Khalid Rehman Hakeem *Editor*

Crop Production and Global Environmental Issues

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Hakeem Abdul Hameed (14 Sept 1908–22 July 1999)

A great philanthropist, thinker, visionary,
and founder-chancellor of Jamia Hamdard,
New Delhi, India

Foreword

For decades, due to increasing food demand together with policies encouraging production, agricultural science has focused on boosting production through the development of new technologies. It has helped farmers to achieve enormous yield gains as well as lower costs for farming. Agriculture has become increasingly intensive. Farmers are becoming capable of producing higher yields using less labor and less land due to many factors, including use of fertilizer and pesticides, introduction of farm machinery, development of hybrid strains, and increased knowledge about farm management practices. Intensification of agriculture has not, however, been an unmixed blessing because this success has come at a high environmental cost. The detrimental effects of intensification of agriculture include water, air, and soil pollution, as well as the loss of wildlife, habitats, and landscape features. As agricultural sustainability means maintaining productivity while protecting the natural resource base, there is increasing general recognition of the need to improve environmental performance in agriculture, through enhancing the beneficial and reducing the harmful environmental effects. The book *Crop Production and Global Environmental Issues* should prove a very timely action in this direction. Agriculture has a complex relationship with natural resources and the environment. Agriculture is a major user of land and water resources, yet needs to maintain the quantity and quality of these resources in order to remain viable. Agriculture does generate waste and pollution, yet it also conserves and recycles natural resources. Many of the environmental effects are confined to agriculture itself, but off-farm effects are also important. The impacts are often concentrated locally and regionally, although some are of national and global significance. As a matter of fact, during the next 50 years, demand for food by a wealthier and 50 % larger global population will be a major driver of agriculturally driven global environmental issues.

The selection of diverse issues in different chapters of this book is in line with the widespread realization that agricultural knowledge, science, and technology can be used to reduce hunger and poverty, to improve rural livelihoods, and to facilitate equitable environmentally, socially, and economically sustainable development. Biotechnologies are techniques that use living organisms to make or modify a product. Some conventional biotechnologies such as plant and animal breeding to create varieties with better characteristics or increased yields are well accepted. Modern biotechnologies change the genetic code of living organisms using a technique called genetic modification. These technologies are being used in industrial applications such as enzyme production but use of genetically modified crops created by inserting genes from other organisms lacks long-term assessments of environmental and health risks and benefits tend to lag behind the discoveries. The chapter on issues and challenges related to genetic modification of crop plants should, therefore, be very valuable. Similarly the chapter on plant mutagenesis and crop improvement constitutes an important contribution.

Agriculture has contributed to climate change in many ways, for instance, through the release of greenhouse gases and conversion of forests to farmland. And now climate change is threatening to damage irreversibly natural resources on which agriculture depends. Although moderate global warming can slightly increase crop yields, overall, negative impacts will increasingly dominate. Floods and droughts become more frequent and severe, which is likely seriously to affect farm productivity and the livelihoods of rural communities, and increase the risk of conflicts over land and water. Climate change is also likely to encourage the spread of pests and invasive species and may increase the geographical range of some diseases. There are three chapters in this book that deal with how climate change is going to influence productivity of food grains as well as horticultural crops. How increasing levels of carbon dioxide are going to influence RuBisCO, an enzyme involved in the first major step of carbon fixation, should make interesting reading. Destruction of stratospheric ozone due to nitrous oxide produced in fields to which nitrogen fertilizers are applied, results in increasing levels of ultraviolet and gamma rays reaching the surface of Earth. The chapter dealing with the effect of gamma rays on crop production should immensely add to our knowledge.

In recent decades, although food production has substantially increased, many people remain undernourished, a problem accounting for 15 % of global diseases. Deficiency of protein, micronutrients, and vitamins prevail in many population groups. Agricultural research and policies need to be devised to increase dietary diversity, improve food quality, and promote better food processing. Different chapters in this book provide valuable information in this regard. Health concerns also include the presence of pesticide residues and heavy metals in agricultural produce. As a matter of fact, agricultural development was geared towards increasing productivity and exploiting natural resources, but it ignored complex interactions between agricultural activities, local ecosystems, and society. Knowledge, science, and technology need to resolve the challenges such as producing healthy crops and quality food grains when soils are polluted with heavy metals and industrial effluents are becoming increasingly available, but putting them into practice requires creative efforts from all stakeholders. Two chapters in the book dealing with these issues constitute a significant step in this direction.

In recent years, wheat production has stagnated in South Asia because new varieties are not able to provide significant improvements in yield potential primarily because of the adverse effects of biotic and abiotic stresses. Modern breeding practices result in relatively little genetic variation in wheat varieties, so that breeders are not able to develop superior adapted genotypes. The wild relatives or alien species of wheat provide a vast and largely untapped reservoir of genetic variation for traits such as tolerance to abiotic and biotic stress, biomass, yield, and photosynthetic potential. This variation can be exploited for the development of new high-yielding varieties adapted to climate change and environmentally friendly agricultural practices. The introduction of alien germplasm that combats these stresses is thus of critical importance for future increases in wheat production. Chapters dealing with biotic and abiotic stresses in wheat and use of alien diversity to combat these stresses provide very useful information. Another chapter on the importance of seed quality in improving crop yields also provides information of practical importance.

Existing agricultural science and technology can tackle some of the underlying causes of declining productivity. But further developments based on a multidisciplinary approach are needed, starting with more monitoring of how natural resources are used. For example, in the 1970s, Malaysia was the biggest cocoa bean producer in the world. The area under cocoa then was >400,000 ha. Since then it has been rapidly decreasing and now the area under cocoa is about 50,000 ha with production not enough to feed its own factories producing cocoa products. As some of the cocoa trees in Malaysia are planted on highly weathered and acidic Oxisols with low fertility, production and quality of cocoa are adversely affected. The chapter on cocoa cultivation in Oxisols of Malaysia contains very valuable information in terms of achieving sustainability in cocoa production. Similarly, the chapter on cracking of cherry fruits contributes a wealth of information that can be useful all over the world where the cherry is grown. As cherries begin the final period of rapid fruit growth, the cuticle becomes thinner and microcracks appear. Contact with water aggravates microcrack formation. With prolonged contact, too much surface water is absorbed, the flesh swells in this localized area, and bowl or shoulder cracks result.

Management of acid sulphate soils and the effect of rhizosphere acidification on nutrient uptake by crop plants constitute a chapter that deals with the soil environment as it is changed due to long-term inappropriate soil management. Sulphur nutrition of oil palms has also been discussed in detail in another chapter. The information contained in these chapters should help manage crop production in a way that natural resources can be maintained for the generations to come.

In 1992, fertilizer use in developing countries surpassed use in developed countries. Eastern Asia is now the world leader, with Southern Asia in second place and North America in third place, respectively. China alone uses more than one third of the synthetic fertilizers applied globally. Overuse of fertilizers in China or anywhere in the world is leading to environmental degradation in the form of nitrate pollution of surface ground water bodies, nitrogen deposition, and nitrous oxide emissions. Without fertilizer use it may not be possible to produce enough food for the increasing population on the Earth. Therefore, the need of the time is that fertilizer use efficiency is enhanced to a level that crop yields remain high and only a small portion of the nutrients applied through fertilizers leave the soil–plant system. This aspect has been amply emphasized in the chapter on fertilizers and the environment.

If as per the United Nation's mid-range forecast global population stabilizes around 9 to 10 billion by 2050, the next 40 to 50 years may be the final episode of rapid global agricultural expansion and intensification. During this phase, crop production activities may exhibit massive and irreversible global environmental impacts. The big challenge ahead, therefore, will be to minimize these impacts, but not at the cost of providing sufficient and quality food to the burgeoning population of the globe. Already different technologies and policies are becoming available that can reduce, or perhaps reverse, many of the trends in environmental degradation that are already identified or will be known in years to come. As significant scientific advances and regulatory, technological, and policy changes will be needed to control the environmental effects of crop production, the information contained in this book will prove useful, but solutions will not be achieved unless enough resources are made available for research and implementation.

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Preface

The world's population is predicted to hit 9 billion by 2050, up from today's total of nearly 7.4 billion, and with it food demand is predicted to increase substantially. There are many factors that affect food production. The post-war "second agricultural revolution" in developed countries, and the "green revolution" in developing nations in the mid-1960s transformed agricultural practices and raised crop yields dramatically, but the effect is leveling off and will not meet projected demand. At the same time, many other factors are having severe impacts on food production: water stress and desertification are reducing the amount of arable land; many pests are becoming resistant to insecticides, but many of the most effective chemical agents are now banned under environmental regulations; underdeveloped infrastructure means that losses increase further during transport and storage; consumption patterns are changing and climate change is bringing new microbial diseases to food-growing regions along with more extreme and unpredictable weather patterns.

Global environmental change (GEC), including land degradation, loss of biodiversity, changes in hydrology, and climate change patterns resulting from enhanced anthropogenic emission of greenhouse gas emissions, will have serious consequences for food security, particularly for more vulnerable groups. Growing demands for food in turn affect the global environment because the food system is a source of greenhouse gas emissions and nutrient loading, and it dominates the human use of land and water. The speed, scale, and consequences of human-induced environmental change are beyond previous human experience, and thus science has a renewed responsibility to support policy formation with regard to food systems.

Estimates vary, but around 25 % of crops can be lost to pests and diseases, such as insects, fungi, and other plant pathogens. Climate change associated with agriculture is also a global issue. Agriculture is a significant contributor to greenhouse gases and is estimated to account for 10–12 % of total greenhouse gas (GHG) emissions. Some estimates are much higher when land-use changes, such as deforestation for farming, are taken into account: up to 30 % of 2004 human-induced GHG can be from agriculture and land use. Many of the issues highlighted are global problems. Meeting the world's food security challenge will require a multinational collaborative effort to integrate the best research from science, engineering, and socioeconomics so that technological advances can bring benefits where they are most needed.

At present, environmental degradation and the consistently growing population are two main problems on the planet Earth. Fulfilling the needs of this growing population is quite difficult from the limited arable land available on the globe. Although there are legal, social, and political barriers to the utilization of biotechnology, advances in this field have substantially improved agriculture and human life to a great extent. Abiotic and biotic stresses greatly affect plant growth and development. When a plant is subjected to abiotic stress, a number of genes are turned on/off, resulting in increased levels of several metabolites and proteins, some of which may be responsible for conferring a certain degree of protection to these stresses. A variety of crops has been engineered for enhanced resistance to a multitude of stresses such as herbicides, insecticides, viruses, and a combination of biotic and abiotic stresses in different crops including rice, mustard, maize, potato, and tomato, among others.

The present volume covers some major global environmental issues that affect crop productivity throughout the globe, particularly in developing countries.

I wish to express my gratitude to all the contributors for readily accepting my invitation for not only sharing their knowledge, but for admirably integrating their proficiency in scattered information from diverse fields in composing the chapters and enduring editorial suggestions finally to produce this venture. I greatly appreciate their commitment. I would like to thank Professor Bijay Singh for writing the foreword and giving useful suggestions during the editing process.

I thank the Springer-Verlag team for their generous cooperation at every stage of the book production

I hope this volume will be useful to all researchers as well as others concerned with agriculture and our environment.

Selangor, Malaysia Khalid Rehman Hakeem

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Heavy Metal Stress and Crop Productivity

**Muhammad Shahid, Sana Khalid, Ghulam Abbas, Naeem Shahid,
Muhammad Nadeem, Muhammad Sabir, Muhammad Aslam,
and Camille Dumat**

Abstract Heavy metal contamination of the environment through anthropogenic activities and/or natural processes is a widespread and serious problem. Heavy metals occur in various forms in soil, which differ greatly with respect to their solubility/bioavailability. The geochemical behavior of heavy metals in soil, their uptake by plants, and effect on crop productivity is affected by various physicochemical properties of soil. Heavy metals mainly accumulate in root cells, due to their blockage by Casparian strips or due to trapping by the cell walls of roots. Excessive heavy metal accumulation in plant tissue impairs either directly or indirectly several biochemical, physiological, and morphological functions in plants and in turns interferes with crop productivity. Heavy metals reduce crop productivity by inducing deleterious effects to various physiological processes in plants including: seed germination, accumulation and remobilization of seed reserves during germination, plant growth, and photosynthesis. At the cellular level, heavy metal toxicity reduces crop productivity by producing reactive oxygen species, disturbing the redox balance and causing oxidative stress. Under heavy metal stress, plants have numerous defense mechanisms to manage heavy metal toxicity and to maintain their productivity, which include reduced heavy metal uptake by plants, sequestration into vacuoles, binding by phytochelatins, and activation of various antioxidants. This chapter presents the effect of heavy metals on physiological reactions in the plants' crop productivity.

Keywords Abiotic stress • Heavy metal • Oxidative stress • Crop product

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1 Introduction

Potentially toxic elements are often presented as “trace metals” or “heavy metals.” Trace metals relate to the elements present in soils in trace amounts (normally described as 1 mol m^{-3}). Heavy metals, a loosely defined group of elements, represent the elements that exhibit metallic properties with atomic mass over 20 (excluding the alkali metals) and specific gravity more than 5 (Rascio and Navari-Izzo 2011). According to some researchers, heavy metals are the elements with an atomic density >6 gcm^{-3} (except for As, B, and Se) (Park et al. 2011). This group mainly includes transition metals, some metalloids, lanthanides, and actinides that can be toxic to living organisms at a low level of exposure. However, the International Union of Pure and Applied Chemistry (IUPAC) technical report has called the term heavy metal a “misinterpretation” due to the contradictory definitions and lack of a “coherent scientific basis.” In this chapter, the term “heavy metal” is used for potentially toxic metals to plants at exorbitant concentrations.

Among the naturally occurring elements, 53 are reported to be heavy metals and the majority of these metals do not have any essential role in plants. Heavy metals have some differences with respect to their biological importance and effects on crop productivity (Kavamura and Esposito 2010). Some heavy metals such as Zn, Cu, Mn, Ni, Se, Co, Cr, and Mo are involved in essential biological functioning, and therefore have positive biological effects in terms of crop productivity (Kavamura and Esposito 2010; Rascio and Navari-Izzo 2011; Salla et al. 2011). However, these metals and those without any essential metabolic function such as Zr, Sb, As, Pb, Hg, and Cd can reduce crop productivity to a great extent when their concentration rises to supraoptimal values (Park et al. 2011; Rascio and Navari-Izzo 2011; Shahid et al. 2013a; Foucault et al. 2013; Xiong et al. 2014; Pierart et al. 2015). The latter four heavy metals (As, Pb, Cd, and Hg) are also regarded as the most toxic metals by the Agency for Toxic Substances and Disease Registry (ATSDR 2003) based on their toxicity, frequency of occurrence, and human exposure potential.

Soil contamination with heavy metals can cause accumulation of these toxic metals in plant parts resulting in decreased crop productivity and threats to animal and human health (Järup 2003; Foucault et al. 2013; Saifullah et al. 2015; Sabir et al. 2015). Many authors have reported the accumulation of heavy metals in food crops when grown on contaminated soil (Uzu et al. 2009, 2010, 2011a; Nabulo et al. 2010, 2011). It has been reported that in many parts of the world, land used for crop production has been polluted with heavy metals, especially by Cd, Pb, and Zn (Singh et al. 2010; Nabulo et al. 2010; Uzu et al. 2010, 2011a; Bai et al. 2011; Foucault et al. 2013; Shahid et al. 2014a). Several previous studies reported that crops grown near urban areas may surpass legal or advisory limits (Yang et al. 2011; Uzu et al. 2011b; Xiong et al. 2014). Adekunle et al. (2009) found higher Pb concentration than recommended values in vegetables for three cities in Nigeria. Similarly, Singh et al. (2010a) reported toxic effects of Zn and Cd due to consumption of vegetables cultivated in heavy metal polluted soil in India. Bigdeli and Seilsepour (2010) forecast an expected hazard in Iran due to daily intake of Cd, Zn, and Pb from heavy metal contaminated sites. Studies based in China (Zhuang et al. 2009), Australia (Kachenko and Singh 2006), and France (Schreck et al. 2011, 2012, 2013; Foucault et al. 2013) reported excessive heavy metal concentration over the food standard limits in vegetables cultivated near metal smelters.

Excessive heavy metal uptake by plants may lead to reduced crop productivity by interfering with photosynthesis, water and mineral uptake, and nitrogen metabolism (Cambrollé et al. 2011; Buendía-González et al. 2010; Dirilgen 2011; Shahid et al. 2011, 2012a, b, 2014b; Austruy et al. 2014; Hasanuzzaman et al. 2014). Exposure to heavy metals results in reduced crop growth and biomass, and in extreme cases causes plant death. It can lead to disorganization of the grana structures, reduced root and shoot growth, and decrease in chlorophyll biosynthesis, interfering with respiration and photosynthesis (Cenkci et al. 2010; Bah et al. 2010; Pourrut et al. 2011, 2013; Ali et al. 2011; Austruy et al. 2014). Necrosis and programmed cell death are seen in many plants under heavy metal stress conditions. The production of reactive oxygen species (ROS), which disrupts the redox status of cells is known to be a major cause of heavy metal toxicity in plants (Duquesnoy et al. 2010; Deng et al. 2010; Antolín et al. 2010; Gill and Tuteja 2010; Körpe and Aras 2011; Pourrut et al. 2011; Shahid et al. 2014c; Ibrahim et al. 2015). The damage to normal biological processes caused by these metals can be either passive or due to their similarity with essential ions (Kramer et al. 2007). To cope with these heavy-metal–induced stresses, plants have evolved a number of defense mechanisms. These mechanisms help crops to sustain the cellular redox state and maintain crop productivity by mitigating the damage caused by oxidative stress (Xu et al. 2011; Xiong et al. 2010; Buonocore et al. 2010; Shahid et al. 2014c; Sabir et al. 2014; Sabir et al. 2015).

In order to better understand the biogeochemical behavior of heavy metals in the ecosystem and their possible effects on crop productivity, it is necessary to establish a link between heavy metal phytouptake and phytotoxicity. How does the phytouptake of heavy metal affect different physicochemical processes inside the plant and in turn reduce crop productivity?

2 Heavy Metal Pollution in Soil

Soil, the basic and most essential part of the ecological system, is heavily contaminated with heavy metals throughout the world (Shahid et al. 2013b; Austruy et al. 2014; Hakeem et al. 2014). Heavy metal polluted sites draw great interest because of their potential risk to food safety and harmful effects on the ecosystem (Lu et al. 2012; Mombo et al. 2015). Reduced crop productivity is also a consequence of soil heavy metal contamination. The soil compartment receives a significant amount of pollutants from different sources every year (Wannaz et al. 2012) throughout the world. Recently high levels of heavy metals in soils have often been reported worldwide (Bolan et al. 2011). Heavy metal contamination of agricultural soils may deteriorate soil health and reduce crop productivity (Cai et al. 2012). Until now over 20,000,000 acres of farmland in China have been reported to be contaminated by high levels of heavy metal (Wu et al. 2010). This causes a loss of crop output by 1,000,000 million tons per year in China (Wu et al. 2010). In the United States and

Europe, almost over 100,000 ha of land are polluted by heavy metals (Lewandowski et al. 2006). According to the European Environmental Agency (EEA) 32 member countries of the European Union have reported that potentially polluting activities have occurred at about three million sites, of which more than 8 % (or nearly 250,000 sites) are highly contaminated and need to be remediated (Guimarães et al. 2010). Moreover, more than three million sites are most probably contaminated, based on knowledge about potentially polluting activities on the site (Jensen et al. 2009). Projections based on the analysis of the changes observed in the last five years indicate that the total number of contaminated sites needing remediation may increase by more than 50 % in 2025.

3 Heavy Metal Uptake by Plants

Bioavailability of a metal in the soil is the part of the total metal content that is readily available or made available in a dynamic manner over time to an organism from its direct environment (Pauget et al. 2012). Generally, most of the heavy metals especially Pb and Cu are relatively less soluble and available for plant uptake (Punamiya et al. 2010; Sammut et al. 2010; Vega et al. 2010; Pourrut et al. 2011). Despite high total heavy metal soil concentration, only a small fraction of these metals is phytoavailable (Sun et al. 2009) due to strong binding with different soil components (Uzu et al. 2009; Sammut et al. 2010; Rascio and Navari-Izzo 2011). However, Cd is relatively more available for plant uptake because it is predominantly found in soil solution or bound to the solid phase (Verbruggen et al. 2009). The bioavailable/mobile fraction of heavy metals can be taken up by plants and other living organisms (Fig. 1) (Sammut et al. 2010; Vega et al. 2010). The metals enter the plants from the soil mainly via the root (Uzu et al. 2009; Pourrut et al. 2011). Foliar heavy metal uptake by crops cultivated near metal recycling industries is also reported to be a major path of metal entrance to plants (Uzu et al. 2010; Schreck et al. 2013). The entrance of metals from soil to roots is not direct; rather they are first adsorbed on plant roots, followed by binding to carboxyl groups of uronic acid around the roots, or directly to the mucilage polysaccharides of the rhizoderm cell surface (Pourrut et al. 2011). Several processes/steps are involved in the uptake of metals by plants including: desorption of metal from soil particles, transport of metals towards plant roots, uptake of metals by roots, and translocation of metals towards shoot (Saifullah et al. 2009).

4 Heavy Metal Translocation to Shoots

Heavy metal transportation towards aerial plant parts is via the xylem (Verbruggen et al. 2009) and is most probably motivated by transpiration (Liao et al. 2006). After penetrating the central cylinder, the metals move towards plant aerial parts via water

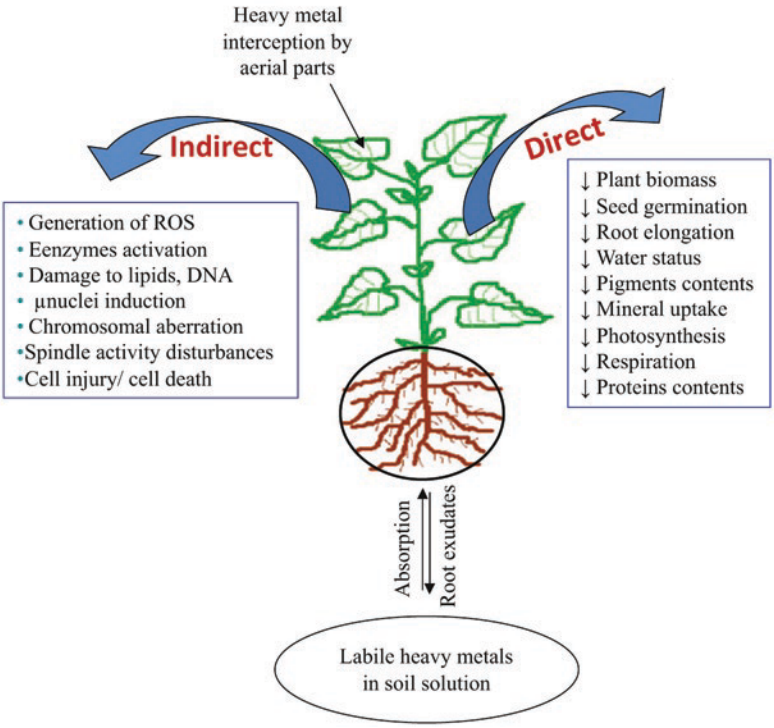

Fig. 1 Heavy metals uptake by plant roots and possible direct and indirect toxic effects resulting in reduced crop production. ↓ indicates decrease

flow of the vascular system (Krzeslowska et al. 2010), where water evaporates and metal accumulates. Inside the xylem, metals such as Pb and Cd may bind with amino acids and form complexes (Maestri et al. 2010; Rascio and Navari-Izzo 2011). Using X-ray mapping, Arias et al. (2010) reported increased deposition of Pb and Cr in phloem and xylem cells of *Prosopis glandulosa*.

For most of the plants, only a small amount of heavy metals is translocated to the shoot tissues. In some cases, 95 % or more of absorbed metal is sequestered in the plant roots unless the plant is a hyperaccumulator or chelate-assisted (Małecka et al. 2008; Gupta et al. 2010; Jiang and Liu 2010; Yan et al. 2010; Duarte et al. 2007; Shahid et al. 2012c). The metal translocation restriction phenomenon is most common to Pb (Pourrut et al. 2011) as compared to other metals. The restricted translocation of heavy metals to aerial plant parts is due to blockage by the Casparian strip (Pourrut et al. 2011), accumulation in plasma membrane (Jiang and Liu 2010), precipitation in intercellular space (Małecka et al. 2008; Pourrut et al. 2011), precipitation as insoluble metal salts within the cell wall (Islam et al. 2008; Arias et al. 2010), or accumulation in the vacuoles of cortical and rhizodermal cells (Kopittke et al. 2007).

However, certain plant species known as metal hyperaccumulators (*Alyssum bertolonii, Thlaspi goesingense*, and *Alyssum murale*) are capable to uptake and accumulate high levels of heavy metals without any toxic impact on their growth processes (Arshad et al. 2008; Shahid et al. 2011). Heavy metal hyperaccumulator plant species are capable to uptake and transport 100–1000-fold higher concentrations of heavy metals compared to nonhyperaccumulating plant species. Moreover, enhanced metal tolerance makes these plants highly suitable for remediation of heavy metal contaminated soils (Xiong et al. 2006; Arshad et al. 2008; Redondo-Gómez et al. 2011; Shahid et al. 2012a).

Enhanced heavy metal translocation to plant aerial parts is governed by specific members of carrier proteins (Rascio and Navari-Izzo 2011). Recently, several studies have reported that the transporter proteins such as ZIP [zinc-regulated transporter proteins (IRTP) and iron-regulated transporter proteins (ZRTP)], Nramp (natural resistance and macrophage protein), CDF (cation diffusion facilitator), and HMA (heavy metal ATPase) are associated with the transport of heavy metals among plant cells (Meyers et al. 2008; Maestri et al. 2010; Siche et al. 2010; Sperotto et al. 2010; Conte and Lloyd 2011). These metal transporter proteins are found in plasma or intracellular membranes and have cell-specific expression proposing that they may have a specific/different function in different plant species. In addition to heavy metal transporter proteins naturally found in hyperaccumulators, several studies have reported increased translocation of heavy metals from root to shoot in the presence of organic ligands (Shahid et al. 2012c, d, 2014d). The natural and synthetic organic ligands, such as ethylene diamine tetraacetic acid (EDTA), ethylene diamine disuccinate (EDDS), nitrilo triacetic acid (NTA), humic substances (HSs), and low molecular weight organic acids (LMWOA) have been reported to increase heavy metal uptake and translocation (Saifullah et al. 2009; Sabir et al. 2014; Sabir et al. 2015; Shahid et al. 2014e, f).

5 Heavy Metal Effects on Crop Productivity

Inside the plants, heavy metals are capable of inducing a range of morphological, physiological, and biochemical disorders, which in turn cause a decrease in crop productivity. However, all these heavy metal-induced toxic effects are the function of exposure duration, stage of plant development, the intensity of stress, studied organ and even species variety, and the concentration of metal exposed to the target organism.

5.1 Effects of Heavy Metal on Germination

Seed germination is one of the most susceptible physiological phenomena in the plant life cycle that is affected by various biotic and abiotic environmental factors and hormonal interactions (Moosavi et al. 2012) including metals. The effect of any metal on germination depends on its capability to penetrate the seed coat and reach embryonic tissues (Ko et al. 2012; Márquez-García et al. 2013). The same applied level of a metal has different effects in different plant species depending on the anatomy and structure of the seed coat (Munzuroglu and Geckil 2002). Metals such as Cu and Cd hamper water uptake and consequently seed germination does not take place (Kranner and Colville 2011). The seed germination test is mostly used for assessing metal toxicity (Munzuroglu and Geckil 2002). After penetration through the seed coat, germination depends on the seed reserves for supplying various metabolites for respiration and this process is interrupted due to oxidative stress caused by metals (Ko et al. 2012). Márquez-García et al. (2013) studied the effects of different levels of Cu, Mn, Ni, and Zn on germination pattern and seedling size in *Atriplex halimus* and *Salicornia ramosissima*. All the metals reduced the germination percentage in *A. halimus* and only Ni reduced germination in *S. ramosissima*. Increasing concentration of Cr reduced the germination rate of *L. perenne* (Chigbo and Batty 2013). However, this reduction was only observed at more than 9.4 ppm Cr concentration. The reduced germination rate was related to the restricted oxygen uptake and physiological disorders in the supply of food reserves.

Plants can take up these metals through roots or via rain and dust (Jozic et al. 2009). Celik et al. (2005) reported four times greater concentration of Fe, Pb, Cu, and Mn in plants along roadsides as compared to control plants. The seeds are particularly susceptible to metallic traffic pollutants. Decreased seed viability and increased number of abnormal embryos were observed in plants growing near heavily trafficked highways (Stvolinskaya 2000). Ganatsas et al. (2011) concluded that the seeds of *Pinus brutia* collected near the polluted road did not germinate even after pretreatment. On the other hand, seeds collected over a longer distance showed normal germination behavior.

5.2 Effects of Metals on Accumulation and Remobilization of Seed Reserves during Germination

A large body of knowledge exists concerning seed biology which is one of the most extensively researched areas in plant physiology (Bewley 1997) in recent decades. The assimilation, concentration, and distribution of heavy metals in seeds have been studied in different crop species (He 2010; Lange-Hesse et al. 1994; Mengchang et al. 2000; Wang et al. 2014). Success or failure of the developing seedlings during early ontogeny depends on restoration of transcriptional and translational machineries (Finkelstein 2010; Mei and Song 2008) and to several other factors including successful remobilization of stored seed reserves (Nadeem et al. 2011, 2012, 2013) that are accumulated in different seed compartments throughout the ripening period (Malan and Farrant 1998); seedling root growth (Enns et al. 2006; Zhu and Lynch 2004); soil, water, and temperature conditions (Louarn et al. 2008; Manz et al. 2005; Miller 2001); and metal concentrations (Chigbo and Batty 2013; Ko et al. 2012; Kranner and Colville 2011; Márquez-García et al. 2013; Wang et al. 2014).

Seed germination is sensitive to the different heavy metals especially the Cd, Cu, Cr, Mn, Ni, and Zn status of the environment (Chigbo and Batty 2013; Kalai et al. 2014; Léon et al. 2005; Ko et al. 2012; Márquez-García et al. 2013). Higher levels of Ni induced the remobilization of macronutrients compared to normal Ni concentrations (Léon et al. 2005), whereas a reduction in the remobilization of stored barley seed phosphorus reserves was reported due to the decrease in the activities of acid phosphatase, α-amylase, and alkaline phosphatase in endosperms mainly due to the concentrations of Cd and Cu (Kalai et al. 2014) during germination. Moreover, Cu and Cd enhanced soluble protein and sugar content and caused lipid peroxidation even at the lowest dose, and caused an accumulation of proline, fundamentally in radicles (Kalai et al. 2014). The decrease in seed germination of barley after exposure to Cu or Cd is not a result of reduced water uptake by seed tissues, but may be due to a failure in reserve remobilization from the endosperm (Kalai et al. 2014).

Increasing concentrations of Cu, Cr, Co, Ni, Mn, Pb, and Zn metals reduced the germination percentage in different crops (Chigbo and Batty 2013; Márquez-García et al. 2013; Wang et al. 2014) and this reduction in germination rate was related to the restricted oxygen uptake and physiological disorders in the supply of food reserves (Chigbo and Batty 2013; Márquez-García et al. 2013).

5.3 Effects of Heavy Metals on Plant Growth

Toxic metal ions enter plant tissues along with nutrients from the soil solution (Dal Corso et al. 2013; Hossain and Komatsu 2013). The most common physiological outcome of heavy metal exposure to plants is the reduction in growth (Hu et al. 2013). Leaf structure and physiology are changed along with the reduction in photosynthesis and respiration. As a result of these changes, metabolism is affected and energy production is reduced. Transpiration and transportation of materials between various organs are also affected (Ying et al. 2010). The ability of roots for nutrient and water uptake is also reduced under metal stress (Poschenrieder and Barceló 2004). Therefore, various developmental processes including flowering, embryogenesis, and seed formation are affected due to changes in the functioning of the root and leaf. Heavy metals are severely toxic for plants causing phytotoxicity which is followed by chlorosis, reduced plant growth, yield decline, and restricted nutrient uptake, and nitrogen fixing capacity is reduced in leguminous plants (Guala et al. 2010). Due to heavy metal pollution agricultural yields are reduced and dangerous health effects are observed upon their entry into the food chain (Schickler and Caspi 1999). Among various heavy metals, cadmium (Cd) is considered very toxic for plants (Waalkes 2000), inhibiting photosynthesis (Qian et al. 2009) and reducing root and shoot growth. Cadmium limits the activity of many enzymes forming a strong affinity with the thiol group (Mendoza-Cozatl et al. 2005). It also results in the production of many active oxygen species including hydrogen peroxide, superoxides, and hydroxyl radicals (Romero-Puertas et al. 2004) together with lipid peroxide, causing harm to cell membranes and biopolymers (Heyno et al. 2008). The higher concentrations of Cu not only reduce the biomass by stirring up the chlorosis (Quartacci et al. 2000), but also interfere with the electron transport system of photosynthesis (Patsikka et al. 2002). Higher uptake of Ni causes many physiological disorders in plants such as chlorosis and necrosis (Pandey and Sharma 2002; Rahman et al. 2005; Sabir et al. 2013; Shahid et al. 2014f). Plants cultivated on Ni-contaminated soil showed impaired nutrient balance and resulted in disorder of cell membrane functions. In this way Ni affects H-ATPase activity and lipid composition of the plasma membranes (Ros et al. 1992; Yadav 2010).

5.4 Effects of Heavy Metals on Photosynthesis

Recently it has been discovered that heavy metals cause many problems in growth and photosynthetic and respiratory activities in the algal model system *Micrasterias denticulata* (Volland et al. 2012; Andosch et al. 2012; Shahid et al. 2014b). Certain metals such as iron, copper, and zinc are essential nutrients of plants and are required for photosynthesis and as cofactors for a large number of enzymes (Kovacik et al. 2010; Shanmugam et al. 2011). Photosynthesis is responsible for providing energy for plants and requires a consistent working of countless molecular and cellular structures that are susceptible to metal pollution. The contents of light-harvesting pigment (i.e., chlorophyll and carotenoids) are reduced on their interaction with heavy metals (Kuzminov et al. 2013) and disruption occurs in energy transfer in light-harvesting antennae. Heavy metals can also affect proteins (composition or structure) involved in photosynthesis such as Rubisco and proteins of the reaction centers (Franco et al. 1999). In this way heavy metals affect the normal functioning of both light and dark photosynthetic reactions. High levels of heavy metals may affect electron transport on the acceptor side of PS II and may inhibit electron transport between PSI and PSII due to toxicity of heavy metals to membrane lipids (Rama Devi and Prasad 2004). Overall, heavy metals have dramatic effects on photosynthesis, however, the main sites and the order of involved physiological modifications are not yet very clear (Bertrand and Poirier 2005; Appenroth 2010). Kuzminov et al. (2013) noticed that Z, Cd, and Cu caused reticence of electron transport between PSI and PSII, followed by a reduction in the energy transfer in light-harvesting complexes, indicating metal effects on the functional integrity of the lipid membranes.

5.5 Effects of Heavy Metals on Chlorophyll

The membranes of the thylakoid are a well-organized system containing chlorophyll and protein complexes. The function of the thylakoid membrane is to couple photo-oxidation of water with electron transport. In this way the availability of ATP and NADPH for the dark reactions of photosynthesis is made possible. The chlorophyll and protein complexes (PSI) and (PSII), surrounded by external light-harvesting complexes, are present hierarchically inside the thylakoid membranes in mega- and supercomplexes (Dekker and Boekema 2005; Croce and van Amerongen 2011). It is well recognized that heavy metals affect the functioning of the photosynthetic apparatus (Shahid et al. 2014b). Several previous studies showed that Cd, Cu, Zn, and Pb affect photosynthesis (Burzynski and Kłobus 2004; Shahid et al. 2012b, 2014b). On the other hand, distorted chloroplast ultrastructure, restrained chlorophyll synthesis, repressed electron transport, and reduced activity of enzymes involved in the Calvin cycle are noticed in plants under Pb stress (Sharma and Dubey 2005; Kalaji and Loboda 2005). Reduced photosynthetic capacity and decreased chlorophyll concentration under Pb stress were also observed in many species (Pinchasov and Dubinsky 2006; Shahid et al. 2014b). Soudek et al. (2014) found that lower concentrations of metals were less toxic to shoots than roots.

At higher concentrations, transport of the metals to the leaves increased which caused a reduction in growth and chlorophyll loss, resulting in metal-induced chlorosis. Marques and Nascimento (2013) observed the changes in the absorption peaks of the chlorophyll fluorescence spectra. The least fluorescence reabsorption was observed in plants grown under the highest Cd level, indicating the sensitivity of chlorophyll fluorescence in detecting changes in the PSII under Cd stress. Padinha et al. (2000) noticed less photosynthetic efficiency in plants grown on polluted sites. Photoinhibition caused due to damage to photosynthetic machinery may be short-term and reversible, or long-term and irreversible (Werner et al. 2002). Photosynthetic pigment content is reduced by elevated metal concentrations (Cambrollé et al. 2011). Reduction in photosynthetic functioning may be due to the adverse effects of excess metals on photosynthetic electron transport, as a result of decreased chlorophyll synthesis or its increased degradation (Marques and Nascimento 2013). Cadmium is very toxic to photosynthesis especially in higher plants. High levels of metals in leaves can deteriorate composition, structure, and functionality of PSI and PSII (Molins et al. 2013; Janik et al. 2010). It is reported that metals can alter the supramolecular conformation of the light-harvesting pigment protein complex of PSII (Janik et al. 2010). Moreover, metals can affect the activities of enzymes of the pigment synthesis pathway and could in turn influence the chlorophyll content (Böddi et al. 1995). Heavy metals cause deficiency of Fe or Mg and are capable of substituting Mg^{2+} in the chlorophyll molecules (Küpper et al. 1998), decreased mesophyll thickness, and stomatal density (Tang et al. 2013).

5.6 Effect of Heavy Metals on Nutrient Uptake

Multiple studies (Gopal and Rizvi 2008; Sharma and Dubey 2005; Chatterjee et al. 2004) showed that Pb exposure significantly affected the nutrient uptake process in plants. It also reduced the concentration of cations such as Mg^{2+},

Zn^{2+}, Ca^{2+}, Fe^{2+}, and Mn^{2+} in leaves of *O. sativa* (Chatterjee et al. 2004), *M. sativa* (Lopez et al. 2006), *B. oleracea* (Sinha et al. 2006), *R. sativus* (Gopal and Rizvi 2008), *Z. mays* (Seregin and Ivanov 2001), and *V. unguiculata* (Kopittke et al. 2007). Xiong et al. (2006) demonstrated that the exposure of lead content significantly diminished the nitrate content in shoots, nitrate reductase, and free amino acid in *B. pekinensis*. Similarly, in soil–plant interaction, Cd manipulates the structural, physiological, and biochemical processes in crops (Feng et al. 2010) by disturbing the functions and fractions of mineral nutrients (Nazar et al. 2012). Cadmium, a nonessential element for plant growth, is taken up by the roots and translocated to the vegetative parts of the plant, degrades the quality as well as yield of crops (Hassan et al. 2005) by inhibiting (1) the absorbance as well as distribution of macro-/micronutrients in crops (Sandalio et al. 2001) and (2) the process of photosynthesis (Nazar et al. 2012; Gussarson et al. 1996). Additionally, Cd inhibits the stomatal openings (Hassan et al. 2011), hence, water uptake and its transportation (Vassilev et al. 1997). Cadmium in the plant system slows down photosynthesis by disturbing the Kelvin cycle enzymes (Nazar et al. 2012), and thus reduces the carbohydrate metabolism (Khan et al. 2009).

5.7 Heavy-Metal–Induced Oxidative Stress

The primary response of plants upon exposure to high levels of heavy metals is the generation of ROS (Mirza et al. 2010; Mou et al. 2011; Radic et al. 2010; Xu et al. 2011; Shahid et al. 2014g). These ROS include hydrogen peroxide (H_2O_2), hydroxyl radicals ($^{\bullet}OH$), and superoxide radicals ($O_2^{\bullet-}$). ROS are produced in different cell organelles such as chloroplast as by-products of different reactions (Corpas et al. 2011; Circu and Aw 2010; Buonocore et al. 2010). The generation of ROS by heavy metals is either directly through Haber–Weiss reactions or indirectly by their interaction with the antioxidant system (Srivastava et al. 2005; Shahid et al. 2014c), disrupting the electron transport chain or the metabolism of essential elements (Qadir et al. 2004). The ROS are basically unstable and very reactive molecules possessing an unpaired electron (Buonocore et al. 2010). Under normal plant growth situation, ROS levels in a plant are controlled by a defensive system that includes antioxidants, enzymes, and GSH. However, when ROS are not properly scavenged, oxidative stress may occur (Table 1). Overproduction of ROS causes oxidation and modification of cellular amino acids, membrane lipids, DNA, and proteins (Yadav 2010; Rascio and Navari-Izzo 2011). These reactions between ROS and cellular components cause mitochondrial malfunction, DNA damage, cell membrane damage, and finally cell death (Reddy et al. 2005; Clemens 2006; Yadav 2010; Shahid et al. 2011; Pourrut et al. 2011).

Table 1 Heavy-metal–induced oxidative stress in different plant species

Metals	Plant Species	References
As	*Zea mays*	Duquesnoy et al. (2010)
Cd	*Spinacia oleracea*	Wang et al. (2011)
	Brassica juncea	Ahmad et al. (2011)
	Ipomoea batatas	Kim et al. (2010)
	Solanum nigrum	Deng et al. (2010)
	Kandelia candel	Huang and Wang (2010)
	Bruguiera gymnorrhiza	Huang and Wang (2010)
	Fontinalis antipyretica	Dazy et al. (2009)
	Rhyzobium leguminosarum	Corticeiro et al. (2006)
	Cicer arietinum	Eyidogan and Öz (2005), Reddy et al. (2005)
	Macrotyloma uniflorum	Reddy et al. (2005)
Cu	*Ipomoea batatas*	Kim et al. (2010)
	Fontinalis antipyretica	Dazy et al. (2009)
	Cicer arietinum	Eyidogan and Öz (2007), Reddy et al. (2005)
Pb	*Najas indica*	Singh et al. (2010)
	Paulownia fortunei	Wang et al. (2010)
	Medicago sativa	Antolín et al. (2010)
	Sesbania drummondii	Israr et al. (2011)
	Medicago sativa	Antolín et al. (2010)
	Sesbania drummondii	Israr et al. (2011)
	Macrotyloma uniflorum	Reddy et al. (2005)
Ni	*Medicago sativa*	Antolín et al. (2010)
	in Sesbania drummondii	Israr et al. (2011)
Zn	*Fontinalis antipyretica*	Dazy et al. (2009)
	Ipomoea batatas	Kim et al. (2010)
	Medicago sativa	Antolín et al. (2010)
	Sesbania drummondii	Israr et al. (2011)

5.8 Heavy-Metal–Induced Lipid Peroxidation

Lipids are vital cellular components and play important roles in many diverse biological processes (Xiao and Chye 2011) such as building cell membranes, energy provision for cellular metabolism, and maintaining of cell and organelle integrity and composition. Heavy metals are known to cause lipid peroxidation via ROS production (Table 2). Lipid peroxidation is the process whereby free radicals produced by heavy metals oxidize lipids and their esters in cell membranes (Shahid et al. 2014c, 2015). The phenomenon is most common in polyunsaturated fatty acids and involves three distinct stages: initiation, progression, and termination. The overall effects of heavy-metal–induced lipid peroxidation are : (1) increase in membrane leakiness to substances that do not normally cross it other than through specific channels, (2) decrease in membrane fluidity that makes it easier for

Table 2 Heavy-metal–induced lipid peroxidation in different plant species

Heavy Metals	Plant Species	References
Ag	*Potamogeton crispus*	Xu et al. (2012)
Al	*Hordeumvulgare*	MohanMurali Achary et al. (2012)
	Carassius auratus	Chen et al. (2012)
	Brassica juncea	Ahmad et al. (2011)
	Brassicajuncea	Szőllősi et al. (2009)
	Solamum lycopersicum	Cherif et al. (2011)
Cu	*Phaseolusvulgaris*	Bouazizi et al. (2010)
	Vetiveria zizanioides	Xu et al. (2009)
	Withania somnifera	Khatun et al. (2008)
	Datura stramonium	Boojar and Goodarzi (2007)
	Malva sylvestris	
	Chenopodium ambrosioides	
	Brassica napus	Baryla et al. (2000)
Hg	*Medicago sativa*	Carrasco-Gil et al. (2012)
Pb	*Spinacia oleracea*	Wang et al. (2011)
	Spinacia oleracea	Wang et al. (2011)
Zn	*Solanum lycopersicum*	Cherif et al. (2011)
	Vetiveria zizanioides	Xu et al. (2009)

phospholipids to exchange between the two halves of the bilayer, and (3) damage to membrane proteins that inactivate the receptors, enzymes, and ion channels.

6 Defense Mechanism of Plants against Heavy Metals Toxicity

To survive and maintain crop productivity, plants have to cope continuously with stress. Heavy metal hyperaccumulator plants have evolved defense mechanisms to cope with metal toxicity and to restrict cell injury and tissue dysfunctioning (Shahid et al. 2012c; Hakeem et al. 2014). These defense mechanisms either operate separately or simultaneously. However, the efficiency and activation of a specific defense mechanism depends on the plant and metal type as well as the level and duration of exposure.

6.1 Antioxidant Enzymes

To combat metal toxicity and thereby prohibit cell injury and tissue dysfunction (Singh et al. 2006), plants have developed numerous protective mechanisms to avoid heavy metal toxicity (Israr et al. 2011; Xiong et al. 2010; Xu et al. 2011; Hakeem et al. 2012; Shahid et al. 2014c; Abbas et al. 2015). First is through reduced uptake of metals to plants by exclusion or binding them to the cell wall and other ligands (Xu et al. 2011; Zeng et al. 2011) which makes metals harmless at the initial stage of their entrance to the plants. The reduced entrance of metals to the roots is considered as the first and major protective mechanism adopted by plants against the harmful effects of metal (Jiang and Liu 2010). Metal complexation with carboxyl groups of pectins, which build plant cell walls is considered as the most important plant cell resistant reaction to most metals such as lead (Krzeslowska et al. 2009, 2010; Jiang and Liu 2010; Pourrut et al. 2013). The secondary defense system for heavy metal detoxification involves several antioxidant enzymes to control overproduction of ROS. These enzymes include catalase (CAT), peroxidase (POD), superoxide dismutase (SOD), and ascorbate peroxidase (APX). In addition to these enzymes, low molecular weight molecules such as cysteine (Cys), proline (PRO), ascorbic acid (AsA), nonprotein thiol (NPT), and glutathione (GSH) are also involved in scavenging different types of ROS (Israr et al. 2011; Gao et al. 2010; Mou et al. 2011; Lomonte et al. 2010; Yasir et al. 2011; Ali et al. 2011; Pourrut et al. 2013; Shahid et al. 2012d).

6.2 Phytochelatins and Metallothioneins

A safe sink of toxic metals is crucial for tolerance when a plant uptakes high amounts of these metals (Wojas et al. 2009; Hassan and Abbass 2011). In this way, the plants can evade the toxic effects of these metals to different cellular processes. Vacuolar sequestration of heavy metals is a vital feature in plant metal homeostasis (Maestri et al. 2010; Xu et al. 2011). The hyperaccumulator plants are especially capable of sequestering heavy metals to molecules to minimize their otherwise harmful effects. In hyperaccumulator plants, metal detoxification is generally achieved by complexation of these metals with ligands and/or by their removal from metabolically active cellular compartments. Vacuolar transporters partly play this role, contributing to the sequestration of heavy metals in the vacuole (Martinoia et al. 2007; Hakeem et al. 2014).

In plants, some natural chelators such as metallothioneins (MTs) and phytochelatins (PCs) are characterized as the best metal-binding natural ligands for transportation of these metals to a safe point (vacuoles) in plant cells (Israr et al. 2011; Xu et al. 2011). PCs and MTs are cysteine-rich heavy-metal–binding protein molecules. PCs and MTs play a vital role in heavy metal detoxification in plants by forming mercaptide bonds with various metals (Maestri et al. 2010) and play a vital role in their detoxification in plants (Verbruggen et al. 2009; Yadav 2010; Gupta et al. 2010; Jiang and Liu 2010).

7 Summary and Conclusions

Soil heavy metal contamination is one of the most severe environmental and human health concerns. Heavy metals occur naturally in Earth's crust but anthropogenic activities have redistributed many of these heavy metals from Earth's crust to different compartments of the environment. Once released into the soil, heavy metals greatly influence environmental quality and risk crop productivity.

Heavy metals enter plants primarily via the roots from the soil solution and travel along the food chain. The majority of the heavy metals absorbed are stored in the roots where they precipitate as insoluble metal salts, immobilized by negatively charged pectin within the cell wall, precipitate in intercellular space, or accumulate in the vacuoles.

Excessive heavy metal accumulation in plant tissue impairs the phytometabolism directly or indirectly, and causes several negative effects resulting in reduced crop productivity. Heavy metal accumulation in plant tissue causes reduced seed germination, decreased root elongation, decreased plant biomass, and inhibition of chlorophyll biosynthesis. While inside a cell, lead affects photosynthesis, respiration, enzymatic reactions, mineral nutrition, and several other physiological factors. One of the most common effects of heavy metal toxicity in plants is the overproduction of ROS, which is the result of heavy metal interference with electron transport activities. Plants have evolved several detoxification mechanisms in order to cope with overproduction of ROS. The reduced uptake of heavy metals into plant roots through their complexation with carboxyl groups of cell wall pectins is the most important reaction of plant cell resistance against heavy metal toxicity.

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Effects of Gamma Radiation on Crop Production

Hafsa Ali, Zoya Ghori, Sandal Sheikh, and Alvina Gul

Abstract The increasing world population has raised concerns over food security. In order to feed the world, the projected target is to double food production by 2050. However, this objective has been interrupted by many global challenges, including climatic change and a reduced ozone layer. The Earth is protected by layers of atmosphere. The stratospheric ozone protects living organisms from harmful radiation. Plants use sunlight for photosynthesis and as a consequence face harmful radiation. Depletion of stratospheric ozone has increased radiation entering the surface of the Earth. Radiation is divided into two types: ionizing radiation, where gamma rays are most prominent; and nonionizing radiation, including UV rays. UV rays (high energetic radiation) cause heritable mutations in the genome of plants that exacerbate plant physiology, environmental factors, plant growth, and affect photosystem and soil properties which ultimately affect crop productivity, leading to the incidence and progress of crop diseases. However, plants have evolved methods to reverse the genetic changes by UV radiation by delaying growth and cell division that helps in DNA repair. There have been further studies on plant responses, including in DNA repair enzymes, endogenous photodamaging molecules, and repair machinery towards UV radiations in crop plants. Gamma radiation is high-frequency rays consisting of high-energy protons that penetrate the cell and cause ionization. Ionization of plant cells causes disruption of the normal processes of the cell ultimately affecting crop yield. Gamma rays are dose dependent, where a low dose has fewer side effects in contrast to a high dose that affects plant phenotype, including various cell organelles and biochemical components. However, there are several biochemical parameters to identify the damage caused by this radiation. Nevertheless, the plant defense mechanism is activated under a low dose of gamma rays to cope with the damage. Gamma rays also have various benefits in all applied fields and are used to create crop mutants. This chapter discusses the effects of radiation, predominantly UV and gamma rays in crops and their benefits.

Keywords Gamma radiation • Crop production • Antioxidant defense system UV rays

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1 Introduction

One of the major global issues is to feed the speedily increasing population of human beings. With the rapidly growing rate of population, the expected rate by 2050 will be 9 billion; therefore, there is a need to increase food production (The Royal Society 2009; Hakeem et al. 2012; Wargent and Jordan 2013). However, due to climate change we are not able to mitigate our food requirement (Godfray et al. 2010; Wargent and Jordan 2013). Earth is surrounded by a layer of gases called atmosphere. It shelters life on Earth by maintaining its temperature and protects life on Earth from the harmful radiation of the sun. The atmosphere has five layers: troposphere, stratosphere, mesosphere, thermosphere, and exosphere (http://eo.ucar.edu/basics/wx_1_b.html). The troposphere starts from the Earth and extends 7 miles above. It is the nearest layer of the Earth. We breathe in this layer and this layer has most of the atmosphere gases. The mesosphere is present 30 miles above the Earth; it is the coldest part of the atmosphere. The temperature of this region is 13 °F (Flannery 2006). The thermosphere is present above the mesosphere; this layer is present 50 miles above the Earth and the temperature of this region is 360°F. The exosphere is the outermost layer of the Earth and extends into space. In this layer satellites revolve around the Earth (Kubesh et al. 2008). The stratosphere separates the lower layer from the upper layers of the mesosphere and thermosphere. Its altitude spreads from 10 to15 km, containing most of the ozone's atmosphere (Campillo et al. 2012). Ozone is divided into two types: ground ozone and ozone layer.

Most of the harmful radiation is absorbed by the ozone layer in order to protect the living organisms that live on Earth. Ozone started accumulating in the atmosphere as a waste gas about 200 billion years ago, and when photosynthetic organisms started releasing oxygen (McMichael 1993) 400 Ma ago evolution occurred and aquatic plants moved to the land to begin terrestrial life. Life on Earth is protected from harmful radiations and sustained by the ozone layer (McMichael et al. 2011). Solar radiations are of different types and range from infrared to ultraviolet. Not all types of radiation reach Earth. Radiations that have shorter wavelengths (UV) are absorbed by the stratospheric ozone (Campillo et al. 2012). Unfortunately, depletion of ozone and climatic change are occurring due to anthropogenic activity (McMichael et al. 2011), resulting in environmental deviations. The industrial revolution has polluted the environment (Kakani et al. 2003a, b, c).

In the late twentieth century industrial chemicals such as chlorofluorocarbon which is used in refrigerator and propellant sprays and their intermediates, hydrochlorofluorocarbon, destroy the stratosphere layer (Minorsky 2004). Chlorofluorocarbon has the largest capacity to destroy the ozone layer. They have a half-life of 50–150 years. According to the US Environmental Protection Agency 1 chlorine molecule can destroy 0.10 million ozone molecules. These chemicals react with ozone to produce free radicals that destroy the ozone (McMichael et al. 2011). It is estimated that six types of hydrochlorofluorocarbon (HCFC) and seven types of chlorofluorocarbon (CFC) compounds have a role in ozone depletion. Although the use of chlorofluorocarbon compounds has been reduced, the ozone layer is reaching its maximum depletion. These radiations have affected not only human lives but also lives of plants and all other living organisms on the earth. Crops are badly affected by these solar radiations (Minorsky 2004).

All living organisms present on Earth are constantly exposed to radiations. Radiations travel in the form of energy from the source. The two main sources of radiations include natural radiations and man-made radiations. Natural radiations include natural resources with sun and lightning as the major causes. However, man-made radiations are the result of anthropogenic activity such as: rays as by-products of industrial activities, radiations from medical and scientific applications, wireless communication, and so on (Ng 2003). Radiations that radiate from the sun are of various wavelengths; most of them are invisible to the human eye. Short wavelength radiations are considered harmful and energetic (http://earthobservatory.nasa.gov/Features/UVB/uvb_radiation.php). Electromagnetic radiations are emitted from the sun, and range from infrared to ultraviolet radiations. Not all types of radiations reach the Earth's surface that only absorbs the radiations having shorter wavelengths. The ozone layer mostly absorbs the radiations and stops these radiations from reaching Earth. Different layers of the atmosphere act as filters for the radiations. These layers of the atmosphere absorb different parts of the radiation and reflect them either to the Earth or back into space (Campillo et al. 2012).

2 Types of Radiations

2.1 Ionizing Radiations

These radiations have wavelengths less than 100 nm (Ng 2003). These radiations are charged high-energy particles such as high-energy photons and electrons. Ionizing radiations are of two types including: gamma radiations and X-rays. Gamma rays are categorized in ionizing radiation because these radiations produce free radicals in the cell when they interact with atoms or molecules. These free radicals damage the cell, but sometimes modify the cells and components. Damage or modification of the cells and components depends upon the level of radiation. These radiations cause changes in the physiology, morphology, anatomy, and biochemistry of the plants (Kim et al. 2004; Kovacs and Keresztes 2002; Wi et al. 2005; Hamideldin and Hussin 2014). The effect of these radiations is dose dependent, as these rays stimulate growth in plants at low dose (Al-Safadi and Simon 1990). Therefore, these radiations are important in modifying the plant genome for crop improvement. It is estimated through studies that overall mutants created from radiation are 2570 and among them gamma rays have produced 1023 crop mutants (Hamideldin and Hussin 2014). X-rays are electromagnetic radiations, ionizing radiations, a photon of energy that resembles gamma rays. Gamma radiation and alpha radiation are emitted from different parts of atoms, but have the same properties. X-rays are radiated from outside the nucleus, whereas gamma rays are emitted from the nucleus (Radiation: Facts, Risks and Realities 2012).

2.2 Nonionizing Radiations

Nonionizing radiations include radiation with wavelengths greater than 100 nm. Nonionizing radiations are further divided into electromagnetic fields and optical radiations. The optical radiations include visible light, UV radiation, and infrared radiations (Ng 2003). Visible light ranges from 360 nm to 760 nm. This visible light has the largest effect on the life of living organisms (Campillo et al. 2012). Plants use visible light in photosynthesis and change carbon dioxide into organic molecules such as glucose, starch, sucrose, and so on. These organic molecules are used in respiration to produce energy (Kovacs and Keresztes 2002). Visible light is important for photosynthesis, but the radiations ranging from 400 to 500 and 600 to 700 are most essential. Radiations between 500 and 600 nm are assisted by accessory pigments as they have low ability to be absorbed in pure chlorophyll (Campillo et al. 2012). Infrared radiation has wavelength ranges from 760 nm to 4000 nm (Campillo et al. 2012). These radiations have small quantum because of their longer wavelength. The biological effects of these radiations depend upon the absorption of the energy. These rays penetrate 20 mm into the tissues (Kovacs and Keresztes 2002).

UV radiations have shorter wave length ranges from 200 nm to 400 nm. These types of radiations are absorbed by ozone, which is present in the stratosphere (Campillo et al. 2012). Generally, these rays are not categorized in ionizing radiation because these radiations only ionize some types of molecules under certain conditions. The absorption and emission of ultraviolet radiation involve larger quanta than the visible light. The ultraviolet photon has much energy to carry out a photochemical reaction by breaking down the chemical bonds (Kovacs and Keresztes 2002). Ultraviolet radiation is found in the category of nonionizing radiations and it is found in 8 % to 9 % of total radiation emitted from the sun. Plants need sunlight for the process of photosynthesis; sunlight comprises ultraviolet radiations. Therefore, plants are directly exposed to the ultraviolet radiations. Plants—being living organisms—respond to UV radiations. UV rays also damage plant processes such as physiological processes and DNA damage (Stapleton 1992).

UV radiation is divided into three types: UV-A, UV-B, and UV-C. UV-A radiations are the less harmful part of ultraviolet radiations. This ray ranges from 320 to 400 nm and has a relatively higher wavelength than UV-A and UV-B; it comprises 6.3 % of solar radiation. The ozone, which is present in the stratosphere, absorbs ultraviolet radiations that have shorter wavelengths, so the depletion of ozone has no effect. The ozone layer is more effective as it absorbs UV radiation shorter than 280 nm; this absorption effectively decreases with an increase in wavelength greater than 280 nm, and at 320 nm it reaches approximately zero (Robberecht 1989). UV-B rays are more harmful than UV-A, but less harmful than UV-C. However, they cause severe damage in plants. The wavelength of UV-B radiation ranges from 280 nm to 20 nm. This radiation comprises about 1.5 % of the total solar radiations. Even a minor decrease in the level of ozone has a large effect on the level of UV radiation (Madronich 1992, 1993). One percent decreases in the ozone increase the

UV-B level, which reaches to the biosphere. UV-C radiation has a shorter wavelength ranging from 200 nm to 280 nm. Among UV radiations, UV-C is the most harmful radiation for living organisms.

3 Effect of UV Radiations on Crop Plants

Ultraviolet radiations (UV) are known to cause significant damages to crop plants and the overall ecosystem. Even small changes in its level can cause devastating effects on life on Earth. There are basically two types of damages inflicted by UV radiations, damage to DNA, which leads towards mutations, and damage to plant physiological and biochemical functions. These damages can either be inflicted directly on the particular process or on the regulatory molecules involved in that process. Examples of such damage include membrane disruptions, protein conformational change, effect on plant hormones and pigments that ultimately affects the plant growth, yield, development, and numerous cellular processes such as photosynthesis and respiration (Zlatev et al. 2012). The damage inflicted by UV significantly depends on the quality and quantity of photosynthetic active radiation (PAR) which is actually the amount of solar radiation required by plants to activate photosynthesis. The balance of UV and PAR is necessary for the protection of plants because the ration of PAR that reaches the Earth remains the same and it is not absorbed by ozone whereas it is the opposite for UV. It has been confirmed that high levels of PAR compensate for the negative effects of UV and serve as an acclimatization factor. Hence, in recent studies PAR is always taken into account while analyzing the effects of UV on crop plants (Gotz et al. 2010).

Many studies have been reported on the effects of UV radiations. Among them UV-B are more common because UV-B levels directly depend on the ozone layer and those levels are continuously increasing due to ozone depletion. The effect of UV-B can be categorized as the effect on morphological, physiological, and biochemical processes and DNA damage and changes in genotype of crops.

3.1 Effect of UV-B on Crop Morphology

UV-B radiations are known to cause many anatomical and morphogenic changes in crop plants, including smaller leaf size, folding, discoloration and browning (Teramura et al. 1984), reduced hypocotyls, and increased thickness of leaves (Adamse and Britz 1996) that lead to plant stunting. These effects are elevated when PAR levels are reduced (Teramura 1983). Further alterations in height, stem diameter, length of internodes, leaf area, stomatal number and length, as well as changes in floral morphology have also been observed. Figure 1 shows the effect of UV-B on leaf morphology. These morphogenic changes are also protective mechanisms of crop plants that prevent them from high levels of UV-B (Jansen et al. 1998).

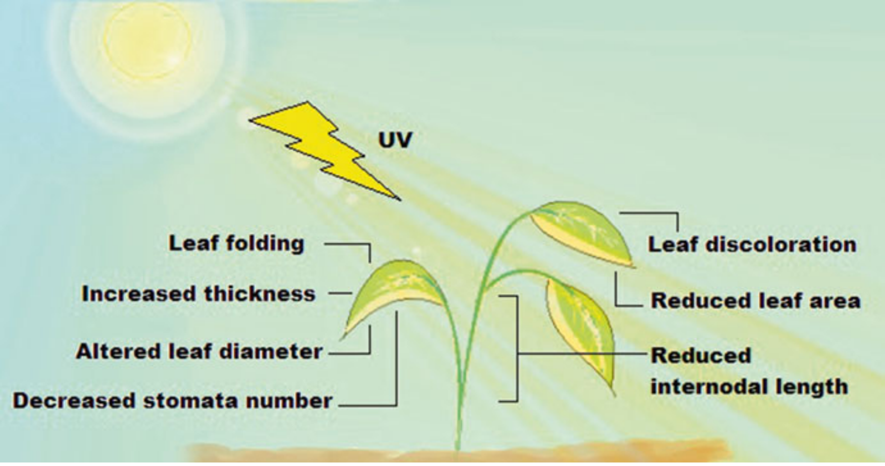

Fig. 1 The effect of UV-B on leaf morphology of crop plants

The introductions of such changes in plants due to the effect of solar radiations are known as photomorphogenic responses. These responses can change the architecture of plants due to the presence of photoreceptors including phytochromes, UV-B photosensory system, and photoreceptors for UV-A/blue light (Briggs and Olney 2001). Different assays have been designed to check the levels of gene expression that are either stimulated or inhibited by these responses (reviewed in Jansen 2002).

Early studies on crop plants show changes in height, leaf blade, and leaf area that have been observed in rice (Barnes et al. 1993). Similar alterations in pea plants with respect to plant height (Vu et al. 1984) and leaf area that resulted in decreased cell division (Mepsted et al. 1996) have been observed as well. Reductions in stomatal number and surface area, and vegetative morphological changes including increase in waxy layer, leaf epidermis (Tevini and Steinmuller 1987), and leaf optical properties (Cen and Bornman 1993) have been studied. Gonzalez et al. (1996) also studied the decrease in the waxy layer due to high-level exposure to UV-B.

Recent studies on crops such as soybean cultivars Jindou and Heidou revealed Heidou to be more sensitive to UV-B radiations and showed morphological changes including smaller and thicker leaf and hairy lamina (Feng et al. 2003). Changes in plant height and stem diameter have been observed due to UV-B radiations. In a study on Tartary buckwheat, decrease in plant heights was observed in eight populations and an increase was observed in four populations. Similar results regarding reductions in stem diameter were also visible in seven populations (Yao et al. 2007). Wheat studies regarding exposure to UV-B also showed morphological changes such as changes in the height of crops, tiller numbers, and alterations in leaf area. When wheat was exposed to the solar spectrum, about 20–24 % increase in height was observed, which corresponded with the increase in the number of nodes and length of internodes. About 50 % increase in leaf area and 114 % increase in the number of tillers was observed (Kataria and Guruprasad 2012b). In a similar study done on southern US rice cultivars, 5–12 % reduction in plant height, 7–10 % increase in length of culm, and a considerable increase in total leaves and leaf area was observed. However, no change in the number of tillers was seen due to high exposure to UV-B (Mohammed and Tarpley 2011).

Research has been conducted to check the effects of UV and PAR on the morphology of barley. In this case, UV/PAR treatment was applied to the crop and effects were calculated after 7 days. When UV + PAR+ treatment was done, reduction in leaf length of young leaves and in leaf area was observed. Under UV + PAR- treatment significant reductions in leaf area and width were observed along with an increase in leaf thickness. In UV + PAR+ and UV-PAR+ treatments decrease in leaf area was studied. This proves the importance of PAR in decreasing the adverse effects of UV-B radiations (Klem et al. 2012). In another study done on leaf anatomy and morphology, the appearance of necrotic patches on leaves visible after 4–5 days exposure to UV-B in cotton was observed but no changes in crop development were seen. A 47 % decrease in plant height, severe reduction of internodes, branch lengths, and leaf area along with a significant increase in the number and lengths of stomata and thickness of waxy layer were observed while studying leaf ultrastructure. Studies on structural morphology showed thinner leaves due to reduced mesophyll cells and increase in air spaces (Kakani et al. 2003b). Mung bean cultivars HUM 1 and HUM 12 also showed cupping and folding of leaves and the development of light purple necrotic patches due to elevated UV-B levels (Choudhary and Agrawal 2014a). Choudhary and Agrawal (2014b) also demonstrated morphological changes due to UV-B in another study on pea cultivars such as decrease in leaf area, root nodules, and root-to-shoot ratio in field conditions.

Floral morphology of crop plants is also observed to change due to UV-B exposure. This in turn affects reproduction of the crop plants which ultimately affects yield. In the same study done by Kakani et al. (2003a), cotton showed a decrease in flower size due to a decrease in the size of the petals, and the number of anthers was also reduced. Floral morphology studies have also been done on soybean which showed decreased petal length and length of staminal column. The flower size was reduced about 31–38 % and flower length about 28 % under different levels of UV. Pollen morphology is also affected by an increase in the UV-B exposure causing shriveled appearance, lack of apertures, and other structural effects (Koti et al. 2005). Hence UV-B has a significant consequence on the morphology of crop plants that can affect their growth and ultimately reduce their yield.

3.2 Effect of UV-B on Crop Physiological and Biochemical Processes

The major effect of UV-B exposure to crop plants results in malfunctioning of the crops' physiological and biochemical functions such as photosynthesis. This can in turn affect the plant's pigment concentration, crop phenology, reproductive processes, biomass and grain quality, and increase environmental stresses including abiotic and biotic factors. UV-B can also affect the metabolite concentration, amino acids, proteins, and total sugar content, and can cause changes in nitrogen levels.

3.2.1 Biomass and Grain Quality

The morphology of plants guarantees their particular biomass. As UV-B affects the morphology of crop plants, it also alters the biomass, the grain quality, and grain number and ultimately affects the yield. It has also been studied that reduction in photosynthesis can also decrease the biomass of crops. There are many crops on which studies of biomass have been conducted. Research on cotton shows that increased exposure to UV-B reduces the biomass of crops (Gao et al. 2003). In a study conducted on soybean cultivars a significant decrease in biomass and dry weight was observed due to the changed morphology of all organs of the plant (Feng et al. 2003). In another study on 20 soybean cultivars altered biomass and grain yield has been observed due to UV-B sensitivity of crop plants (Yanqun et al. 2003).

In rice there is a variation among the varieties on the effect of the UV-B. Some are more tolerant than others such as in different southern US rice cultivars and that's why biomass production varies in them (Teramura et al. 1991). However, in a recent study on rice, a dry weight decrease of 23 % was observed for aboveground parts. Alterations in grain weight were also seen that significantly decreased the yield in ranges from 13 % to 79 % in different cultivars as compared to plants grown under a UV-B free environment (Mohammed and Tarpley 2011). The reason for the decrease in plant dry matter is basically due to a decrease in the rate of photosynthesis and stomatal conductance, which are explained further in Sect. 1.2.2.2. A research conducted on maize revealed decreases in grain yield when exposed to UV-B for different time periods. The maize yield was less affected when exposed to UV-B for a short-term period of 1 week as compared to maize plants that were exposed to UV-B for 4 weeks. In contrast the grain quality was enhanced due to increase in grain protein content (Yin and Wang 2012).

UV-B also affects the biomass in Tartary buckwheat. It is calculated to be decreased in six populations and the difference between the control plants and affected plants ranged from 3 to 5.2 times. An increase in biomass in some populations and their yield enhancement has also been observed. The thousand grain weight calculation of the same plants showed a decrease in six populations whereas specific leaf area was increased (Yao et al. 2007). Another study by Yao et al. (2006) also showed reduced thousand grain weight, seed yield, and biomass in both spring and autumn varieties of Tartary buckwheat. Research conducted on red and green lettuce revealed reduction in growth and biomass due to high UV-radiation. The plants showed higher weights of 47 % when placed under UV blocking film and their vegetative growth significantly increased as compared to when the same plants were placed under transparent film. Among the lettuce types, red lettuce showed lower dry weight as compared to green lettuce. The rate of growth and dry weight also depends on the period at which plants were transferred from under UV-blocking to UV-transparent film (Tsormpatsidis et al. 2010).

The grain quality of wheat has also been under consideration. Although the positive effects of UV-B enhancing grain quality have been studied in 10 wheat cultivars (Zu et al. 2004) and rice (Hidema et al. 2005), negative effects have also been reported in maize (Gao et al. 2004). But recent studies have shown that biomass and grain quality and grain yield of wheat largely depend on the crop phenology and developmental stages, that is, at what period the plant was exposed to UV-B radiation (Calderini et al. 2008). However, in a study done in 2009, wheat varieties under increased UV-B radiations did not show any change in crop phenology as compared to control plants. In contrast to these results, the aboveground biomass, particularly leaf blade biomass and grain yield were negatively affected by UV-B and a decrease of 11–19 % and 12–20 %, respectively was observed (Lizana et al. 2009). In another study on wheat by Feng et al. (2007) spring wheat growth, economic yield, and biomass were also reduced by high UV-B levels.

Reductions in biomass with alterations in plant organs were reported in sorghum varieties due to a decrease in the process of photosynthesis. Similarly the grain number, grains per panicle, and length of panicle showed increased growth when exposed to solar radiation free of UV-B (Kataria and Guruprasad 2012a). Another study done by Kataria and Guruprasad (2012b) on wheat varieties showed significant increase in aboveground biomass and grain yield. In a study on mung bean cultivars HUM 1 and HUM 12, grain and yield reductions of 8.5 and 10.6 %, respectively, were observed (Choudhary and Agrawal 2014a). Similarly 29 and 19 % reduction in biomass and seed yield of pea cultivars HUP-2 and HUDP-15, respectively, were observed in field conditions which also showed that UV-B can have a considerable effect on crop quality and economic yield (Choudhary and Agrawal 2014b). Hence UV-B has negative effects on plants, plant biomass, and agronomic traits such as growth and yield.

3.2.2 Photosynthesis and Photosynthetic Pigments

UV-B has a major impact on the rate of photosynthesis and its pigments. As mentioned in the above sections UV-B stressed crops undergo many physiological and morphological changes which inhibit photosynthesis that in turn alter the crop biomass and subsequently affect the crop's yield. The decrease in the photosynthesis process occurs due to the damage on the molecular mechanisms of the process or due to the decrease in photosynthetic pigments such as chlorophyll and carotenoid content. Biochemical changes include alterations in leaf RuBisCO level (Ziska and Teramura 1992) and binding proteins of Photosystem II along with alterations in physiological factors such as stomatal number, rate of transpiration, and water-use efficiency that are also negatively affected by UV-B. The stomatal conductance and the opening and closing of the aperture are known to associate with environmental factors such as light and humidity, and on plant hormones such as abscisic acid. Thus a stressful environment with increased UV-B can affect the stomata's function

(Jansen and Van Den Noort 2000; Teramura 1983). Thylakoids and grana in the chloroplast are also affected as UV-B can break their membranes and rupture them completely (He et al. 1994; Kakani et al. 2003a).

UV-B radiation at low PAR levels has also greatly affected the process of photosynthesis. The process is inhibited by the inactivation of photosystem II that normally occurs in the thylakoid membranes of chloroplasts. Photosystem II is a part of the electron transport chain that functions to generate ATP required for plant functions. Inhibition of this system will inhibit the synthesis of ATP and affect the photosynthetic activity. The photosystem II reactions are mediated by D1 and D2 proteins. They are very sensitive and degrade due to high UV-B levels, which can be another factor for the decrease in photosynthesis rate. UV-B is also known to affect RuBisCO (Ribuose-1, 5-biphosphate carboxylase oxygenase) during the Calvin cycle for fixing CO_2 into sugar molecules. The reduced synthesis of sugars is due to limited triose-P usage, which resulted in decreased RuBP regeneration and hence CO_2 fixation capacity of the plant decreases (reviewed in Kakani et al. 2003b and Zlatev et al. 2012). Figure 2 shows the effect of UV-B on photosystem II and Calvin cycle.

Numerous studies have been reported to check the activity of photosynthesis in the presence of excessive UV-B in crop plants. In a study on wheat by Lizana et al. (2009), a considerable decrease in chlorophyll content was observed. Chlorophyll a

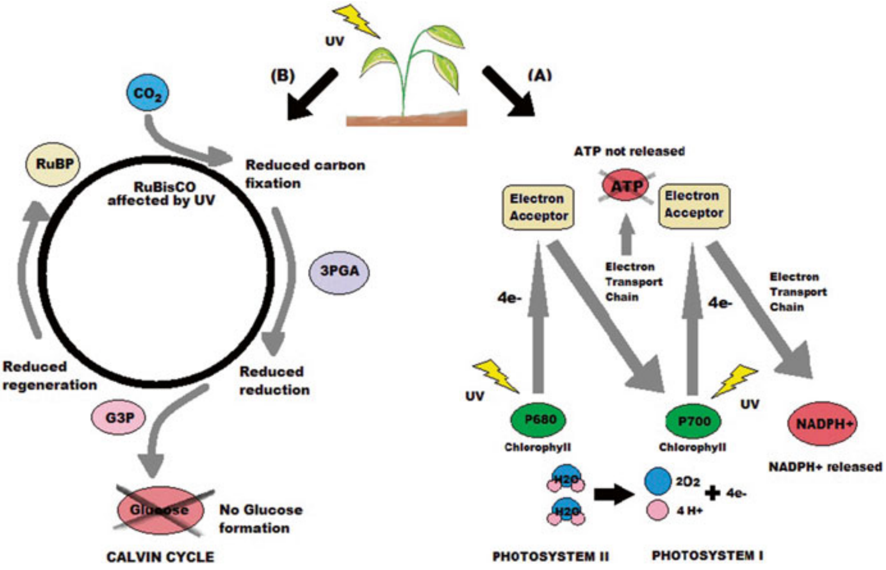

Fig. 2 The effect of UV-B on the process of photosynthesis. (**a**) Photosystem II affected by UV-B stress at the end of which ATP is not released. However, photosystem I is not affected by UV-B and NADPH+ is released at the end of the process. (**b**) Calvin cycle affected by UV-B in which RuBisCO is affected. This in turn reduced the carbon fixation, reduced reduction from 3PGA to G3P which leads to reduced regeneration of RuBP

was found to be more sensitive than chlorophyll b but a considerable decrease in a/b ratio was observed by increased UV-B exposure. Similar results were seen when carotenoid concentration was measured. The reason for the decrease in pigments was due to the lack of compounds or antioxidant enzymes that have the capacity to absorb UV-B radiations and hence affect the thylakoids, photosystem II, and yield of the wheat crop. Similarly chlorophyll a and b, ratio a/b, as well as carotenoids were found to be higher when sorghum varieties were exposed to solar radiation in exclusion of UV-B. Because chlorophyll a content was found to be greater than chlorophyll b, the a/b ratio was decreased. This resulted in an increase in photosynthesis rate and in turn increased the biomass and growth of crop plants (Kataria and Guruprasad 2012a). Similar results regarding the negative effects of UV-B on photosynthetic pigments have been seen in wheat (Feng et al. 2007). A moderate reduction of carotenoids such as neoxanthin, xanthophylls, and luten and in chlorophyll a and b were also seen in cucumber varieties whereas a significant decrease in all the pigments was observed in soybean (Yao et al. 2006).

During the process of photosynthesis II, naturally occurring isotopes of carbon are used that are ^{12}C and ^{13}C. ^{12}C is more commonly incorporated by plants than ^{13}C during the assimilation process. But there are several studies which report that an isotope $\delta^{13}C$ is also used and its uptake by the plant during carbon fixation is affected by UV-B and found to be decreased which further lowers the rate of photosynthesis (Naidu et al. 1993). Some studies have reported no significant change in $\delta^{13}C$ due to UV-B exposure (Kim et al. 1996). However, in 2003 it was studied that $\delta^{13}C$ composition in plants decreased due to UV-B exposure, which resulted in the decrease in the rate of photosynthesis and stomatal conductance. Consequently, it affected the photosynthetic pigments such as chlorophyll and carotenoid content. Inasmuch as there was no change in the concentration of $\delta^{13}C$ in the environment, the UV-B stress was the only factor that affected its uptake by plants (Feng et al. 2003). Studies on spring wheat exposed to UV-B have also shown a reduction in carbon stable isotope $\delta^{13}C$ composition along with decreased water-use efficiency and in stomatal conductance that consequently affected the photosynthesis rate (Zhao et al. 2009).

Photosynthetic pigment concentrations were also found to be negatively affected by UV-B in Tartary buckwheat. Total chlorophyll content and carotenoids were decreased mostly in young leaves. The populations with higher levels of pigment content were found to be more affected by excessive UV-B (Yao et al. 2007). Another study on Tartary buckwheat showed a decrease in photosynthetic pigments in high UV-B as compared to ambient UV-B and spring buckwheat was much more affected than autumn buckwheat (Yao et al. 2006). Elevated UV-B has also led to a decrease in chlorophyll and pigment concentrations in both HUM and HUM 12 cultivars of mung bean, which was due to disruption of the chloroplast structure (Choudhary and Agrawal 2014a, b). Another study on the grapevine plant showed the negative effects of UV-B exposure in the short- and long-term period in which leaf chlorophyll levels and carotenoid concentrations were severely reduced. However β-carotene levels were significantly increased due to high UV-B level (Martinez-Luscher et al. 2013).

Various studies on rice cultivars have been done to identify the decline in photosynthesis rate due to high UV-B irradiance. In research done in 2010, the photosynthesis rate was observed to be reduced by the decline in CO_2 assimilation in all cultivars under study. This was also found to be due to the reduction of RuBisCO as well as a significant reduction in photosystem II and the electron transport chain. However, no changes in photosystem I were calculated (Fedina et al. 2010). In another study on nine cultivars of rice, UV-B exposure resulted in decreased rates of photosynthesis and chlorophyll a and b at the grain filling period but the leaf carotenoid levels did not show any difference. The decrease in photosynthesis was more visible in inbred cultivars in comparison to hybrids (Mohammed and Tarpley 2011). In the leaves of *Oryza sativa* (rice), the rate of photosynthesis was also found to decline due to UV-B exposure in the leaves because of reduced stomatal conductance and gaseous exchange. The leaf fluorescence when calculated to check chlorophyll levels was recorded to be majorly affected. Chlorophyll a was more strongly affected in leaves than chlorophyll b which decreased the chlorophyll a/b ratio. Among the pigments, xanthophylls pigments were less severely affected and carotenes showed minor deviations from normal levels. However, the leaves of crop plants formed after the exposure showed no significant effect. This confirmed the insensitivity of rice leaves to excessive UV-B (Lidon and Ramalho 2011).

In two varieties of barley, the effects of PAR and UV-B have been studied on chlorophyll levels and stomatal conductance. When the UV + PAR-condition was applied, chlorophyll content was reduced, photosystem II was targeted, and a decrease in photosynthetic enzyme activity, RuBisCO content, and stomatal conductance were observed. However, in PAR+ condition, chlorophyll a and b were not affected (Klem et al. 2012). In a similar study on lettuce, plants grown under UV transparent film showed no difference as compared to those grown under UV blocking film. However, when they were transferred from UV blocking to UV transparent film, the plants' stress condition decreased due to the change in environment. In the second experiment, no significant differences were measured when the stomatal conductance and rate of photosynthesis were measured. This showed that ambient UV treatment was not able to affect red and green lettuce cultivars (Tsormpatsidis et al. 2010).

It was also studied that the photosynthetic capability of the plant is affected by nitrogen concentration inasmuch as nitrogen is associated with photosynthetic enzymes, membrane proteins, and chlorophyll and carotenoid composition (Field and Mooney 1986). In a study on maize reported in 2005, UV-B affected the photosynthetic rate and stomatal conductance. Activities of enzymes, pigments, RuBisCO concentration, as well as chlorophyll a and b were severely affected. However, the nitrogen levels when measured were also found to be reduced. This in turn affected photosystem II as the pool size of electron acceptors decreased. Thus, the study proved that the rate of photosynthesis is dependent on the plant's nutrition and correlates with nitrogen levels (Correia et al. 2005).

When the plants are exposed to high levels of UV-B, they become stressful and release signaling molecules that are required for plant defense. One such molecule is jasmonic acid (JA) that is released due to biotic and abiotic stresses (Dar et al. 2015).

In this study on wheat the effect of UV-B was observed in the presence and absence of JA. Results showed that photosynthetic pigments and chlorophyll florescence were minimized when UV-B was exposed to the plant in the presence of JA. This also proposed that photosystem II which was affected by UV-B exposure was remedied by the application of JA. Therefore JA is involved in increasing the tolerance of plants exposed to high UV-B (Liu et al. 2012). Hence UV-B can affect the photosynthetic activity of crops and can reduce them significantly under high irradiance. Various photosynthetic processes and pigments are altered and if not controlled by UV-B exposure can lead to severe yield loss and poor crop quality.

3.2.3 Flavonoid Levels

Plants under stress conditions initiate many mechanisms to protect themselves from impairment. One such mechanism is the alteration of flavonoid levels, which are normally synthesized with the help of chalcone synthase (CHS) enzyme (Batschauer et al. 1991). When the plant is exposed to stress, changes in physiological and biochemical functions and DNA damage cause many pigments to release. In the case of UV stress, the photo repair is mediated by an enzyme called photoreactivating enzyme (PRE) which undergoes this mechanism by monomerizing cyclobutane pyrimidine dimer (CPD) known to cause DNA damage if not degraded. The formation of CPD initiates the flavonoid biosynthesis pathway and PRE activity which damages the CPD thus limiting its function. It is also known that PRE acclimatizes flavonoid biosynthesis due to UV-B irradiation stress (reviewed in Sancar 1994). Flavonoids also serve as the reactive oxygen species (ROS) scavenging secondary metabolites that protect the plant against oxidative stresses (Frohnmeyer and Staiger 2003) and are secondary to antioxidant enzymes to regulate the ROS level inside the plant under stress (Agati and Tattini 2010; Fini et al. 2011). There are many types of flavonoids that are present in plants. Table 1 shows some flavonoids and their functions.

Basically, there are two mechanisms by which these secondary metabolites protect the plant. Firstly by reducing free radicals such as O_2, H_2O_2, and $OH^{\cdot}$ or by chelating them with metals, thus stopping their formation and secondly by inhibiting ROS synthesizing enzymes and increasing UV-B absorption capacity (Pietta 2000). Because they reside inside the vacuole, the vacuole has a major role in ROS homeostasis and in regulating the activity of various oxidants (Mittler et al. 2004). Apart from flavonoids and antioxidants, plants also release some phenolic compounds that are induced when the plant is irradiated with high UV-B. Hydroxycinnamic acid (HCA) is a phenolic compound involved in protecting the plant from UV-B. These compounds also function by absorbing UV-B at specific wavelengths, but allow PAR to transmit to initiate photosynthesis (Morales et al. 2010).

As the accumulation of flavonoids in plants decreases ROS generation, it has been observed that flavonoid synthesis is induced more in plants that are sensitive to stress as compared to those less sensitive. It means that sensitive plants will encounter more oxidative stress (Tattini et al. 2005). In severe conditions flavonoid

Table 1 Different types of flavonoids and their known functions (Winkel-Shirley 2002)

Types of flavonoids	Functions
Isoflavonoids (e.g., naringenin)	Helps in the formation of nodules and in defensive roles
Aurones	Role in pigmentation of leaves
Flavones (e.g., luteolin, tangeritin)	Helps in nodule formation and defense
Anthocyanins (e.g., cyanin, malvin)	Role in pigmentation that helps to attract pollinators and enhance seed dispersal
Deoxyanthocyanidins	Role in pigment production and defense
Flavonol glycosides (e.g., Quercetin, kaempferol, myricetin)	Involved in protection against UV-stress, in producing purple pigment, male fertility, and signaling
Proanthocyanidins	Role in pigmentation and defense

biosynthesis is increased and more flavonoid accumulation becomes inversely proportional to the presence of other antioxidative enzymes, meaning that when antioxidants deplete in the plant due to stress, flavonoid activity is induced, making up the secondary antioxidative system (reviewed in Agati et al. 2012).

Various studies on crops have been reported that specify the stimulation of flavonoids due to UV-B stress. In a study on *Brassica napus*, low PAR levels and high UV-B stress increased the flavonoid accumulation in the plant. When UV-A stress was studied, it was found that UV-A only induced a low level of flavonoids as compared to UV-B (Wilson et al. 2001). In a similar study on white asparagus, activities of antioxidant enzymes PAL (phenylalanine ammonia lyase) and POD (peroxidase) were checked under UV-B irradiation. PAL levels did not demonstrate any significant activity at high UV-B concentration, but at low UV-B high PAL was observed. In contrast, POD activity was elevated due to UV-B stress. Such differences were also seen in other parts of the plant. In apical meristems high POD levels were observed, and in the basal region PAL activity was high. The flavonoid level was also increased with an increase in quercetin activity (Eichholz et al. 2012). In a study on mustard cotyledons UV-B affected the flavonoid concentration and the levels of the PRE. The results indicated that radiations for a short period of time can induce anthocyanin production whereas flavonol biosynthesis occurred due to radiation exposure for a long time. PRE was found to be induced by far-red light and long-term exposure (Buchholz et al. 1995).

Research on *Ligustrum vulgare* plants also showed flavonoid accumulation due to high light stress. The plants when placed in sunlight exclusive of UV-B showed a severe decrease in oxidative enzymes that was also enhanced by salinity stress. The oxidative damage led to the initiation of synthesis of flavonoids that reduced the ROS accumulation (Agati et al. 2011). A study in 2012 in maize leaves indicated that nitric oxide (NO) colocalizes with flavonoids. It was found that flavonoids and NO were accumulated in the upper epidermis of leaves irradiated with UV-B as compared to leaves that were nonirradiated. It also indicated that both NO and flavonoids are systematically produced as a result of UV-B stress (Tossi et al. 2012).

Thus the above studies prove that flavonoids have a major role in photoprotection of plants and their mechanism is initiated by high levels of UV-B.

3.3 DNA Damage and Repair Mechanism

As mentioned before, UV-B can cause DNA damage in crop plants. Under stress conditions two adjacent pyrimidine bases form a pyrimidine dimer that affects the DNA replication and transcription processes. Photodamage by UV-B occurs by the construction of the cyclobutane pyrimidine dimer (CPD) and pyrimidine, pyrimidone 6-4 photoproducts (6-4 PPs) that are formed between two carbons of adjacent pyrimidines C_6 and C_4. UV-B exposure to crop plants can also alter the concentration of thymine dimers (TD) inside the leaf. It has been observed that high UV-B exposure increased TD levels and subsequently increased DNA damage, but the repair mechanism was too slow such that it could only repair low levels of TD and not the high concentration. TD levels were also found to be reduced under negative UV-B condition. Hence it has been proved that DNA damage is stimulated at high UV-B (Schmitz-Hoerner and Weissenbock 2003).

Plants have evolved many repair mechanisms to counter the damage induced by UV stress. There are basically two mechanisms by which photorepair can occur in plants. Firstly, by the accumulation of flavonoids that are UV-absorbing compounds, and phenolic compounds in the epidermis of leaves so that mesophyll cells can be protected and the photosynthesis process is not affected (Kolb et al. 2001), and secondly, by excision of pyrimidine dimers (CPD or 6-4 PPs). Photolyases are the enzymes that initiate photorepair mechanisms and can remove the defected pyrimidine dimers (Britt 1996). These dimer formations result in the accumulation of antioxidants as mentioned in Sect. 1.2.2.3. It has also been studied that pyrimidine dimers can cause cell death by interfering with the DNA replication and transcription process if not removed and if somehow they bypass the repair mechanism, they are translated and lead to the development of mutations. There are many mechanisms for the repair of DNA damage. Among them two are most common, photoreactivation (PR) and nucleotide excision repair (NER; Tuteja et al. 2001). The first DNA repair pathway is a light-dependent photoreactivation repair mechanism or the PR pathway in which CPD or 6-4 PPs dimer formation occurs. Photolyases that undergo the repair mechanism are of two types, CPD photolyase and 6-4 photolyase. These photolyases carry flavin cofactor FAD which acts as an electron donor and breaks the CPD or 6-4 PPs dimer in the presence of light (Britt 2004). Figure 3 shows the photoreactivation pathway for pyrimidine dimer repair.

The second method for repairing DNA is nucleotide excision repair. It is an evolutionary conserved mechanism in which DNA damage induced by radiations and other environmental factors is repaired. Figure 4 shows the NER mechanism for the repair of DNA damage. NER has two mechanisms by which UV-induced DNA damage can be repaired. First is the NER-global genome repair (NER-GGR) which is able to repair damage to DNA in the entire genome that is untranscribed.

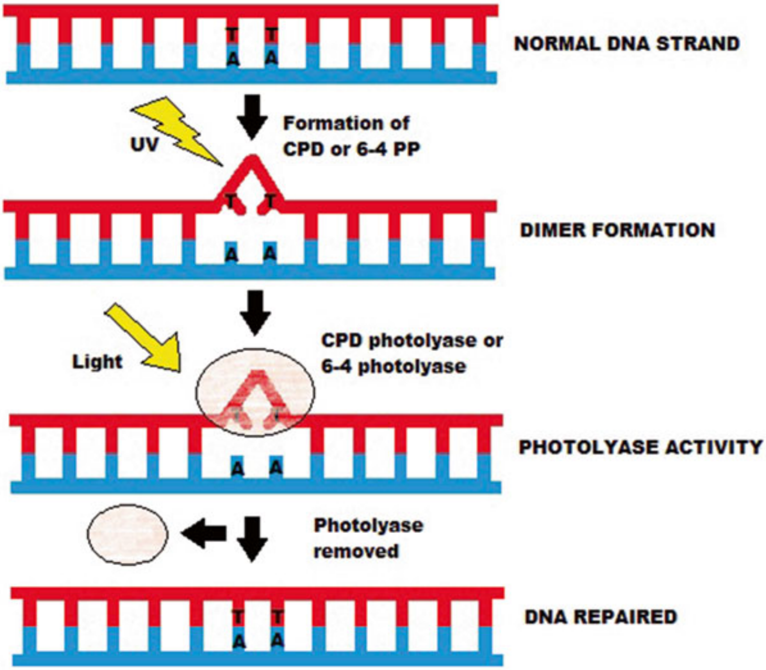

Fig. 3 Photoreactivation (PR) pathway for the repair of pyrimidine dimers mediated by photolyases (explanation from text)

Second is the NER-transcription coupled repair (NER-TCR) which can only repair DNA damage in transcribed strands but does not interfere with the transcription process. In the NER-GGP, the damage is recognized by the UV-damage binding protein (UV-DDB) and a complex of *xeroderma pigmentosum* complementation group C (XPC) and RAD23. However, in a review by Tuteja et al. (2009), NER-GGP recognizes UV-B induced damage to DNA by XPC/hHR23B. Contrastingly, in the NER-TCR pathway, damage recognition is mediated by Cockayne syndrome A and B (CSA and CSB) which are in turn activated when RNA polymerase reaches the site of damage.

After recognition both NER-GGP and NER-TCR unwound the DNA helix by a transcription elongation factor-IIH that includes other subunits such as *xeroderma pigmentosum* complementation group B (XPB), *xeroderma pigmentosum* complementation group D (XPD), and *xeroderma pigmentosum* complementation group A (XPA). After unwinding excision proteins, namely *xeroderma pigmentosum* complementation group F/excision repair cross-complementation (XPF/ERCC1) and *xeroderma pigmentosum* complementation group G (XPG) excise the 20–30 base oligonucleotides on the damaged strand. The undamaged strand is held intact by replication protein A (RPA). RPA prevents the excision of the complementary undamaged strand and enables it to be used as a template for the repair synthesis of the damaged strand. The last step of NER is the gap filling stage in which proliferating

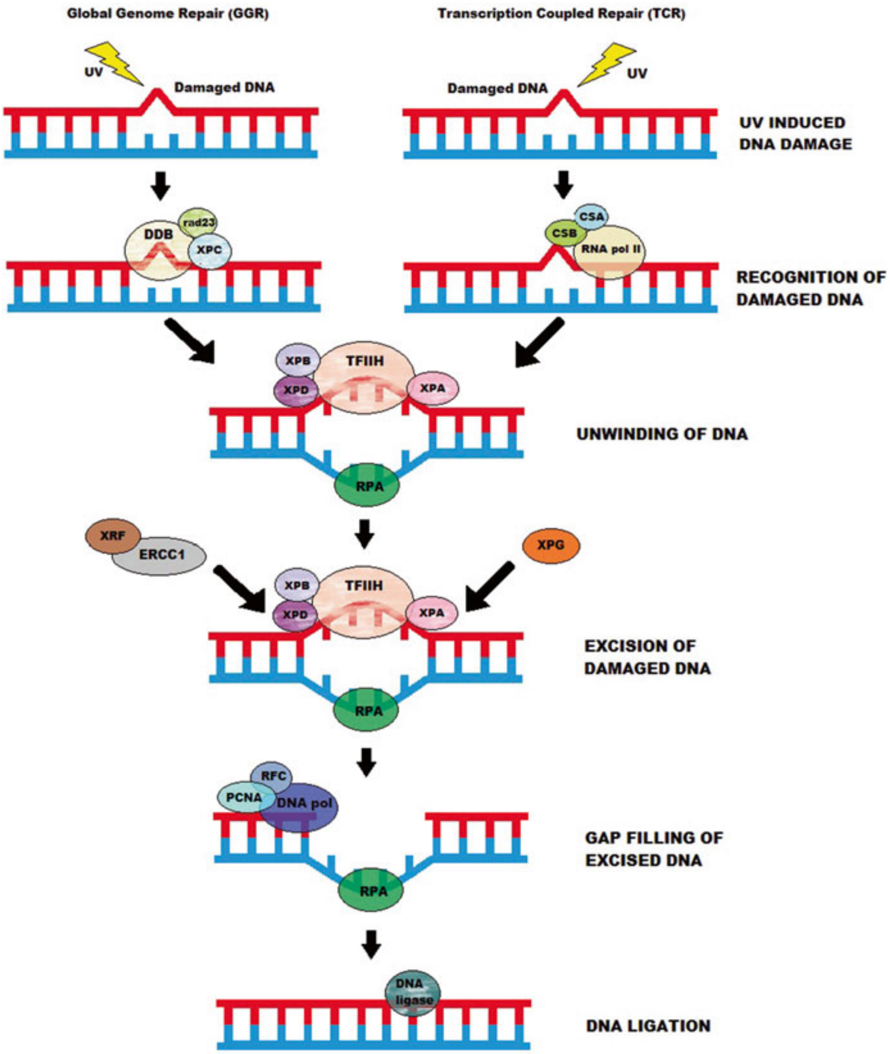

Fig. 4 NER mechanism for the repair of DNA damage induced by UV-B (explanation from text)

cell nuclear antigen (PCNA) and replication factor C (RFC) carry out repair synthesis of excised strands mediated by DNA polymerase subunits δ and ϵ. The strands are then ligated by DNA ligase I (Britt 2004; Kimura and Sakaguchi 2006; Tuteja et al. 2009; Balestrazzi et al. 2011).

Different studies have been reported in plants, particularly *Arabidopsis*, which explains how UV-B can cause DNA damage. A study shows that temperature and environmental factors can affect the photorepair mechanisms and can increase DNA damage. It was found that CPD and 6-4 PPs formation were not affected by normal temperature and direct UV-B stress and their concentrations remained normal.

However, the photorepair mechanism, particularly of 6-4 PPs was reduced under high temperature and UV-B exposure as compared to CPD concentration which was measured to be minutely decreased. This shows that repair mechanisms of a plant are directly dependent on temperature (Li et al. 2002). CPD activity has also been observed in spinach due to UV-B exposure. Expression of the photolyase gene was found to be higher in leaves and flowers as compared to roots in both male and female plants (Yoshihara et al. 2005). In research on *Arabidopsis*, mammalian Cockayne syndrome As (CSA) orthologue ATCSA- 1, involved in NER-TCR was discovered. It was found to be working simultaneously with DNA binding protein 2 (DBP2). It was studied that in normal conditions the ATCSA-1 expression was stronger than DDB2 but under UV-stress, DDB2 expression was increased and ATCSA-1 expression remained constant. Hence this showed the importance of both ATCSA-1 and DDB2 in the NER-TCR mechanism (Biedermann and Hellmann 2010).

In *Arabidopsis*, UV-B has been shown to affect the expression of DNA that regulates the cell cycle. Under UV-B stress, the expression of marker genes revealed that UV-B downregulated the histone H4, E2Fa genes and the transcript CYCD3; 1 which mediate the G1-S transition whereas a gene transcript KPP2 that normally reduces the G1-S transition showed increased expression. The transition from the G1-S phase is also shown to be affected by CPD formation and not by ROS. In another study on *Arabidopsis* and maize, DNA damage has been found to be repaired by the mismatch repair system (MMR) which is involved in recognition of mismatched or unmatched bases. In this study MSH2 and MSH6 genes were found to be contributing to the DNA damage and also affected cell cycle regulation and their expression was found to be upregulated. However, MSH2 and MSH6 mutants when compared to wild-type also showed more accumulation of CPD which confirmed that they are involved in response pathway to DNA damage (Lario et al. 2011).

4 Introduction to Gamma Radiation

There is a constant exposure of radiation that all the living organisms face every day, including cosmic radiation and natural radiations occurring from rocks and soils, radionuclides. Moreover, anthropogenic activities are the main cause of producing absorbed radiations through radioactive waste storage, nuclear radiation accidents, and nuclear power production (Vanhoudt et al. 2014; Daly and Thompson 1975). Electromagnetic radiations are of various types such as gamma rays, X-rays, visible light, and UV rays (Wi et al. 2005). These radiations have different frequencies and energies. Among all radiations gamma rays are considered to be the most energetic form of radiation with an energy level starting from 10 KeV to several 100 KeV. This quality makes them more penetrable than alpha and beta rays (Kovacs and Keresztes 2002). Gamma radiation (electromagnetic radiation with high frequency) is an important ionizing ray, as it comprises high-energy photons. High penetration properties of photons cause ionization of matter and plants by indirect interaction

(Vandenhove et al. 2010. Previous studies show that these rays cause modification in growth and development, cause DNA damage, and interrupt the metabolic pathway (Esnault et al. 2010; Kovalchuk et al. 2007; Vandenhove et al. 2010) consequently causing deleterious effects on the plant. Nevertheless, useful reports have also been published on growth stimulation by the effect of a low dose of gamma rays (Marcu et al. 2013; Miller and Miller 1987).

Plants, sessile organisms, constantly face fluctuations in environmental conditions, for instance, different harmful radiations of sunlight, air pollutants, and other abiotic stresses. Any changes in the somatic cells are represented as mutations in gametes, as plants lack reserved germline and meiotic cells are produced in late development (Walbot and Evans 2003). Gamma rays are ionizing rays that react with atoms and molecules present inside the cells to produce free radicals. Production of free radicals depends on the irradiation level that causes damage or modification of components in plants, ultimately affecting morphology, physiology, anatomy, and biochemistry of plants. As a result, physiology and metabolism are affected such as altered photosynthesis, expansion of thylakoid membrane, accumulation of phenolic compounds, and variation of the antioxidative system (Kim et al. 2004; Kovacs and Keresztes 2002; Wi et al. 2005).

4.1 Effects of Gamma Radiations on Plants

4.1.1 Effects on Phenotype of Plants

Chaudhuri (2002) found that a high dose of gamma rays reduces root and shoot length. Kiong et al. (2008) reported that the rate of seed germination depends on the level of chromosomal damage caused by increasing doses of radiation. It was determined that radiations reduce growth regulators such as cytokines by breaking them down or not synthesizing, thereby increasing plant sensitivity. Kim et al. (2004) determined that the low dose of gamma rays ranging 1–2 Gy when exposed on *Arabidopsis* seedlings slightly enhanced their growth, in comparison to seedlings exposed to high radiations of 50 Gy. He hypothesized that a low level of gamma rays helps the plant to overcome daily stresses during growth conditions, including variations in light intensity and temperature. Low levels of gamma rays induce growth stimulation signals by increasing the antioxidative ability of cells or by changing the hormonal signaling in plants (See Fig. 5). Gamma ray treatment in the early stages of seed germination triggers the activation of RNA or protein synthesis (Abdel-Hady et al. 2008). Toker et al.'s (2005) findings show that radiations up to 200 Gy increase shoot length, but further increase to 400 Gy causes despair in shoot length. Melki and Marouani's (2010) research also concluded that a low dose of 20 Gy gamma radiations enhances the root length and number by 18–32 %. Rashid and Daran's (2013) findings showed that increasing duration of gamma rays decreases the average germination rate in ginger (44 %), which was not as severe as that of the maximum exposure period of 150 s. Gamma rays decrease the growth rate with an increase in radiation dose due to mutations in DNA that synthesize DNA at the interphase leading to plant bud disruption and resulting interruption of cell differentiation. They estimated that increasing doses are injurious to the plant cell and ultimately interfere with the growth of plants. However, Konzak (1984) described that doses reducing 25 % of seedling height are considered useful rays

A high dose of gamma radiations is not only injurious to the ultrastructural organelles, but also affects the phenotype of the plant. Wi et al. (2007) determined that treating pumpkin plant with a high dose of gamma radiations (1 kGY) can cause an imbalance of plant growth regulators and result in curling and yellowing of leaves. Pumpkin tissues were found sensitive to gamma radiations (Micron 38 (2007). A high dose of gamma irradiations (100, 200, 300, and 400 Gy) decreases the germination process in seeds, but does not affect already germinated wheat seed (see Fig. 5). Borzouei et al. (2010) demonstrated that germination capacity decreases with increase in irradiation. Melki and Marouani (2010) also verified that irradiated and nonirradiated wheat seed showed no significant differences at low dose. Borzouei et al. (2010) stated a low dose of 100 Gy showed no central changes in root weight; nevertheless a high dose up to 200–300 incredibly lowered the root weight compared to controls. Melki and Salami's (2008) findings were contradictory to Borzouei et al.'s (2010) results that a radiation range of 15 Gy causes improvements in chickpea dry weight in contrast to 0 Gy doses of gamma rays.

Majeed and Muhammad (2010) reported that a high dose of 70–80 kGy delays initiation and completion of germination in *L. sativum,* as a result of inhibitory effect of rays on seed dormancy (Fig. 5). Such high radiations are injurious to seeds

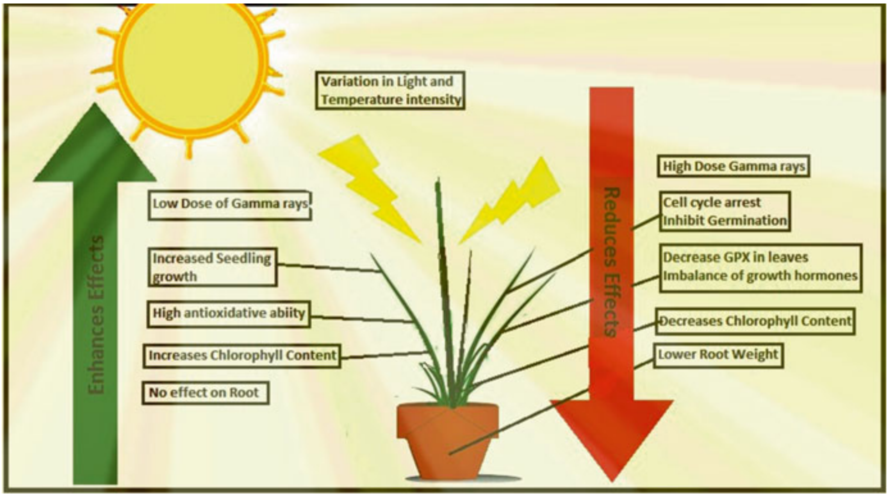

Fig. 5 Comparison of high dose and low dose of gamma radiations effects: high dose of gamma radiations that effects phenotype, ultrastructural organelles, causing cell arrest of the plant, whereas low dose of gamma rays enhances seedling growth and helps cell fight back daily stresses in its growth. It also increases the antioxidative ability of cells (Wi et al. 2007; Melki and Marouani 2010)

and have the ability to cause inhibitory effects on seeds of angiosperms and gymnosperms (Thapa 1990). However, germination can also increase as a result of the stimulating effects of RNA or protein synthesis (Kuzin et al. 1976) or due to eradication of the bacterial population along with spores and other fungi (Gruner et al. 1992). Borzouei et al. (2013) reported that gamma rays above 200 Gy in Roshan wheat prevent seed germination. Marcu et al. (2013) also investigated the role of different gamma radiation doses in causing morphological abnormalities in maize. He described that rays from 0.1 to 1 kGy affect maize germination up to 11–62 %, shoot length of maize is decreased to 9–62 %, and the root length is reduced from 9 to 71 %. Radiation ranging from 0.5, 0.7, and 1 kGy inhibited maize seed germination, however, 0.1, 0.2, 0.3 kGy lessens the content of photosynthetic pigment. Vanhoudt et al. (2014) presented that different doses of gamma rays caused changes in root and leaf weight but growth was not inhibited. These changes were the result of biological changes taking place in plants, instead of effects of radiations. A chronic dose (a low dose for a long time) affects *A. thaliana* more than an acute dose, a high dose for short time. Kurimoto et al. (2010) demonstrated that older plants are more tolerant towards these radiations as they are fully equipped with internal structure and biomass when irradiated. However, immature plants are not completely established which makes them sensitive to radiation stress.

4.1.2 Effects on Ultracellular Organelles

Wi et al. (2005) reported that gamma rays ranging from 1, 5, and 50 Gy cause certain changes in the ultrastructure of the *Arabidopsis* stem when observed under TEM. The cortical cells of the stem were highly vacuolated forming a thin separation between cell wall and vacuoles. The cytoplasm containing various organelles was reported to comprise high-density electrons. Nevertheless, the cytoplasm and chromatin material were well dispersed and well persevered in all the irradiated plants. At 50 Gy range plasmalemma gets separated from the cell wall. In short, low irradiations do not affect the morphology of the plant cell organelles, in contrast to high irradiations that cause prominent changes in the organelles, especially chloroplasts. Kovacs and Keresztes (2002) described that gamma rays interact with the atoms of water and produce radicals; these radicals have the ability to damage plant physiology, morphology, anatomy, and biochemistry (Ashraf et al. 2003).

Kim et al. (2000) determined the symptoms caused by different doses (high and low) of gamma irradiation involved in enhancement or inhibition of germination, seedling growth, and various biological responses (Wi et al. 2005). Preussa and Britta (2003) stated that a high dose of gamma radiations contributes in cell cycle arrest during G_2/M phase, inhibiting growth during cell division. Radiation causes damages to cell organelles that can be observed with the help of a microscope. Fenech (2000) defined that radiation induces damages which can be observed in micronuclei, nuclear material that arises from chromosomal fragments or when the chromosome is not present in the nuclear membrane. Micronuclei were first investigated in China rice seeds when bombarded with gamma radiations, and other ions including Ar and Fe ions of different doses. Exposure of different radiations with the pollen cells showed that micronuclei are most sensitive to the radiations (Mei et al. 1994). Takatsuji et al. (2010) demonstrated the effects of gamma rays on onion seedlings where a low dose increased the amount of micronuclei. However, a high dose of gamma radiations decreased the amount of micronuclei.

Wi et al. (2007) determined the damage caused by gamma rays at the ultrastructural level. The result provided knowledge about how the ionizing radiation affects the cellular mechanism of plants. At 1–5 Gy irradiation the chloroplast present in stems was well arranged; however, when the irradiations were amplified to 50 Gy, chloroplast in the cortical cells of the stems were altered with swollen and destructed thylakoids, but with the same size as that of chloroplast exposed to low irradiated gamma rays. Some of the changes affect the cellular structure of plants such as thylakoid membrane, which reduces photosynthesis ability that further causes accumulation of phenolic compounds (Kovacs and Keresztes 2002; Kim et al. 2004). Kim et al. (2004) designated that gamma rays after 50 Gy cause ultrastructural changes in the irradiated plant cell, which shows that chloroplasts are sensitive to gamma rays as compared to other organelles present in the plant cell. Plastids were also found to be affected as senescence was inhibited and due to differentiation into the agranal stage (Kim et al. 2004). Wi et al. (2005) demonstrated that the chloroplast structure was intact under a low dose of gamma rays (1–5 Gy) displaying well-organized thylakoid and membrane. However, the chloroplast structure at high gamma radiation displayed altered cortical cells of stems with swollen and destructed thylakoid membrane.

Gamma rays cause dose-dependent changes in plants by inducing production of harmful free radicals in cells (Kovacs and Keresztes 2002) that further damage the nucleic acid, proteins, and lipids present in the membrane (Bolwell and Wojtaszek 1997), which results in reduction of membrane integrity (Lee et al. 1998). Affecting the plant cell on a cellular level leaves a wide impact in minimizing the plant development that reduces the yield (Ogawa and Iwabuchi 2001). A high dose of radiations also increases numerous plastoglobuli in the chloroplast by increasing their size in the stroma of the cell. Wi et al. (2005) also reported the deposition of starch grain in the chloroplast at a high dose of gamma rays, but a low dose of radiation-treated cells was similar to controls. The damage and disorientation of thylakoids and grana influence carbohydrate transport by inhibiting it (Carmi and Shomer 1979; Bondada and Oosterhuis 2003). Chloroplasts are more sensitive to high doses of gamma radiations, as numerous plastoglobuli on chloroplast are produced as a result in stems, along with accumulation of starch grains (Wi et al. 2007) indicated that the accumulation of starch in the chloroplast along with damaged grana and thylakoid affect the carbohydrate transport. Other radiations and environmental factors also cause a similar disruption (Molas 2002; Quaggiotti et al. 2004).

The size of both the chloroplasts irradiated with high and low doses of gamma rays remained the same. Similarly, the cristae of mitochondria were also well organized under a low dose of gamma rays, and the high dose of gamma rays (50 Gy) caused distortion in mitochondria and distended the endoplasmic reticulum membrane (Wi et al. 2005). Mitochondria remained well-organized, but slightly enlarged when exposed to a low gamma dose; although a high dose increases the endoplasmic reticulum and distorts the mitochondrial shape, its size is not changed (Wi et al. 2007).

A high dose of gamma rays on seeds also causes certain morphological disruptions in protein synthesis, hormone balance, leaf gas exchange, water exchange, and enzyme activity. Irradiated seed also shows defective chloroplast which decreases the chlorophyll a and b ratio; such leaves show white stripes on affected areas (Abe et al. 2002; Palamine et al. 2005; Mei et al. 1994, 1998). Ionizing radiation affects the plants by producing free radicals that cause oxidation of atoms and results in plant cell damage (Zaka et al. 2002). Reactive oxygen species have basal expression inside the plant cell, but in a very low amount, however, the induction of the radiation increases the amount of ROS to maintain cell homeostasis (Polle 2001). These result in reduction of the photosynthetic electron transport chain as reductants of Calvin cycles are reduced. This condition leads to photo-oxidation by the increase of electron flux to O_2 that produces superoxide, H_2O_2 and hydroxyl radicals (Foyer and Mullineaux 1994). These high reactive species are responsible for creating damage to the photosynthetic apparatus; Agarwal et al. (2008) also reported that *Cyanobacterium anacystisnidulans* irradiated with ionizing radiations have high levels of ROS.

4.2 Effect of Gamma Irradiation on Biochemical Parameters

Gamma radiations result in the production of a reactive oxygen species that induces oxidative stress, and ultimately affects structural and functional molecules of a plant by causing a disturbance in normal metabolic pathways (Al-Rumaih and Al-Rumaih 2008; Ashraf 2009; Noreen and Ashraf 2009). Radiation causes radiolysis of water present inside the cell resulting in the production of reactive oxygen species such as hydrogen peroxide (H_2O_2), superoxide anion, hydroxyl radicals (OH), and singlet oxygen [O] (Kovacs and Keresztes 2002; Luckey 1980; Miller and Miller 1987; Quintiliani 1986). When a gamma ray acts on a crop it disturbs various morphological features of plant that are easily visible, but to countercheck the effect of various gamma ray doses on plants different biophysical parameters are adapted to measure the disastrous effects. The prominent measurable parameters are the content of chlorophyll, proline, and starch.

4.2.1 Chlorophyll Content

Gamma radiations affect many biophysical contents of the plant, where photosynthesis is widely studied. Radiations also affect the wide range of autotrophic organisms (Angelini et al. 2000; Esposito et al. 2006; Rea et al. 2008) including plants (Mei et al. 1994; Palamine et al. 2005). Gamma rays are responsible for causing different alterations in physiology and biochemical properties of plants at various doses, and disturb hormonal balance, enzymatic activity, and leaf exchange at a high level (Kiong et al. 2008). Photosynthesis begins with the absorption of light energy by plants in order to manufacture their own food. Different components of photosynthesis altogether such as pigment protein complexes which play a role in absorbing the light, enzymes reduced for the carbon reduction cycle, and electron transport carriers. This photosynthetic complex responsible for performing various activities is altered by the radiations. Ionizing radiations decrease the capabilities of the photosynthetic apparatus by damaging the photosystem (Angelini et al. 2000). Under high light intensities the plant's photosynthetic antenna complexes play an important role in combating variable intensities. These complexes allow photosynthesis by capturing light energy, protect photo-oxidative damage of chlorophyll from ROS, and release excess energy as heat (Niyogi 1999).

Borzouei et al. (2013) determined the high dose of gamma rays on cv-Roshan and Bam varieties of wheat. Where the chlorophyll content in cv-Roshan was increased after exposing it with radiations of 100 Gy and more, the chlorophyll content was decreased in Bam cultivar from 12.8, 26 and 29 %. Gamma radiations also damaged the photosynthetic pigments that reduced photosynthetic capabilities of plants (Kiong et al. 2008). A high dose of gamma rays up to 500 Gy decreases chlorophyll content by 80.91 % and decreases the organized pattern of grana and stroma thylakoid (Alikamanoglu et al. 2011). The intensity of chloroplast damage caused by the ionizing radiations depends on the plant growth stage, species, and the intensity of the dose. Holst and Nagel (1997) supported that woody species are less sensitive to acute radiations as compared to herbaceous plants that easily get damaged by radiation exposure, where a lethal dose to *Arabidopsis thaliana* that causes severe damage is 150 Gy (Kurimoto et al. 2010). The banana fruit thylakoid membrane is dilated on exposure above 0.2 kGy and further results in loss of grana stacks (Strydom et al. 1991).

Kovacs and Keresztes (2002) demonstrated that a high dose of gamma rays has an adverse effect on chlorophyll synthesis of wheat. Kim et al. (2005) demonstrated that carotenoid pigments immediately recover from the irradiation as they are highly radiosensitive. Found that red pepper irradiated with 16 Gy significantly increases the chlorophyll content. Additionally, Khodary et al. (2003a, b, c) confirmed these results that radiation of 20 Gy on dry seeds improves total chlorophyll content, which increases chlorophyll activity and increases the amount of soluble sugar. A comparative study was done on the chlorophyll content in treated and control *Paulownia tomentosa* seedlings when exposed to radiations along with controls. The chlorophyll content was increased with an increase in the radiation until it reached 100 Gy. Furthermore, an increase in radiation had no effect on the chlorophyll a, b levels, but the amount decreased to 81.36 % at 400 Gy, and 500 Gy gamma ray exposure caused an 80.91 % reduction (Alikamanoglu et al. 2007). Borzouei et al. (2013) demonstrated that the chlorophyll content rises in two cultivars of wheat by increasing the gamma radiations after 100 Gy. However, radiation reaching 200 Gy prevents wheat Roshan cultivar germination in soil, and comprises minimum chlorophyll. Borzouei et al. (2013) noted that chlorophyll a contents are higher than chlorophyll b, as a result of the high radiation dose above 100 Gy which depresses the chlorophyll content level in wheat cultivars.

The chlorophyll level is increased when exposed to low levels of radiation as a result of an activated enzyme system (Ferreira-Castro et al. 2007). Zeerak et al. (1994); Osama (2002) reported high chlorophyll content in plants including tomato (*Lycopersicon esculentum L.*), maize (*Zea mays L.*), rice (*Oryza sativa L.*), and wheat (*Triticum aestivum L.*) along with improved yield when exposed to variable radiations. However, Soehendi et al. (2007) described that gamma rays affect leaf canopy and seed yield of mung bean; especially those having a larger area of leaf are highly exposed to photosynthesis which results in greater yield rate. According to Rashed et al. (1994) gamma rays change the protein pattern in the protein band. described an increasing gamma rays dose that affects the pigments on leaves of *Holcuslanatus L.* Gamma radiations harm the pigment for photosynthesis as a result of damaged thylakoid and chloroplast and cause disorganization in the pattern of grana and thylakoid (Kiong et al. 2008; Borzouei et al. 2010; Marwood and Greenberg 1996).Borzouei et al. (2010) described that 100–200 Gy of radiations increases the level of chlorophyll a, b up to 64.5 % in wheat seedlings. Radiation at 100 Gy showed an increase in level of chlorophyll a as compared to b. However, a high-level 300 Gy decreases the total chlorophyll a and b content. A low level of chlorophyll indicates selective destruction or degradation of chlorophyll b precursors (Kiong et al. 2008). Kim et al. (2004) have evaluated that 16 Gy radiation in red pepper plant stimulates growth, and changes in photosynthesis can be the cause (Wi et al. 2007). Vanhoudt et al. (2014) determined the effects of gamma rays on chlorophyll, specifically on photosystem II (PSII). He reported that the capacity of PSII remains constant when different dose rates of gamma radiation were applied on *A. thaliana*, in contrast to cadmium stress which decreases photosystem II capacity (Dias et al. 2013). Vanhoudt et al. (2014) reported that carotenoids protect the photosystem II by deactivating triplet chlorophyll and neutralizing the effect of singlet oxygen. Therefore, measuring the level of chlorophyll content after treating them with gamma rays helps to evaluate the impact of radiation in crops.

4.2.2 Effects on Biochemical Content

Radiations are responsible for breaking the bond between chains, cross-linking DNA molecules and protein molecules. Seedling growth contributes to the nutrition of the plant which comprises proteins, carbohydrates, and vitamins (Marin-Huachaca et al. 2002). Different levels of gamma radiations pose different effects on morphology, and biochemical characteristics such as producing amino acids (proline), stimulating seedling growth, and promoting germination. Amino acid contents are indicators to determine the effects of gamma rays on the crop plant. Amino acids are essential for human diets and the essential ones are required to be taken in the form of food to fulfill the requirement of normal growth. In amino acids, amino group (–NH2) is radiation sensitive (Siddhuraju et al. 2002). Satter et al. (1990) irradiated a low dose (0.10 kGy) of gamma rays and determined the level of amino acids in soybean, where a low dose increases protein content by inhibiting protein synthesis assembly (Reuther 1969). Inoue et al. (1975) reported that amino acids are released in irradiated rice at a low dose of 0.10–0.40 kGy. Ananthaswamy et al. (1971) described amino acids inside cells are decreased in irradiated wheat where free amino acid due to a low dose of radiation depends on the sensitivity of the exposed plant. The results were contradictory by Siddhuraju et al. (2002), who described that particular amino acid content (phenylalanine leucine and arginine) was increased at low dose 0.5–5 kGy and many other amino acids were reduced by high dose (5 kGy) of gamma rays in wheat, maize, mung bean, and chickpea. However, described that comparing the cowpea amino acid content with its controls were found reduced in amount as a result of an increase in gamma radiation.

Proline is a hydrophilic solute that helps in water shortages by replacing water around nucleic acid, protein, and membrane, where proline and nonaqueous tails of protein surface interaction help in increasing protein stability (Irigoyen et al. 1992). Prolines are important solutes that act as osmoregulators by contributing in stress tolerance, protection, hydrophobicity, active oxygen scavenging, and maintaining cell pH (Kuznetsov and Shevyakova 2007). Proline functions to scavenge the hydroxyl radical and acts as a cytosolic osmoticum that helps in regulating and stabilizing various structure and functions such as DNA, protein, and membranes (Kishor et al. 2005). Proline is not the only component involved in stability; it along with other compounds is referred to as “compatible solutes” to maintain the osmolality of cells in various organisms (Yancey 2005). Therefore, the more high proline content is present in a cell, the more it is protected against various stresses. Al-Enezi and Al-Khayri (2012) described radiations on *Phoenix dactylifera* with X-rays result in high proline content that helps to overcome the stress by radiations. confirmed the increased content of proline by increasing radiations, where the highest concentration of proline was recorded by treating with 100–200 Gy in *T. arjuna*. Therefore high proline content guarantees it as a compatible solute.

Falahati et al. (2007) reported that radiations promote the amount of antioxidants; as a result extra proline is not required to face damages caused by oxidative reagents. But Borzouei et al. (2010) contradicted this research by his findings that a slight increase in proline content was observed when wheat seedlings were treated with gamma radiations. Borzouei et al.’s (2010) results showed that proline content of wheat seedlings irradiated up to 300 Gy were not significantly different from nonirradiated seedlings, although in wheat of different genotypes the proline level was raised; however, in wheat -cv. Roshan a high level of proline was observed at 100, 200, and 300 Gy. The result shows that Roshan wheat is sensitive to rays (Borzouei et al. 2010). Borzouei et al. (2013) determined that gamma rays of (500 Gy), high dose, increases the amount of proline to 16 %, whereas 100 Gy on wheat cultivars (Bam and Roshan) decreases proline to 9.3 and 23.6 %. Proline is involved in various functions such as preserving enzyme structure and activities; it reduces enzyme denaturation caused by environmental stresses including heat, NaCl, and the like (Ashraf and Foolad 2007; Kishor et al. 2005). Therefore, defining the amount of proline in the plant can be helpful in creating mutants.

Another biochemical parameter used to determine the effect of radiations is proteins. Seeds comprise all the important basic nutrients, where the seed of *Oryza sativa* comprises 14–20 % of protein, with 80 % of glutein as a total rice protein (Chrastil and Zarins 1994). Other protein components make up the rest of the 20 % including (1–5 %) of albumins with globulins about 4–15 % and 2–8 % of prolamins (Hulse 1989). Inoue et al. (1975) described that radiation inhibited protein synthesis which decreases the total amount of protein and carbohydrates at high dose in wheat and rice plant. Muskmelon (*Cucumismelo L.*) fruit retains the protein in its plasma membrane after 1 kGy of gamma rays (Lester and Whitaker 1996). This irradiation somehow activates the self-defense mechanism in plants (Marchenko et al. 1996). This mechanism works by increasing the production of certain enzymes as superoxide dismutase and compounds that contain sulfur (cysteine), which helps either to remove or neutralize the free radicals formed inside plants (Qui et al. 2000). Radiations also increase the amount of sucrose in potato tubers when treated with 3–4 kGy (Hayashi and Kawashima 1982).

Maity et al. (2009) observed the influence of gamma radiations on important proteins, where total protein content was affected by the radiations. This depletion was the result of a high dose (1 kGy) of gamma rays on *O. sativa.* However, when *C. arietinum* was irradiated with 1 kGy of gamma rays a 3 % reduction in soluble proteins was observed where 6 kGy showed the loss up to 27 % of proteins. Aziz and Mahrous (2004) described the effects on wheat and bean when a low dose of gamma rays was applied, where the protein content was not affected. Maity et al. (2004) compared the effects of gamma rays on protein contents *O. sativum* and *Cicer*, where the rice showed radiation resistant activity against the degradation of protein content. The amount of protein concentration helps to determine the lethal dose of radiation and its side effects on plant crops. Borzouei et al. (2013) demonstrated gamma radiation effects in the protein content of two wheat cultivars and they concluded that protein content increases after applying rays between 300 Gy and 400 Gy doses in the wheat–Bam cultivars, where, gamma rays of 200 Gy increased soluble protein content in Roshan cultivars and other Bam wheat cultivars comprised soluble protein content (38.91 ug/g Fw) were more than the nonirradiated wheat cultivars. Consequently, plants activate and keep on developing their defense system in response to gamma radiation (Qui et al. 2000; Jan et al. 2012). Al-Rumaih and Al-Rumaih (2008) concluded that the high content of proteins acts as a protective mechanism to fight the harmful effects of gamma radiation. However, inasmuch as an outcome of exposure to radiations causes radiolysis of water by radical oxygen, proteins are consequently fragmented and aggregate, forming cross-linking, and oxidation (Kiong et al. 2008; Afify et al. 2011). Although, Stajner et al. (2007) described that high doses up to 10 kGy slightly disturb the water component such as sugar, minerals, proteins, and the like Borzouei et al. (2013) explicitly described that reduction in protein content by exposure of 200 Gy is due to increase in proline and starch content for the defense and protection of protein against oxidation.

Described that treating with ionization radiations causes variation of concentration in the crop such as phenylalanine, valine, and glutamic acid. He described that after gamma radiation exposure most of the amino acids in millet pearl were stable except for leucine, glutamic acid, and phenylalanine, whose content was decreased from 32 to 23 mg/g on 5 kGy. This aromatic amino acid, phenylalanine, is dose-dependent and high rays of gamma radiation cause modification in this compound and lead to the formation of decarboxylation, hydroxylation (formation of amine in aqueous solution), or formation of complex compounds (Cataldo et al. 2011). The radiation induces the splitting of peptide bonds that form free radicals (Aziz et al. 2006). However, the protein content including proline, glutaminic acid, and valin was slightly decreased in millet flour at high radiation. According to Aziz et al. (2006) it is negligible and similar to nonirradiated flour. Many previous studies show that as the gamma radiations are increased the total amount of protein and carbohydrate content is decreased due to metabolic activities and hydrolyzing enzyme activities (Barros et al. 2002; Maity et al. 2004). Reported that gamma rays increase glucose absorption and decrease acetate and succinate absorption in carrot, and reduce all amino acids except serine and valine, whose amount was increased at 1 Gy. Reported the reduction of pectin and alginate viscosity. Demonstrated the degradation of oligosaccharides in legumes of Bengal gram (*Cicerarrietinum L.*) and cowpea (*Vignaunguiculata (L.) Walp*) between control and treated. Gamma rays are also considered to produce amino acids by breaking seed proteins (Maity et al. 2004; Kiong et al. 2008).

The original content of starch has low thermal resistance, low shear, and ability to retrogradation. Gamma rays are helpful tools in improving starch to enhance the physicochemical characters to starch in crops. Yu and Wang (2007) determined that gamma rays can be useful in cross-linking, grafting, and degradation techniques of polymer material. Gamma rays are responsible for breaking glycoside bonds that results in smaller fragments from the larger molecules. It is considered a useful technique due to its rapidity and effectiveness (Kang et al. 1999; Yu and Wang 2007). When gamma rays act on the starch they hydrolyze its chemical bonds and cause the formation of small polymers. The water binding capacity of starch along with high solubility and low viscosity is considered useful in food applications, and paper and textile materials (Kang et al. 1999). Akulova et al. (1970) investigated different effects of gamma rays in changing the properties of corn starch. Roushdi (1981) supported the previous findings that an increase in gamma ray dose decreases the starch content in corn up to 10 %.

Gamma rays break the glycosidic bonds apart into starch granules, which are further decomposed to produce macromolecules with small chains. This decreases crystalline content and distribution of amylose and amylose pectin in granules of corn (Ciesla et al. 1992). This modification changes the physical and chemical properties of native starch to improve its function that can be useful in food application (Hermansson and Svegmark 1996). Chemical modification in starch is common in food applications, however, physical modification of starch by radiation is widely accepted as it does not produce any by-products and is safe to consume (Bemiller 1997). Induction of gamma rays produces free radicals that cause fragmentation of starch and result in molecular changes (Grant et al. 1991), although increasing the radiation does not affect the moisture content of the starch with the increased dose of rays. Sokhey and Chinnaswamy (1993) reported that gamma rays of 20 kGy reduce the moisture to 28.3–23.07 % in lotus starch. This result is due to excess degradation of the amylose fraction that results in reduced amylose content by decreasing iodine binding (Sokhey and Chinnaswamy 1993). Abu et al. (2005) found that gamma radiations modify the starch content of cowpea and decrease swelling and pasting properties. Water absorption capacity, carboxyl content, and solubility are increased as a result of degradation of amylose (Gani et al. 2013).

4.3 Antioxidative Defense

Plants cells have a defensive, ROS regulating, system that consists of enzymes such as peroxidases (PX), catalase (CAT), superoxide dismutase (SOD), and ascorbate and glutathione; this system allows cell signaling while avoiding cellular damage (Mittler et al. 2004). Former studies show that under irradiation conditions, antioxidative defense systems regulate cellular stress responses (Kim et al. 2005; Vandenhove et al. 2010). Whenever a plant is exposed to gamma radiations superoxide dismutase (SOD) plays a defensive role in converting superoxide to hydrogen peroxide (McCord and Fridovich 1969). Additionally, catalase and peroxidases hunt for hydrogen peroxide produced during the reaction.

Halliwell (1974) specified that among all the reactive oxygen species H_2O_2 is always present in a standard amount inside the cell under normal growth conditions but whenever the amount of H_2O_2 is increased as a result of radiation it causes lethal effects inside the cell. Production of radicals causes disorder of the metabolism as the cellular structure in plants is disrupted due to induction of gamma rays and causes the following disturbances: expansion of thylakoid membrane, modulation of the antioxidative system, amount of phenolic compound increased variation in photosynthesis, and increase in phenolic compounds (Kim et al. 2004; Kovacs and Keresztes 2002; Wi et al. 2007). Gamma irradiation is highly effective and penetrating causing conformational changes, oxidation, formation of free radicals, and breaking of covalent bond with exposure to plant cells (Cheftel et al. 1985). Hydroxyl ions and superoxide anions produced as a result of radiations causes modification in lipids and proteins (Stajner et al. 2007). Changes in the molecular properties of proteins caused by gamma rays include oxygen radicals by radiolysis of water, fragmentation, and cross-linking of protein (Cho and Song 2000).

Changes in biochemical activities through production of various metabolites are quite prominent when a plant is exposed to gamma radiations. Cellular activity is disturbed due to production and accumulation of peroxides that cause oxidation of lipid membrane (Mead 1976). Ikeya et al. (1989) identified the physiological effects of gamma rays in plants. Voisine et al. (1991) described that free peroxidation of unsaturated fatty acid produces peroxyl radicals. Wi et al. (2006) described that pumpkin leaves and petioles showed high deposition of hydrogen peroxides when reacted by a high dose of 1 kGy. Middle lamella of parenchyma cells were the center of deposition, however, plasma membrane and vessels also deposit hydrogen peroxides. This accumulation is associated with high POD activity in the middle lamella of parenchyma cells (Wi et al. 2007).

Nevertheless, Zaka et al. (2002) determined that a protective cellular mechanism is present inside all organisms—plants, microorganisms, and animals—against the prominent effects of ROS produced by radiations. Calabrese and Baldwin (2003) reported that those plants are under constant influence of different radiations but they have the ability to cope with various stresses to a certain extent after which the ability decreases. Chakravarty and Sen (2001) proved that exposure to 140 Gy gamma ray decreases the glutathione–nonenzymatic antioxidants; consequently a low dose increases the activity of glutathione reductase. An oxidative mechanism helps the plant cell to avoid oxidative damage and to counteract the effects of ROS (Kiong et al. 2008). Plant cells cause certain alterations in gene expression to defend themselves that lead to defensive metabolic pathways. Synthesis of osmolytes is one of the most important protective mechanisms that requires proline synthesis and is essential for plant growth. Irradiated plants show a high level of proline involved in osmolyte synthesis. Alteration in proline content in environmental stresses and gamma radiation proved its involvement in protective mechanisms. (Esfandiari et al. 2008; Al-Rumaih and Al-Rumaih 2008).

Plants show protection against radiations by removing H_2O_2 and lipid hydrogen peroxides through the action of peroxidase, which shows higher efficiency of peroxidases than catalase. However, a low dose of gamma radiation activates and stimulates the peroxidase activity that helps the plant recover from initial degradation in chickpeas, and affect the peroxidase's isozymatic composition (Khanna and Maherchandani 1981; Shen et al. 2010). Peroxidase activity contributes in radiation and can help to understand radiation's role in plant growth inhibition, where damage due to irradiation causes different peroxidase isozyme patterns. Jain et al. (1990) described the effects of irradiation in the callus culture of *Daturainnoxia Mill* that had high peroxidase enzymatic activity. Later, Wada et al. (1998) also confirmed the isozyme activity of POD in *Nicotianadebneyi domin* and *Nicotianatabacum L. Nicotianadebneyi domin* with SOD activity and *Nicotianatabacum L.* with CAT activity as a result of gamma radiations. Vandenhove et al. (2009) reported that gamma rays enhance activity in (*Raphanussativus L.*) radish; CAT, POD, and SOD had boosted effects when irradiated at 10 kGy of gamma rays, however, they inhibit CAT activity. Determined that activities such as SOD, CAT, and POD can be stimulated in *Viciafaba L.* seeds when irradiated with gamma rays as they all effectively remove free radicals and prevent peroxidation of the lipid membrane. CAT inactivation leading to a drop in catalase activity is compensated by the APX activity, where H_2O_2 is decomposed by the activity of peroxidase. This research supports Pasternak (1987), who reports that cellular CA^{2+} levels are shifted due to peroxidase activity in the injured membrane. The gene expression of APX in cells is enhanced when low gamma rays are irradiated (Zaka et al. 2002). This research supported Foyer et al.'s (1997) findings that enzymes play a role in the upregulation of genes in enzyme activity.

Soybean seeds consist of a high amount of phenol content with wide use in pharmaceutical industries. Validated that antioxidants are affected inversely under different doses of irradiation. A low dose decreases the activity of CAT and GSH-Px, however, an increase in SOD, GPx, and LP is due to irradiation treatment taking place, even though nonenzymatic antioxidants did not affect soluble protein biosynthesis in soybean seeds. Irradiation of high dose, 200 Gy, stimulates oxidative stress and produces OH-ions. They showed that different antioxidant enzymes are activated depending on the amount of dose irradiated to defend the cell.

Vanhoudt et al. (2014) demonstrated the role of ROS-scavenging enzymes, SOD, CAT, ascorbate, peroxidase (APX), guaiacol peroxidase (GPX), and syringaldazine peroxidase (SPX) in roots and leaves of *A. thaliana* and reported that enzyme capacity gets affected in roots making them more radiosensitive. In contrast, leaves' enzymatic capacity is less affected making them less radiosensitive. He formulated that the GPX capacity of root starts to decrease even at a low dose of radiation as compared to leaves, whereas the GPX capacity of leaves was decreased when exposed to a high dose of radiation. The result showed that enzymatic activity at particular regions of plants also helps in tolerance against rays.

4.4 DNA Repair Mechanism

Energy absorbed and deposition of energy affects the biology of the cell due to ionizing radiations. Plant repairs the DNA by activating the cell cycle to look for damage in the cell (Cools and De Veylder 2009). Dose rate is important in the regulation of defensive mechanisms in the plant. When *Arabidopsis thaliana* was exposed to acute irradiations (1 Gy in 1 day) genes for DNA repair genes were activated as they play a role in regulating oxidative stress response and pathways of signal transduction. However, when *A. thaliana* was exposed to chronic irradiations (1 Gy in 21 days) the DNA repair and antioxidant gene's expression was not altered (Kovalchuk et al. 2007). Coyle et al. (2002) described that the plant cell in defense also produces certain antioxidants such as metallothioneins (MTs; metal binding protein); they hunt for hydroxyl radicals and actively prevent DNA damage. Furthermore, this research was proven, showing that MTs play a role in protection of creatine kinases by acting as chaperones against oxidative stress that inactivates enzymes (see Fig. 6).

Kam and Banati (2013) reported that mitochondrial DNA is more susceptible to ionizing radiation than the nucleus DNA. The DNA of mitochondria is damaged when part of the DNA is deleted as a result of radiation but it has the ability to overcome the damage by producing more copies of DNA to overproduce the mitochondrial proteins (Kam and Banati 2013). This elevated protein increases the production of superoxide as the activity of the electron transport chain is altered. Increased superoxide diffuses into other mitochondria that amplify the damage by signaling which further produces superoxide and eventually leads to the damage of nuclear DNA (Kam and Banati 2013).

Vegetables and fruits have antioxidants that have important health benefits and also act as free radical scavengers including polyphenols and ascorbic acid (Bland 1995; Surh 2003). Found that vegetables rich in ascorbic acids protect the plant against thymine oxidation promoted by gamma rays. Moon and Song (2001) found that ascorbic acid is helpful against gamma ray-induced ovalbumin and ovomucoid aggregation. Green onions are rich in ascorbic acids and are frequently exposed to gamma rays in increasing their shelf life and eliminating pathogens (Fan et al. 2003).

Dona et al. (2013) found that a variable dose rate of IR leaves different impacts on Petunia x hybrida cells' ability. A low ionizing dose is less effective in activating the protective DNA repair mechanism and ROS hunting. However, a high dose of gamma irradiations boosts Petunia's defense system. According to Pages and Fuchs (2002) DNA polymerase ensures the replication of DNA sections by assisting the replicative enzymes. This mechanism is more likely to generate high-frequency mutations (see Fig. 6). Dona et al. (2013) hypothesized that DNA damage with a low dose of gamma radiation was not completely repaired, as enzymes repair DNA lesions and create mutations afterwards. However, long-lasting irradiation maintains production of reactive oxygen species and the threshold that is required to activate the enzymes. However, acute irradiation causes severe stress—DNA damage—that activates the metabolic pathways and defense mechanism by attaining high activity of gene upregulation (Kovalchuk et al. 2007; Gicquel et al. 2011).

Jimenez et al. (2011) determined in their research that green onion having polyphenols and ascorbic acid, sacrificial radical compounds, are capable of preventing DNA damage by reacting with free radicals induced by gamma rays. The decrease in amount of ascorbic acid to 45 % (213 1 M) in green onion from 364 1 M after exposure to the radiation showed that they actively protect DNA (Jimenez et al. 2011). They formulated that the decrease in the amount of ascorbic acid after exposure to gamma rays for food preservation purposes reduces their nutritional properties.

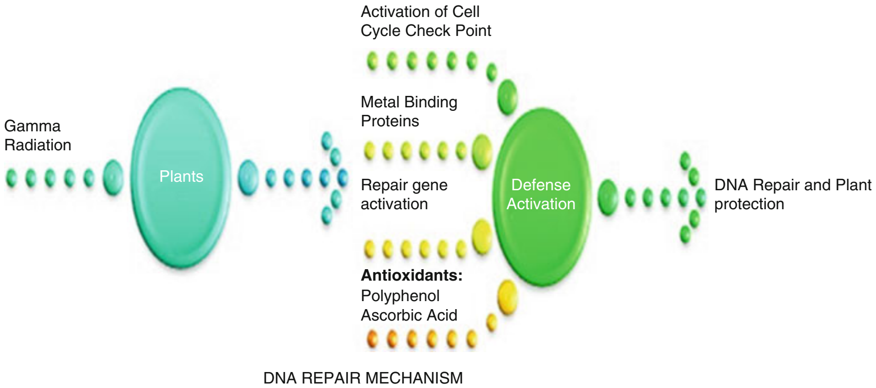

Fig. 6 DNA repair mechanism: gamma radiation results in activation of various plant defense pathways such as cell cycle check points activated and working to repair DNA (Cools and De Veylder 2009), metal binding protein called metallothioneins (MTs) starts hunting for hydroxyl radical to prevent DNA damage by chaperoning it. Antioxidants—naturally present in plants including polyphenols and ascorbic acid scavenge for free radicals—produced as a result of gamma rays and lethal to cells

Thus, ascorbic acid plays a significant role in protection of DNA due to its antioxidant nature (Jimenez et al. 2011).

4.5 Mutated Plants from Gamma Radiations

Mutagenesis is the process in which heritable changes occur in the genetic material that sometimes is repaired in the DNA repair process. Mutations are of two types; either occurs spontaneously in the DNA or is induced by various methods such as chemicals, radiation, or viral infections to make the genome adaptable to environmental changes. Gamma ray induction (physical mutagen) in causing mutation is widely used to improve crop production by creating diversity in the crops. On the molecular level these ionizing radiations are responsible for creating many types of mutations on the DNA base pair to chromosomal aberrations. According to the record of FAO/IAEA mutant varieties database, 3000 mutant crop varieties have been created by inducing gamma rays as a mutagen (Jain 2010).

Radiations are always considered harmful, but with proper care these radiations can help in bringing much advancement in plants by increasing genetic variability (Jan et al. 2012). With the help of advanced plant molecular tools and radiations crop productivity can be increased. Plants face changes in environmental factors as external stimuli that are induced as signals and affect plant physiology. With rapid change in climatic changes on a global level, and feeding the huge population, gamma rays for creating mutants can be handy (Jan et al. 2012). To make the plants survive all the environmental fluctuations certain radiations can help to enhance the germplasm of the plants (Jan et al. 2012). Any structural changes in DNA lead to functional changes, which are the result of DNA damage mostly after exposure to ionizing radiations. Variation in phenotype of an organism is the result of damage in the DNA molecule that causes altered gene expression. DNA modification ranges from changes in single base, substitution, and deletion, to epigenetic modification (Tanaka et al. 2010). Described that genetic stability in plants such as *Nicotiana tabacum* and *Arabidopsis thaliana* can be induced by homologous rejoining (HR) that helps to restore their normal genetic function by exposing them to acute or chronic radiation. Radiation exposure to plants results in homologous rejoining as the free radical production increases that activates the metabolism of *Arabidopsis*.

Ionizing radiations can be used as important tools to bring about genetic variability in breeding purposes. Recently, desirable traits or mutation efficiency can be increased using phenotypic molecular responses to IR (McKim and Hay 2010). Mutations bring varieties in crops and are used as a mode of genetic modification of useful fatty acid present in rapeseed. Successful rapeseed mutants have been developed using radiations (Bhatia et al. 1999). However, Erkkz and Allen (1961) concluded that success of mutant development depends on unchanged environmental conditions that keep the original genetic constitution unaffected.

Gorgidze (1980) described that irradiation by using gamma rays causes mutations in cultivated wheat that gets deviated from its normal path by increasing the chromosome number causing polyploidy in wheat, or by reversing the polyploidy to tetraploidy, morphological changes by aneuploidy, and many mutations in genes. Grain spike and weight were increased incredibly in generations after exposure to radiation (Gorgidze 1980). El-Shafey et al. (1991, 1993) describe that radiation by using fast neutrons helps in creating mutants by regeneration of the cell wall, and protoplast development. Much research also proved that the use of high neutron irradiation helps in developing high-yield cultivars (Duggal et al. 2000; Koebner and Hadfield 2001; and Al-Maaroof et al. 2003). But if the proper dose of radiation is not maintained, injurious affects can be seen on the plant, as it will inhibit plant growth ultimately leading to reduced production of the crop. Therefore it can be concluded that different doses of radiation help in deciding whether the rays will have a positive or negative impact (Kon et al. 2007). Described that a new form of species is generated when a low neutron acts to increase the protein concentration. Many studies also show that mutations induced by optimum neutrons result in generating variable phenotype varieties (Kharkwal 2001; Wu et al. 2005).

Nuclear technique uses are prominent in plant breeding; the majority of mutant crops created using irradiation include: beans, cotton, peanut, rice, barley, and wheat. However, FAO/IAEA establishment has led to the creation of 1800 cultivars produced by directly creating mutations or by crossing the mutant varieties (Maluszynski et al. 1995). Radioactive labeled probes in DNA recombinant have been used in creating transgenic varieties; in India rice-induced mutants (series “PNR”) with high yielding properties were released (Chakrabarti 1995). In China for 10 years rice mutants “Zhefu 802” were grown. In 1977, in Thailand aromatic *indica* variety of rice RD6, a mutant created from gamma radiation was released. This variety was so successful that even for years after its creation it was grown in extensive regions of Thailand. *Japonica* rice mutant created by thermosensitive genic male-sterile mutation is induced by a single recessive gene caused by gamma radiation (Maruyama et al. 1991). These mutants show successful results and increase the yield of crop and are used as parent cultivars, for example, barley mutants “Diamant” and “Golden Promise” are used in the brewing industry in Europe and used as parent cultivars. In Pakistan “NIAB-78,” a cotton mutant variety release sustained the textile industry in 1987. This cotton mutant variety has several features such as heat tolerance, and prevents bollworm attack during the early maturity stage (Green 1986; Dribnenki et al. 1996; see Table 2)

In China high-yielding peanut mutant varieties were released under the label “Yueyou” produced as a cross of mutant cultivars. India also released a similar peanut mutant variety “TG-26” with high production up to 9.4 t/h (Green 1986; Dribnenki et al. 1996). Gamma radiations are the efficient ionizing radiations that modify plant phenotypes to create improved mutant properties with high production of metabolites, and high productivity (Sato et al. 2006; Naito et al. 2005; Eroglu et al. 2007). These radiations are important in enhancing the production of secondary metabolites despite various biological damage it causes on the plant

Table 2 Crop mutants generated by gamma radiations worldwide

Crop variety	Modification	Country	References
Rice—Zhefu 802	High yield	China	Maruyama et al. (1991)
Rice mutant'RD6'	Aromatic *indica*	Thailand	Maruyama et al. (1991)
Japonica rice mutant	Thermosensitive	Japan	Maruyama et al. (1991)
Cotton mutant "NIAB-78"	Texture, heat tolerant, and prevents bollworm attack	Pakistan	Green (1986), Dribnenki et al. (1996)
Peanut mutant variety—Yueyou	High yielding	China	Green (1986), Dribnenki et al. (1996)
Peanut mutant variety "TG-26"	High production	India	Green (1986), Dribnenki et al. (1996)
Centella Asiatic	Flavonoid contents		Moghaddam et al. (2011)

cell (Kim et al. 2005). Moghaddam et al. (2011) tested the flavonoid contents in control and treated plants of *Centella Asiatic*;, the irradiated plant showed a high concentration of flavonoid content with 8 weeks of the gamma radiation treatment of 20–30 Gy (see Table 2).

Demonstrated that a high dose of gamma radiation, 1200 Gy, reduces the quantity of oleic acid and generated mutants in rapeseeds with less genetic variability, and results in a high level of undesirable fatty acids, although low-dose gamma radiation, 800 Gys, produces mutants with high variability and also increases the amount of oleic acid in rapeseeds. Gamma radiations have been widely used in creating mutations in maize (*Zea mays*) and barley (Stadler 1928). High-yielding *Brassica juncea* mutant has been created by treating with gamma rays (750–1000 KGy); these rays are successful in creating stress-resistant varieties (Khatri et al. 2005; Wang et al. 2007a, b). Other research by Shah et al. (2001) reported the production of another high yielding and (*Alternaria blight* and white rust) resistant variety by exposure to high gamma rays (ranging from 1.0 to 1.2, and 1.4 KGy).

With all the climatic changes adversely affecting crop productivity, drought plays a chief role in limiting the yield of sugar beet (Donini and Sonnino 1998). Previously, Shah and Sharif (1994) reported the production of drought-tolerant sugar beet varieties by in vitro mutagenesis particularly by gel electrophoresis, and by molecular markers. However, in his findings created a drought-tolerant sugar beet mutant using gamma radiations in vitro culture, and confirmed his results using various biochemical parameters and isozyme variations. Genetic variability to create genotypes in a population helps to withstand various biotic and abiotic stresses (Uddin et al. 2007). Described that gamma radiations are a successful technique for creating drought-tolerant mutants in in vitro cultures when treated with 20 Gy of radiation. Induction of gamma rays causes changes in antioxidant enzymes that were detected using a spectrophotometer and by determining the level of isozyme variations, considered to be the reason for generating mutants from the ionizing rays, in control in treated sugar beet crop.

5 Beneficial Aspects of Radiations

Gamma rays have various applications in the medical, industrial, and agricultural fields. One of the common benefits of gamma radiations is the use of different doses in exploiting the agriculture field. These radiations are useful in bringing about genetic change, morphological or physiological changes, and biochemical changes by applying a different intensity of gamma ray dose. Plant breeding using different techniques helps to improve individual crop productivity by reducing disease incidence by various pathogens including viruses, bacteria, fungi, nematodes, and insects. The reduction of various diseases increases the yield of the crop and makes it better quality. However, the plant faces various stresses on a daily basis to improve and protect from various fluctuations; improving the genetic potential of the crop is important.

Nuclear techniques have broadened the scope of crop improvement in agriculture. Irradiated seeds result in genetic variation that allows plant breeders to improve and select new genotypic characteristics such as tolerance to salinity, improved yield and quality, and precocity. Consequently, gamma radiations are helpful in bringing about useful physiological characters (Kiong et al. 2008). Irfaq and Nawab (2001) started wheat improvement by mutation induction that improved the desired traits. Gamma radiations were applied in 1960 in North America for the purpose of food preservation. Gamma radiations are also used in food irradiation to eliminate harmful microorganisms, insects, fungi, and pests with doses up 1 kGy (Variyar et al. 2003) by creating harsh environment tolerant varieties (Al-Rumaih and Al-Rumaih 2008). Controlled exposure of gamma rays is still popular and is used for various purposes such as sterilization of medical equipment (Shokyu 2002).

Fan et al. (2003) and Niemira and Fan (2006) showed that shelf life of celery and other vegetables can be increased if the proper amount of gamma rays (1.0 kGy to 7 kGy) is applied that actively kills *Escherichia coli*. Aziz et al. (2007) described the uses of high doses of gamma radiation in sterilizing the seeds from all kinds of microbial contaminants; there are many reports on gamma rays as a fungicidal agent. Low energy doses of gamma rays (0.15 kGy) are beneficial in the storage of onion by inhibiting sprouting (Niemira and Fan 2006). Described the importance of gamma radiation in extending the shelf life of fruits and vegetables that helps in reducing the decay time of the edibles. These radiations are quite known for their sterilization ability to prevent the colonization of various bacteria and provide durable protection to perishable vegetables against insects. Gamma rays are also used in the storage of fruits to prevent spoilage caused by fungal pathogens by maintaining the proper physiology of the fruits. Determined the useful role of gamma rays against nematodes *Botryosphaeriadothidea, Botrytis cinerea,* and *D. actinidiae* in kiwifruit.

Mashev et al. (1995) described the use of gamma rays in wheat that can help to reduce height to tolerate windy environments and to prevent lodging; that can reduce the annual loss of the wheat crop by increasing the yield. The high irradiation dose of gamma rays of about 5000–15,000 not only reduces plant height but increases the efficacy of wheat to give better and higher yields by increasing the content of proteins and essential amino acids over the nonradiated plant (Mashev et al. 1995). However, Din et al.'s (2003) results on different wheat varieties found that an increased dose up to 35 kGy can induce abnormalities in wheat. Nevertheless, concluded that increasing the dose can help to improve the physiology and morphological characteristics of the wheat crop. The rays were found to improve wheat height with increased yield by improving the number of ear-bearing tillers.

Millet crops are a main focus of public authorities due to high fungal and mycotoxin contamination that causes massive loss in its production (ISO Standard 6322-1 1996). Various methods have been incorporated to sustain the trade of crops and by innovating preservation technologies. Methods for decontamination by using various fumigation products, ethylene oxide or methyl bromide, are at its peak along with radiations especially gamma rays. Use of gamma radiations at 1–10 kGy in preservation and decontamination of microorganisms is the most promising and safest process that at the same time works to improve the shelf life of millet flour (Codex Committee on Food Additives and Contaminants 2001; Aziz et al. 2006). Optimum amount and time period of gamma radiations exposed to the bulk of food products helps in controlling and preventing microbial growth, and slows down fruit maturation by preventing biochemical reactions taking place during maturation (Singh and Pal 2009). Optimum selection of radiation is very important as some radiations have toxicological side effects and result in production of toxin that further reduces the freshness of the crop and increases the degradation of organoleptic properties, decreasing the nutritional content of the food (International Atomic Energy Agency 1999).

Ferreira-Castro et al. *(*2007) described that among all the treatments used for the decontamination of the millet crop, irradiation by using gamma rays was the most promising. They evaluated effects of different doses ranging from 1 to 5 kGy on millet flour that proved to reduce the presence of many pathogens including bacteria, yeast, and mould. Lapins (1983) reported that gamma radiations are useful in enhancing physiological characteristics. Gamma radiations are considered to be disinfectant for microbial treatment and are widely used to enhance biochemical properties of millet flour at 2–3 kGy and increase shelf life (Ferreira-Castro et al. 2007).

UV light in addition to being harmful also has some advantages. There are many studies reporting the use of UV light against plant biotic stresses and in increasing the crop's productivity. Nevertheless if UV light can be used effectively and its disadvantages can be controlled, it can prove to be quite beneficial. A major benefit of UV is its effect against plant pathogens that are known to affect crop quality and yield. UV light is used as a biological control that provides protection to plants from fungal, bacterial, and viral pathogens. Because pathogens are sensitive to high levels of UV, they can serve as an effective biological control to counter pathogens (Paul and Gwynn-Jones 2003). It has been reported that growth of fungal pathogens are severely reduced in the presence of UV due to a decrease in germination of fungal spores and mycelia growth (Willocquet et al. 1996; Jug and Rusjan 2012). Those environments that have reduced UV exposure can also lead to reduction in insects such as whiteflies but this can result in the major reduction of insect pollinators thus affecting pollination and seed dispersal of plants (Paul and Gwynn-Jones 2003).

UV is also known to increase the growth of commercially valuable crops by increasing the length of stems, by improving flower colors of ornamental plants (Oren-Shamir and Levi-Nissim 1997), and by improving seed ripening (Bacci et al. 1999). This can be made possible by growing the plants under such chambers and greenhouses that transmit UV light. UV light can also be used to increase nutraceuticals in plants by increasing their phenolic content, terpenoids and alkolids. It can also be used to increase a plant's capacity to make industrial products and herbal medicines (Hajnos et al. 2001). In a study on grapevine, it has been shown that increase in the production of antioxidants due to UV-B stress and accumulation of secondary metabolites such as flavonoids can give advantages to human health including providing anticancerous drugs and by providing protection to the cardiovascular system of humans (Dzhambazova et al. 2011). Increased UV levels are also known to stimulate the concentration of stillbenes that are also beneficial for human consumption (Jug and Rusjan 2012).

Another study on *Lactuca sativa* has been reported that showed an increase in plant growth rate if UV light is steadily provided to the plants. However, if a high and sudden exposure on the plant is done, the plant growth decreases (Wargent et al. 2011). Hence UV can provide little benefits to humans to protect the crops against biotic and abiotic stresses. A better study on the application of UV to plants especially postharvested crops may lead to improved nutrition that can be ultimately useful for humans (Wargent and Jordan 2013).

6 Future Perspective and Conclusion

Ionizing radiation has various aspects in all applied fields. Gamma ray usage in improving the shelf life of fruits and vegetables to the sterilization of microbial contaminants are quite prominent. They help to delay ripening and browning of fruits, and improves their quality. They are beneficial in controlling fungal diseases in postharvested crops. Radiations are used instead of chemical fumigates to treat fungus in seeds (Paul and Gwynn-Jones 2003). Resistance to UV radiation in crop plants has increased the yield. Introduction of the photolyase gene in crop plants can make plants resistant to UV radiations (Yoshihara et al. 2005). More efficient studies on cell cycle regulation need to be done that can provide strong proof of UV-B effect on crop productivity. The effect of UV-rays on postharvest crops can help to improve nutrition, and also has increased nutraceuticals in plants by UV radiation. The role of radiations in creating mutants and radioactive agents pave new ways in creating different aliments.

Arora et al. (2005) described the development and potential use of radiation-protected plants in treating various diseases. Radiation-protected mutant plants are expected to protect against radiation damage, therefore, these plants can be helpful in treating ailments caused by the production of free radicals. Consequently, development of new drugs from plant extracts in treating radiation injury can lead to novel advancement of health sciences. Further studies, development, and application of drugs using bioactive compounds can make a possible difference in treatment with fewer side effects (Arora et al. 2005).Driscoll et al. (2014) described the advances in the use of ionizing radiations in wood biomass. The biomass of wood is widely distributed throughout the world and has an important role in various applications, especially the hemicellulose and lignin being abundant synthetic polymers, and has various applications in the paper and lumber industries. But the woody biomass in fuels and chemicals requires undergoing proper treatment before their usage due to their crystalline nature; this method increases their usage in defined industry. Induction of gamma rays breaks the bond and initiates the chemical reaction. The use of gamma rays in this method can be helpful to integrate the use of woody biomass into many fields (Driscoll et al. 2014). Keeping the negative impact of radiations in view, further advancement and studies can help to make the proper use of these rays in various fields beneficial for mankind.

Earth is constantly facing radiations; depletion of the ozone layer has resulted in absorption of harmful rays into the Earth's surface. Among all radiations, UV rays and gamma rays are considered to have negative impacts on the living organisms of Earth. Hence UV-B can affect many physiological, biochemical, and molecular pathways inside the plant. Crop plants have evolved to defend themselves from UV-B stress by initiating DNA repair mechanisms and the flavonoid biosynthesis pathway. They can also change their morphology and limit the rate of photosynthesis and prevent photosynthetic pigment alterations and changes in biomass. These protective mechanisms can prevent crops from losing their quality and yield but are still not effective if crops are exposed to high levels of UV-B. Therefore improvement of the crop's defensive mechanisms is the utmost requirement so that crops can be protected against light radiation stresses. Similarly, exposure of gamma rays affects seed germination, plant growth, cellular structure, and biophysical content present in plants. Ionizing radiations have detrimental effects on photosynthesis by affecting the function of PSII. Nevertheless this radiation if maintained and delivered at a proper doses boosts the antioxidant enzymes by protecting plants against radiation. Despite much irreversible damage caused by radiation, gamma rays can still be considered to improve the genetic variability of the crop to increase sustainability of crops. Rapid and harsh fluctuations in the environment have increased stresses in plants, therefore, creation of diverse mutants can help in increasing the yield.

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Pesticide Tolerance and Crop Production

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Abstract In the early twentieth century, various plant pathologists demonstrated the capability of plants to treat diverse contaminants from soil and water without any obvious mechanism. Conversely, the treatments of recalcitrant organic compounds generate incoherent consequences for biotreatment by plants because of varied recalcitrant compound structures from naturally occurring molecules. Several pesticides generally attack the target enzymes, which are normally inhibited; this may be due to overexpression or overstimulation of the target proteins. The enzymes of nontarget organisms and microbial enzymes can also be inhibited by a few pesticides. This makes the herbicide/pesticide tolerance a more intricate process connecting the profuse machinery of a plant. These include phytochromes, antioxidant machinery, glycoproteins, and the metabolic interface of various processes. Genetic heterogeneity of wild populations and weedy species growing on pesticide-contaminated soil provides a source of plant species tolerant to these conditions. In this section, we deal with various aspects of herbicide/pesticide resistance mechanisms found in plants. The herbicide resistance pathway in plants is affected by various components such as enzymes and heredity. In fact, some genes conferring tolerance to inconsequential effect might be amplified under herbicide selection, which exerts a corresponding effect on survival of HR plant species. This chapter provides insights into the main hurdles that could be raised as a result of increased pesticide tolerance to achieve increased crop production.

Keywords Resistance • Pest • Insecticide • Pesticide tolerance • Crop production

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1 Introduction

About 10,000 years ago, since the beginnings of agriculture, farmers have had to compete with harmful organisms—animal pests (insects, mites, nematodes, rodents, slugs and snails, birds), plant pathogens (viruses, bacteria, fungi, chromista), and weeds (i.e., competitive plants), collectively called pests—for crop products grown for human use and consumption. Plant and phytophagous insects have evolved a very long and close relationship (Oerke 2006). During the process of evolution, plants have developed several defense mechanisms against harmful insects. The population of these harmful insects is restricted either by other insects such as natural enemies or toxic chemicals such as insecticides or by the plant defense mechanism. The increased use of insecticides in agriculture has posed several problems including the development of an insecticide-resistant population, the resurgence of treated pest population, elevation of secondary pest to a status of primary importance, deletorious effects on the population of nontarget organisms, and general pollution of the environment.

A nonchemical approach of crop resistance to insect pests offers the potential of a user-friendly, environment-friendly, and consumer-friendly method of crop protection to meet the demands of sustainable agriculture in the twenty-first century. Although recent information on pest resistance is scarce due to the lack of consistent and carefully designed studies, we tried to cover the information on pest resistance to pesticides in this chapter. Also the nonchemical approach for crop production is also covered with a brief conclusion on the impact of information on pest resistance and crop production in the modern era.

2 Definition and Classification of Pest

Any insect, nematode, rodent, weed, or fungus or any other form of aquatic or terrestrial plant or animal life, or microorganisms such as virus, bacteria, and the like that harms or kills crops is known as a pest that can reduce the crop value before and after harvests. Pests can be classified in the following categories:

(a) ***Vertebrates***: It includes all animals including birds. It is known that animal damage inflicted less damage than any other category of pests. In some cases, they can be devastating; for example, rodents cause heavy losses in rice- and sugar-growing areas in Southeast Asia, and kwela-kwela birds take a heavy toll on sorghum and millet grown in East Africa.

(b) ***Insects***: There are about 900,000 known insect species which is three times greater than other species. Insects include *Phasmidia* (leaf insects and stick insects), *Aculiata* (ants, bees, wasps), and *Trichoplira* (caddis flies). Survival and growth rates of insect populations flourish in all climates. Semi-arid areas are favorable for the growth of locusts and midges, whereas the brown plant hopper has devastated rice harvests in the moist tropics.

(c) ***Weeds***: These are commonly unwanted plants competing with crops for soil nutrients and space. One of the more obscure aspects of pest management is the ecology of weeds as they tend to be site-specific and difficult to deal with. They interfere with food and fiber production in agriculture, and in order to prevent losing or diminished crop yield they must be controlled.

(d) ***Pathogens***: These include infectious agents capable of causing diseases among crops. They include bacteria, viruses, fungi, and helminthes. Growth of pathogens flourishes in the tropics. In basic food crops, such as maize, the incidence of diseases is much higher in Africa than in other regions (the maize streak virus). Pathogens have been the most difficult pests to control, especially in the tropics. Plant breeding technique has contributed significantly to the reduction of potential losses from pathogens of resistant and well-adapted varieties in both developed and developing countries.

3 Emergence of Pest Resistance

The use of pesticides has often led to increased and unnecessary pest outbreaks and increased crop losses because of the unintended destruction of natural enemies of the pests that lead to the emergence of both pest resistance and secondary pests. Resistance and increased outbreaks have put farmers to use ever-increasing and stronger pesticides to kill mutating pests. The resistance problem has worsened over time. In 1938, several species of mite and insect species were known to be resistant to pesticides. In the 1940s, the use of synthetic pesticides led the initiation of resistance. Farmers were using more and more synthetic pesticides to kill pests. This procedure actually hastens insect evolution because resistant individuals come to dominate and propagate exponentially.

In 1984, hundreds of pests were known to be resistant, of which some were the most destructive pests that damage the crops. In the late 1980s, the number of resistant weeds reached nearly 48, which were not known before 1970 (Farah 1994). Resistance to 900 species of insects, pathogens, and weeds occurs due to the application of common pesticides. In several parts of Asia, farmers are spraying as much as 800 times the recommended dosage of pesticides in order to reduce crop losses (Farah 1994). Increased spraying to overcome resistance is also common in parts of Central America and Africa (Thrupp 1996).

Due to the indiscriminate use of pesticides, the ecological balance between pests and their predators has been disturbed in developed and developing countries. Destruction of beneficial natural enemies of pests that damage US cotton and apple crops has led to the outbreak of numerous primary and secondary pests, including cotton boll worm, tobacco budworm, cotton aphid, cotton loopers, European redmites, San Jose scale, and rosy apple aphid. The additional pesticide applications required to control these pests, plus the increased crop losses they cause, are estimated to cost the United States about US$520 million per year (Pimentel 1995). Even with the recommended dosages of 2–4, D on corn in the United States, the impact on nontarget pests has increased threefold in aphids, a 35 % increase in corn borers, fivefold increase in corn smut disease, and the total loss of resistance to southern corn leaf blight. The tropical climate of most developing countries seems favorable for the more rapid development of pest resistance and is more serious than in the temperate climates of the developed countries. Excessive use of pesticides led to increased resistance, which led to increases in the use of stronger pesticides, subsequent increases in costs of production, declines in yields, and finally to the near destruction of the productive capacity of the area. Van Veen et al. (1997) reported the excessive use of pesticide had increased the resistance to many cotton pests that resulted in lower production in China. Other countries such as Mexico and Nicaragua have also suffered the destruction of the cotton crop due to the indiscriminate use of pesticides. In the 1960s, the land under cotton fell from 280,000 ha to 400 ha in Mexico due to the resistance developed in bud worm resistance to all pesticides. In Nicaragua, the excessive use of insecticide in cotton for 15 years resulted in lowered yields by 30 % over the next four years owing to the development of pest resistance to pesticides (Farah 1994).

In India, the excessive and indiscriminate use of pesticides also led to the development of pest resistance. In 1963, the first reported case of resistance came out in DDT and benzine-hexachloride (BHC). *Herlithesis armigera,* which preys on cotton, chickpea, and pigeonpea, has also developed resistance in recent years. The increase in resistance adds substantially to the indirect costs of using pesticides and lends weight to those who favor pest management systems that pay adequate attention to pest ecology, biological agents, and farmer training, rather than focusing solely on chemical agents to control pests.

3.1 Natural Pest Resistance

The increased usage of pesticides in agriculture has posed several problems such as the development of insecticide-resistant populations, the resurgence of treated pest populations, elevation of secondary pest to primary importance, deleterious effects on populations of nontarget organisms, and general pollution of the environment (Dhaliwal and Arora 2001). Plants evolved an impressive array in their long association with pests and pathogens. At the same time, pests and pathogens developed mechanisms to compromise plant resistance mechanisms in what must have been an evolutionary game of ping-pong. The mechanism of natural pest resistance occurs in higher plants. Agricultural pest control throughout this century has attempted to find mechanisms wherever possible. Natural resistance has several obvious advantages over the use of chemical pesticides or other methods for pest control. These include nominal genetic permanency, negligible cost once cultivars are developed, and quite high efficacy. The major downside of natural pest resistance is the reality that selection pressure is placed on pest populations to develop means of overcoming the resistance, thus practically limiting the time of effectiveness. Natural pest resistance can be classified into preformed resistance mechanisms and inducible resistance mechanisms.

3.1.1 Preformed Resistance Mechanisms

These are categorized into preformed structural, morphological, and chemical factors. In entomology, morphological and anatomical features such as the presence of trichomes, leaf and flower color, and even the cuticle texture may be responsible for resistance mechanisms. Anatomical features may also deter or discourage insect feeding. These include the degree of secondary wall thickening, stelar structure, toughness and thickness of the plant stem, and other aspects of basic plant structure. They all fall under the category of preformed resistance mechanisms. Plant pathogens include viruses, fungi, bacteria, and nematodes, all of which must gain entry into the plant and contact living plant cells in some way for success. Accordingly, structural and morphological barriers could be expected to provide resistance against many potential invaders. Recognized examples include features as sophisticated as stomatal guard cell anatomy, for instance, the height of the lips of the guard cells.

The nonglandular trichomes are known to affect locomotion, attachment, shelter, feeding, and survival of insects. Trichomes are one of the important morphological parameters for insect resistance against the host plant. Larvae of tobacco budworm, *Heliothis virescens*, were found resistant to cotton cultivars with trichomes on upper and lower leaf surfaces and petiole (Ramalho et al. 1984). *Pectinophora gossypiella* confers resistance due to hairiness in cotton (Smith et al. 1975). Adult whitefly, *Bemisia tabaci*, were found trapped by the glandular hairs on tomato leaves (Kisha 1984). Glandular hairs provide resistance against the attack of *Hypera postica* in alfalfa (Shade et al. 1975). Length and density of hair on the lamina of cotton leaves are the important characteristics in impairing resistance to cotton jassid, *Empoasca devastans*. Incidence of cotton leaf roller, *Sylepta derogate*, was higher on varieties that have long, erect, and more dense hairs than those with short, less erect, and fewer number of hairs (Mahal et al. 1980). In potato, resistance to the leaf hopper, *E. Faba*, the orientation of the hairs was more important than the number of hairs (Broersma et al. 1972). Removal of glandular trichomes and trichome exudates from leaflets of wild potato, *Solanum berthaultii*, increased the proportion of larvae of Colorado potato beetle, *L. decemlineata*, that fed and also led to decreased mortality when trichome exudates were removed (Neal et al. 1989). Removal of the trichomes reduced the percentage of abandonment and increased the total proportion of time probing (Musetti and Neal 1997). The resistance of *L. decemlineata* and *Manducasexta* (*Johannsen*) was associated with the foliar glandular trichomes (Sorenson et al. 1989).

Variation in plant structures also contributes towards insect resistance. Rice varieties with tight leaf sheath wrapping were found less susceptible to Asiatic rice borer, *C. Suppressalis* (Patanakamjom and Pathak 1967). *Hydrellia griseola* were resistant to spring wheat with tight leaf sheath and dense hairs with thick waxy leaf hairs (Zhu 1981). In sugarcane, *Melanaspis glomerata* were resistant due to the low number of stomata per unit area (Agarwal 1969). Rajarajeshwari and Subbarao (1997) found that the bollworm, *H. armigera*, had a negative relation with the gossypol gland on a leaf and ovary surface of cotton. Balley et al.

(1984) observed that the nectariless character of cotton significantly reduced plant bug, *Lygus lineolaris*, nymphal population from 64 to 40 %. Nectariless plants also had a significantly low infestation of pink bollworm, *P. gossypiella*, and cotton leaf worm, *Alabama argillacea*, than the nectaried plants (Butler and Wilson 1984). Wilson (1989) found that nectariless and okra leaf traits provide low levels of resistance in cotton, *G. hirstum*, to pink bollworm, *P. gossypiella*. Sorghum varieties having an axil of leaf tightly fixed to the stem had a low infestation of shoot bug, *Peregrinus maidis* (Agarwal et al. 1978). Diarisso et al. (1998)reported the tightness of glume closure as the major cause of sorghum resistance to sorghum midge, *Stenodiplosissorghicola*.

Silica contents absorbed by the plants are deposited in the tissues of several plant species. Several workers reported the deposition of silica content in certain plant tissues which contributes to the resistance to insect pests (Lanning et al. 1980). In sorghum, cultivars with high silica content in the fourth and sixth leaf stage had low incidence of shoot fly, *A. soccata* (Bothe and Pokharkar 1985). In rice, a highly significant negative correlation was recorded between the silica content of the stem in various cultivars and the susceptibility to the Asiatic rice borer, *C. suppressalis*. High silica content appears to interfere with feeding and boring of the larvae and could cause defacing of their mandibles (Hanifa et al. 1974).

Toughness and thickness of plant stems has been found to alter insect–plant interactions. Ntanos and Koutroubas (2000) reported that infestation of pink stem borer, *Sesamia nonagrioides*, in rice cultivars was significantly and positively correlated with the stem diameter. In wheat, stem sawfly, *Cephus cinctus*, were resistant to solid-stemmed cultivars (Wallace et al. 1974). In sugarcane, shoot borer *C. infuscatellus*, confers resistance in combination with rind hardness with fiber content (Rao 1967). The squash borer, *Melittia cucurbitae*, was resistant to *Cucurbita moschata* by hard, compact, woody stems with closely ranged tough vascular bundles (Howe 1949). In sorghum, shoot flies were resistant to long and thin stems and glossy leaves during the seedling stage (Verma and Singh 2000).

The hardness of various plant tissues has been reported to be correlated with the resistance to insect pests. In sugarcane, *S. nivella* were resistant with very strong, hard midribs in their leaves (Adlakha 1964). Pali (1965) found a close association between resistance in sugarcane and its midrib lignification: the higher the lignification of the midrib, the greater would be resistance to the top borer. In brinjal, jassid, *A. biguttula* infestation was positively correlated with leaf thickness, midrib thickness, and leaf area (Gaikwad et al. 1991).

Color-related insect resistance in plants does not exist, but genetic manipulation of plant color usually has an effect on some fundamental physical plant processes (Norris and Kogen 1980) *P. rapae*, *P. brassicae*, *M. brassicae*, *B. tabaci*, and *B. brassicae* were much attacked as green-foliaged cultivars as compared to red-foliaged brassica species (Elsey and Farnham 1994). The development of *L. eyrsimi* was resistant to Brassica genotype with purple foliage and apetalous flowers (Rohilla et al. 1999). Agromyzid bean fly, *Ophiomyia centrosemat* was found resistant to wild soybean cultivars having purple pigment in the stem epidermis (Chiang and Norris 1984). In cabbage, females of root fly, *Delia radicum*, laid the most eggs around the base of bright green or yellow models having a stem, vertical folds, and covered with a thin layer of paraffin (Roessingh and Stadler 1990).

The plant cuticle consists of wax, pectin, and cellulose. It plays an important role in feeding and oviposition behavior of insect pests. Young cuticle is usually preferred over mature cuticle by insect pests for feeding and oviposition. Larvae of *H. zea* preferred to feed on the older leaves of soybean plants over the younger ones throughout the season (Nault et al. 1992). De Kogel et al. (1997) reported that reproduction in thrips, *Frankliella occidentalis*, was strongly correlated with resistance of mature plants of greenhouse cucumber, *Cucumis sativus.* Walker (1988) concluded that the inability of bayberry whitefly, *Parabemisia myricae*, to feed on mature lemon leaves resulted from inhibitory properties of mature cuticle rather than lack of probing stimulants.

Some secondary metabolites include phenolics, terpenoids, and steroids produced as directly toxic preformed chemicals by the plants whereas glycosides exist as conjugates that become toxic following disruption of the conjugates. An enzyme vacuolar glycosidase releases as a result of hydrolyzation of plant glycosides. Some plant preformed compounds are toxic as glycosides, but lose toxicity when deglycosylated.

3.1.2 Inducible Resistance Mechanisms

These resistance mechanisms function against insect pests as an energy-requiring process that results in the production of proteins or metabolites. This process has been best studied in regard to plant pathogens. Such resistance mechanisms are called the hypersensitive response (HR). Invocation of the HR requires that the plant recognize at least one molecule produced by the invading pest that will act as an elicitor produced by the pest or pathogen as peptides or proteins, fatty acid derivatives, sterols, or low molecular weight chemicals, and so on. Elicitors initiate the active plant defense response in the absence of living pests. The disease resistance genes in the plant have been used in agriculture to avoid the use of chemical pesticides but it is unfortunate that certain plants do not have an identified resistance gene against important pests. Within the last few years, several plant disease resistance genes have been cloned and sequenced, the leucine-rich repeat (LRR) class of proteins which has nucleotide binding sites, leucine zipper domains, or kinase domains suggestive of signal transduction functions. A few LRR plant disease resistance genes have been shown to exhibit dual specificities, that is, the plant harboring them either recognizes two different pests or two different elicitors. Especially exciting was the recent finding by Valerie Williamson and colleagues at the University of California, Davis (Rossi et al. 1998), that the cloned *Mi* resistance gene in tomato against the root knot nematode also recognizes a species of aphid.

Although we have incomplete knowledge of signal transduction in the HR, several genes have been identified based on mutagenesis or biochemical studies. These genes include protein kinases and phosphatases, and calmodulin, that lead to transcriptional activators of defense response genes.

3.2 Chemical Pest Resistance

Chemical insecticides that are commonly used for the control of mosquito became resistant and have remained an important issue in India. Insecticide resistance occurs due to excessive and indiscriminate use of insecticides for vector and pest control. DDT and HCH were introduced in India under the public health program in 1950s, but mosquitoes developed resistance to these insecticides. In the 1990s, synthetic pyrethroids were introduced in some parts of India for the control of various insecticide-resistant vectors (Singh et al. 2002). Due to low mammalian toxicity and remarkable potency at low levels the synthetic pyrethroids quickly immobilize, kill, and repel insects (Prasittisuk 1994; Chareonviriyaphap et al. 2002).

3.2.1 Insect Resistance

The resistance developed by an insecticide is an evolutionary process due to indiscriminate use of insecticide. It is also defined as the ability of an insect population to withstand a toxicant to a greater degree than a normal population and to transmit this characteristic from one generation to another.

According to the WHO, “Resistance to insecticides in the development of an ability in a strain of insects to tolerate doses of toxicant which would prove lethal to the majority of individuals in a normal population of the same species.”

Biological Mechanism of Insect Resistance

Insect resistance to insecticides has been observed in all classes of compounds, including microbial-based agents and insect growth regulators (hormone mimics; Hemingway et al. 2004). In general, response to insecticides can be categorized into two major types: physiological resistance and behavioral responses. These responses of mosquito vectors to insecticides are critical aspects of the chemical-based disease control equation (Chareonviriyaphap et al. 2013).

Physiological Mechanisms

Many vectors and mosquitoes have developed resistance to all the major groups of insecticides, including biocides. Major insecticides used to control mosquitoes on a selective basis for impregnated bed nets, indoor spraying, long-lasting insecticide-treated nets, and larviciding have therefore been accepted as a global strategy by the WHO. Some populations of *Ae. aegypti* have been found to be physiologically resistant to several synthetic compounds (Chareonviriyaphap et al. 1999; Somboon et al. 2003). Sarkar et al. (2009) investigated the physiological resistance to the insecticide deltamethrin in a colony of *Culex quinquefasciatus* Say (Diptera: Culicidae) mosquitoes, which are vectors of *Bancroftian filariasis* in India, after selection with deltamethrin. Physiological resistance is shown by the low mortality of offspring from parents that survived the selective pressure in preceding generations. Li et al. (2002) studied with larvae of Culex pipiens pallens selected with deltamethrin and showed that a nearly 531.85-fold increase in resistance could develop after the F9 generation. Gayathri and Murthy (2006) studied the development of resistance against deltamethrin in *Anopheles stephensi*, a 151-fold increase in LC_{50}, and 100-fold increase in LC_{90} from larval selection. In another study, Kumar et al. (2004) reported a 60-fold increase in *An. Stephensi* larval resistance to deltamethrin when selected for 40 successive generations. Rapid development of physiological resistance against synthetic pyrethroids was also reported for adult *Anopheles minimus* by Chareonviriyaphap et al. (2002), who found a 27-fold increase in LD_{50} after continuous selection with deltamethrin for 10 generations. In another report, Peoporn et al. (2004) found that there was a 62.29-fold increase in RR after three generations of deltamethrin selection in adult *Aedes aegypti*.

Behavioristic Resistance

Unlike physiological resistance, accurately measuring behavioral responses remains elusive and difficult to detect. Some agricultural and medically important insects, including malaria vectors, have allegedly demonstrated what has been termed "behavioral resistance" following repeated exposure to sublethal concentrations of DDT (Lockwood et al. 1984). The first study on the irritant effect of DDT residual deposits was conducted using *Anopheles quadrimaculatus* where females were found to be irritated shortly after making contact with the treated surfaces resulting in a rapid escape response from a treated house before taking a blood meal (Gahan and Lindquist 1945).

There have been few cases of behavioristic resistance recognized as a mechanism of resistance to insecticides. Kongmee et al. (2004) studied the behavioral responses of nine *Aedesaegypti* (L.) strains, six from field collections and three from laboratory colonies. All nine strains showed significant behavioral escape responses when exposed to deltamethrin at the standard field dose (0.02 g/m^2). They summarized their studies that after exposing deltamethrin directly to *Ae. aegypti*, contact irritancy was the major behavioral response and that rapid flight escape from areas exposed to space sprays or surfaces treated with residual pyrethroids could have a significant impact on the effectiveness of adult mosquito control and disease transmission reduction measures. Numerous behavioral responses of *Ae. aegypti* population sex posed to a series of pyrethroids (deltamethrin, permethrin, alpha-cypermethrin, cyphenothrin, D-tetramethrin, and tetramethrin) have been investigated. In general, all tested populations have exhibited moderate to strong irritancy when compared to repellency (Paeporn et al. 2007; Chareonviriyaphap et al. 2006; Grieco et al. 2005; Thanispong et al. 2009; Thanispong et al. 2010).

3.2.2 Weed Resistance to Herbicides

The use of herbicides is an effective weed management tool, however, overreliance on a single herbicide (or group of herbicides with the same site of action) is likely to result in weed populations that are resistant to that herbicide or group of herbicides

(Tranel and Wright 2002). Various weed species have evolved resistance to a number of herbicides. There are two important mechanisms by which resistance can be evolved. The most widely documented mechanism is the target site resistance (i.e., monogenic) where high rates of herbicide have been applied (Zelaya and Owen 2004). The other has been labeled "creeping resistance" (i.e., polygenic) and is attributable to reduced herbicide rates (Gressel 1995). Several strategies have been proposed that may effectively have an impact on the evolution of herbicide resistance: the alternation of low and high herbicide application rates, the rotation of herbicides with different modes of action, or the use of herbicides in combination (Gardner et al. 1998).

The herbicide glyphosate resistant to many weeds has been aggressively debated for a number of years. Weed scientists from different public sectors felt strongly and adamantly that due to the general lack of metabolism in target species and unique site of action, resistance of glyphosate would evolve slowly. The problem of resistance of the *Lolium* species to glyphosate and research has been conducted on the subject. The resistance of *Lolium* sps. to glyphosate was reported in the late 1990s. The high level of resistance of rigid ryegrass [*L rigidum* (Gaud)] was reported regarding numerous herbicides including acetyl-CoA carboxylase (ACCase, EC6.4.1.2) and ALS-inhibiting herbicides (Llewellyn and Powles 2001). Glyphosate resistance of *Lolium* sps. was reported after 15 years of repeated applications in a specific cropping system in Australia (Powles et al. 1998). Resistance level was reported to be seven- to elevenfold compared with the susceptible rigid ryegrass population.

Italian ryegrass (*L. multiflorum* Lam) has become resistant to glyphosate in Chilean fruit orchards after 8–10 years of use (Perez and Kogan 2003). Recently Neve et al. (2003a, b) viewed the evolution of glyphosate resistance in rigid ryegrass, which was predicted to occur at a relatively high rate (an estimated 90 % of rigid ryegrass populations) in a no-tillage environment. When the complexity of the crop rotation was increased, the evolution of resistance was not predicted to occur. Other factors such as application timing, inclusion of other herbicides, and rotation of herbicides also had a negative impact on the evolution of glyphosate resistance.

Common waterhemp (*Amaranthustuberculatus*) control with glyphosate has been variable with anecdotal reports of resistant populations. The first investigated reports of control problems were in 1998 from Badger and Everly, Iowa and resulted in an assessment that portions of the common waterhemp population in those fields were not responding to multiple applications of glyphosate, whereas the majority of the population was sensitive (Zelaya and Owen 2002). Reports from other Midwest states corroborated the findings from Iowa and suggested that common waterhemp plants survived glyphosate applied at 6.72 kg ha^{-1} and produced viable seed (Smeda and Schuster 2002).

Goosegrass [*Eleusineindica* (L) Gaertn] is resistant to glyphosate (Lee and Ngim 2000). The population evolved after an estimated 10 years of selection pressure attributable to repeated applications of glyphosate, and demonstrated a two- to fourfold resistance compared with the sensitive biotypes.

3.2.3 Pathogen Resistance to Fungicide

Fungicides are essential for the maintenance of healthy crops and reliable yields of high-quality produce. However, their effectiveness has been seriously affected in some situations by the development of resistance in target pathogens. Resistance to fungicides usually results from an alteration at the site of fungicidal action in the target pathogen. Thus, knowledge of the mode of action can indicate risk. A single rather than a multiple site of action, and a site of action known to have become resistant to other fungicides, are both positive indicators of risk. Recently, Hobbelen et al. (2014) studied a model structure to describe the emergence of resistance in a sensitive pathogen population, which was parameterized for *Mycosphaerella graminicola* on winter wheat and used to evaluate the effect of fungicide dose rate on the time of emergence of resistance for a range of mutation probabilities, fitness costs of resistance, and sensitivity levels of the resistant strain.

Fungicide-Associated Risk

Structural Class The problems of fungicide resistance indicate clearly the risk of resistance by considering the chemical class to which a fungicide belongs. Each chemical class is characterized by a typical resistance behavior pattern. Certain major classes of fungicide, based on copper (e.g., copperoxychloride and cuprous oxide), phthalimides (e.g., captan and folpet), and dithiocarbamates (e.g., mancozeb, maneb, zineb, and thiram), have very rarely if ever been known to encounter practical resistance, even after many years of use. By contrast, in some other classes, such as benzimidazoles (e.g., benomyl, carbendazim, thiabendazole), phenylamides (e.g., metalaxyl, oxadixyl), dicarboximides (e.g., iprodione, procymidone, vinclozolin), and strobilurin analogues (e.g., azoxystrobin, kresoxim-methyl, pyraclostrobin), all the members met serious resistance problems that arose in most of their target pathogens within 2–10 years of the commercial introduction of each class. Resistance to azoles (e.g., triadimefon, flutriafol, epoxiconazole) has developed more gradually, and only in certain pathogens.

Mechanisms of Action A single target site can be rendered resistant through one mutation changing a single DNA-base in the target gene and, consequently, just one amino acid in the target protein. Formerly it took a long time to identify a mode of action. Thirty years after the introduction of dicarboximides into commercial use, their mode of action has been identified (Leroux et al. 2002). It is now usual for a new fungicide group to be introduced with some information on its mode of action (e.g., benzophenones, which include metrafenone; Schmitt et al. 2006; Opalski et al. 2006).

Much research has been done in the mode of action of azole (DMI) fungicides inasmuch as resistance to antifungal drugs has become a significant problem in human medicine. The mechanisms contribute to azole resistance, including changes in the sterol 5-6-desaturase, overexpression of the target sterol 14 α –demethylase (Schnabel and Jones 2000), and increased expulsion mediated through increased activity of ABC transporters (De Waard et al. 2006).

There are a few fungicides in agricultural use, such as tricyclazole and pyroquilon, used to control rice blast disease, which specifically affect the penetration of the pathogen (*Magnaporthe grisea*) into the host plant through inhibition of reductase steps in melanin biosynthesis needed for the normal function of appressoria. Thus far no resistance problems have arisen with these melanin biosynthesis inhibitor-reductase (MBI-R) fungicides, but there is no obvious reason why not; resistance to carpropamid (melanin biosynthesis inhibitor–dehydratase or MBI-D fungicide), occurred soon after its introduction in Japan (Kaku et al. 2003).

A nontarget type of QoI-resistant mutation in a laboratory mutant of *Mycosphaerella graminicola* involved a nuclear gene and the enhanced production of an alternative oxidase, allowing respiration to bypass the QoI target site (Ziogas et al. 1997). It was considered unlikely to cause practical resistance because this laboratory mutant proved more sensitive than the wild-type to azoxystrobin in vivo. Subsequently, partially resistant isolates of *M. graminicola* with increased alternative oxidase activity have been obtained from QoI-treated wheat crops (Miguez et al. 2004) and it has been suggested that this change rescues the pathogen sufficiently from the effects of QoI fungicides to allow further selection of more highly resistant target-site mutations (Avila-Adame and Köller 2002; Wood and Hollomon 2003).

Some examples of recombination studies are those reported by Butters et al. (1986) and Brown et al. (1992) for ethirimol and triadimenol resistance in barley powdery mildew and by Shattock (2002) for metalaxyl resistance in *Phytophthora infestans*. Phenylamide-resistant field populations of *Phytophthora infestans* arose within 2 years from the first commercial use of these fungicides. Thus, in this case serial transfer experiments were less useful than mutagenic experiments as an indicator of practical risk. Another long-term field study over 11 years also involving the cereal eyespot pathogen (*Oculimacula* spp.) examined the effects of intensive selection on the development of resistance to the aniline pyrimidine fungicide, cyprodinil (Babij et al. 2000).

Whenever baseline studies are done, some variation in sensitivity between isolates is found. *Mycosphaerella graminicola* showed tenfold range of sensitivity to azoxystrobin when tested in vivo, (Godwin et al. 1999), whereas isolates of barley (Hollomon et al. 1996) and grape (Green and Gustafson 2006) powdery mildews showed a much broader, 100- to 1000-fold, range of sensitivity against quinoxyfen. All such isolates are easily controlled by application of the fungicide at concentrations well below the recommended rate of application.

4 Nonchemical Technology Approach in Crop Production

There are technological approaches to improving pest management that do not necessarily depend on chemical pesticides. These include plant breeding, the use of biological control agents, and biotechnology, all of which are discussed separately below although elements of all these technologies are often used together, frequently with chemical pesticides.

4.1 Plant Breeding

In the ecosystem, plants have had some natural resistance to plant pathogens. As time passed plant breeders have crossed varieties of plant species to produce improved varieties with increased pest resistance. In the present century, plant breeders succeeded in improving the resistance of crops, more to diseases, less to insects, and least to weeds. Breeders have been able to breed many crop varieties that exhibit resistance to fungal diseases affecting the parts of the plants outside the soil, as well as to nematodes and viruses. The breeding of high-yielding varieties of crops such as wheat, rice, and corn with built-in resistance to a number of pests has been an important part of the strategy to increase and stabilize yields. Agricultural scientists at national and international agricultural research stations and, more recently, in the private sector, have played a major role in developing pest-resistant varieties in the important food crops grown in developing countries. The initial focus of most of these early breeding efforts, based on Mendelian principles, was to increase yields of basic food crops. Breeding and agronomic improvements have, on average, achieved a linear increase in food production globally, at an average rate of 32 million metric tons per year (Alston et al. 2009). However, to meet the recent Declaration of the World Summit on Food Security (Food and Agriculture Organisation (FAO 2009) target of 70 % more food by 2050, an average annual increase in production of 44 million metric tons per year is required, a 38 % increase over historical increases in production, to be sustained for 40 years. This scale of sustained increase in global food production is unprecedented and requires substantial changes in methods for agronomic processes and crop improvement. Achieving this increase in food production in a stable environment would be challenging, but is undoubtedly much more so given the additional pressures created by global environmental changes (Tester and Langridge 2010).

4.2 Biotechnology and Plant Protection

Biotechnology plays an important role in agriculture. It involves the alteration in traits of plants and animals through manipulation of its cells or molecules. The consequences of the invention of DNA-based molecular techniques and their application to agriculture have been pervasive, both within the agricultural sector and outside it. Increased food production and profits were probably the primary hoped-for results by scientists who pioneered agricultural biotechnology and widespread public skepticism and even vociferous opposition probably were not anticipated (Herdt 2006). The basic tools used in agricultural biotechnology for plant production and protection are given below:

1. Genetic engineering inserts fragments of DNA into chromosomes of cells and then uses tissue culture to regenerate the cells in a whole organism with a different genetic composition of the original cells. This is also known as rDNA technology; it produces transgenic organisms.

2. Tissue culture manipulates cells, anthers, pollen grains, or other tissues; therefore they live for extended periods under laboratory conditions or become whole, living, growing organisms; genetically engineered cells may be converted into genetically engineered organisms through tissue culture.
3. Somatic hybridization removes the cell walls of cells from different organisms and induces the direct mixing of DNA from the treated cells, which are then regenerated into whole organisms through tissue culture.
4. Marker-aided genetic analysis studies DNA sequences to identify genes, QTLs (quantitative trait loci), and other molecular markers and to associate them with organismal functions, that is, gene identification.
5. Marker-aided selection is the identification and inheritance tracing of previously identified DNA fragments through a series of generations.
6. Genomics analyzes whole genomes of species together with other biological data about the species to understand what DNA confers what traits in the organisms. Similarly, proteomics analyzes the protein in a tissue to identify the gene expression in that tissue to understand the specific function of proteins encoded by particular genes. Both, along with metabolomics (metabolites) and phenomics (phenotypes), are subcategories of bioinformatics.

4.3 Biopesticides

Biopesticides are preferred by many to use safely, because they do not leave harmful residues in the environment. They are target-specific and do not destroy beneficial organisms. Also, they promote the growth of natural enemies of pests. Against these advantages, biological pesticides may not be as efficient or as cheap as chemicals. There are several biopesticides that are commercially available in the market for the use of farmers. There are approximately 175 registered biopesticides available globally. The list of biopesticides registered in India for agriculture and public health is shown in Table 1.

5 Conclusion

Incessant accomplishments for greater production have provoked scientists to formulate new herbicides/pesticides. Pesticide application is still the chief and conventional mode of plant protection from pests, and has added considerably to improvements in crop productivity and yield. Consequently, the upcoming exertion on herbicide/pesticide resistance could be potent if it entails the recognition of metabolites responsible for detoxification of these applied xenobiotics, diverse enzymes, their controlling genes, and the rhizosphere bacterial species responsible for herbicide/pesticide tolerance. The pursuit of biotechnology to discover resistance accountable genes could also be potent, which in turn could be transferred to

Table 1 List of biopesticides registered in India

A. For agricultural use	
Biofungicides	
Crop	Common Name of the Disease
Neem oil based EC containing *Azadirachtin* 0.030 % (300 ppm)	
Bhindi	Powdery mildew
***Pseudomonas fluorescens* 1.75 %, 0.5 % WP**	
Wheat	Loose smut
Groundnut	Late leaf spot
Rice	Leaf and neck blast (*Pyricularia oryzae*)
Chili seedlings	Damping off (*Pythium aphanidermatum*)
Tomato	Wilt (Fusariumoxysporum f.sp.)
***Trichoderma harzianum* 0. 50 % WS, 2.0 % WP**	
Cardamom	Capsule rot (*Phytophthora meadii*)
Maize	Root rot Fusarium wilt (*Fusarium moniliforme)*
***Trichoder maviride* 1 % WP, 5 % WP**	
Pigeonpea	Wilt, root rot
Cowpea	Root rot
Chili seedlings	Damping off (*Pythium aphanidermatum*)
Urd bean	Root rot (*Macrophomina phaseolina*)
Pigeonpea	Root rot (*Macrophomina phaseolina*)
Chickpea	Wilt (*Fusarium oxysporum*) Root rot (*Rhizoctonia solani & Sclerotium rolfsii*)
Paddy	Sheath blight (*Rhizoctonia solani*)
Cauliflower	Stalk rot—*Sclerotina sclerotiorum*
Brinjal	Root rot/wilt/damping off *Rhizoctonia bataticola, Sclerotium rolfsii, Fusarium oxysporum, Rhizoctonia solani* Root rot/wilt/damping off *Rhizoctonia bataticola, Sclerotium rolfsii, Fusarium oxysporum, Rhizoctonia solani*
Cabbage	Root rot/collar rot *Rhizoctonia solani*
Tomato	Seedling wilt *Fusarium oxysporum* Damping off *Pythium aphanidermatum, Rhizoctonia solani*
Bengal gram	Seedling wilt *Fusarium oxysporum* Damping off *Pythium aphanideramatum, Rhizoctonia solani*
Sunflower	Seed rot *Scletotium rolfsii* Root rot *Sclerotium rolfsii*
Cowpea	Wilt (*Fusarium oxysporum*)
Groundnut	Stem rot (*Sclerotium rolfsii*)
Bioinsecticides	
Azadirachtin 0.15 % W/W Min., 0.3 %(3000 PPM) Min. 5 % w/w Min Neem Based E.C.	

(continued)

Table 1 (continued)

A. For agricultural use	
Cotton	Whitefly Bollworm
Rice	Thrips Stemborer Brown planthopper Leaf folder
Cotton	American bollworm
Tea	Thrips Red spidermites
Tomato	Fruitborer (*Helicoverpaarmigera*)
Brinjal	Fruit and shoot Borer (*Leucinodesorbonalis*)
Cotton	Bollworm (*Helicoverpa Armigera*) Aphids
Rice	Leafroller Stem borer BPH
Bengal Gram	Pod borer (Heliothis)
Red gram	Pod borer (Melangromyze)
Cotton	Aphids Jassids White flies Bollworms
Okra	Fruit borer Whiteflies Leafhopper
Brinjal	Shoot and fruit borer Beetles
Cabbage	Aphids, DBM Cabbage-worm Cabbage-looper
Jute	Semilooper Hairy caterpillar
Tea	Caterpillar Pinkmite Red spider mites Thrips
Tobacco	Tobacco caterpillar Aphids

(continued)

Table 1 (continued)

A. For agricultural use	
Rice	Brown plant Hopper Leaf folder Stemborer
Cotton	Whitefly Leafhoppers Heliothis Aphids
Cauliflower	Spodoptera Diamondback moth Aphids
Bhindi	Leafhopper Whitefly Aphid Pod Borer
Tomato	Aphids Whitefly, Fruit borer
Bacillus thuringiensis var. galleriae	
Tomato	Fruit borer (*Helicoverpa armigera*)
Cabbage and Cauliflower Bhendi	Diamondback moth (*Plutella xylostella*) Fruit borer (Earias spp.)
Chilliies	Fruit borer (*Spodoptera litura*)
Cotton	Bollworm (*Heliothis armigera*)
Rice	Leaf folder (*Cnaphalocrocis medinalis*)
Bacillus thuringiensis-k	
Cotton	Bollworm
Bacillus thuringiensis Serovar Kurstaki (3a,3b, 3c) 5 % WP	
Cotton	American bollworm Spotted bollworm
Red gram Cabbage	Pod borer Diamondback moth
Bacillus thuriengiensis var Kurstaki 0.5 % WP serotype 3a, 3b, 3c, Strain	
Caster	Caster semilooper (*Achaeae janata*)
Chickpea	Chickpea podborer (*Helicoverpa armigera*)
Bacillus thuriengiensis var Kurstaki 2.5 % AS. (Spicbio-Btk AS)	
Gram	Grampod borer (*Helicoverpa armigera*)
Bacillus thuringiensis var. Kurstaki, Serotype H-3a, 3b, Strain Z-52	
Cotton	Bollworms Spodoptera
Rice	Stem borer Leaf folder
Gram	Heliothis
Pigeon Pea	Heliothis

(continued)

Table 1 (continued)

A. For agricultural use	
Soyabean	Spodoptera, Heliothis, Spilosoma, Semilooper, Leaf miner
Tobacco	Spodoptera, Heliothis
Castor	Hairy caterpillar, Aheajanata
Teak	Dfoliater (Hyblaeapured), Skeletonizer (*Eutectona machaeralis*)
Beauveriabassiana 1.15 % W.P.	
Cotton	Bollworm
Rice	Rice leaf folder (*Cnaphalocrosis medinalis*)
Beauveriabassiana **1 % WP**	
Chick pea	Pod borer (*Helicoverpa armigera*)
Okra	Fruit borer/spotted bollworm
MetarhiziumAnisopliae 1.15 % WP	
Rice	Brown plant hopper (BPH) (Nilapavatalungens)
VerticilliumLecanii 1.15 % WP	
Cotton	Whiteflies
Citrus	Mealybugs (*Planococcus citri*)
Nuclear polyhedrosis virus of Helicoverpaarmigera 0.43 % AS	
Cotton	Helicoverpa Armigera
Tomato	Helicoverpa Armigera
NPV of *Helicoverpaarmigera* 2.0 % AS	
Pigeon pea	Pod borer (*Helicoverpaarmigera*)
Gram	Pod borer (*Helicoverpaarmigera*)
Chick pea	Pod borer (*Helicoverpaarmigera*)
Tomato	Fruit borer (*Helicoverpaarmigera*)
NPV of *Helicoverpaarmigera* 0.43 % AS	
Cotton	*Helicoverpaarmigera*
Tomato	*Helicoverpaarmigera*
NPV of Spodoptera litura 0.5 % AS	
Tobacco	Spodoptera Litura
B. For public health use	
Mosquito Larvae	**Habitat**
Azadirachtin 0.15 % EC	
Mosquito Larvae	Stagnant water, drainage, water puddle, iron containers, machinery scraps, iron box, iron tanks, plastic scraps, pit
Bacillus thuringiensisvar.israelensis WP	
Anopheles and Culex (larvae)	Clean water, cement tanks
Culex	Polluted water, cesspits, cement tank, stagnant and flowing drains
Anopheles	Paddy fields, ponds, pools

(continued)

Table 1 (continued)

A. For agricultural use	
Aedes	Tree holes, disused tires
Culex	Drains, cesspits, casuarina pits, disused wells
Bacillus thuriengiensis var. sphaericus	
Anophles species Culex species	Drains, cesspits, cesspools, paddy fields, ponds
Anophles species Culex species	Casuarina pits, unused wells, unused overhead tanks, domestic wells (not for drinking requirements)
Bti 12 % AS (Vectobac)	
Anopheles	Clean water, cement tanks
Culex	Polluted water, cesspits, cement tanks, stagnant and flowing drains
Bacillus sphaericus	
Anopheles species Culex species	Drains, cesspits, cesspools, paddy fields, ponds
Anopheles species Culex species	Casuarina pits, unused wells, unused overhead tanks, domestic wells (not for drinking requirements)

transgenic plants for improvising resistance. Among with main resistance machinery, the significance of enzymes such as the Cyt P450 in plants in the metabolism for the detoxification of herbicides should be emphasized more. The detoxification and metabolism of herbicide-catalyzed enzymes of Cyt P450 present an exceptional resistance mechanism found in HR plants. Comprehension of the pesticide resistance mechanism in plants and other microbes is fundamental for formulating a secure preparation for pesticide utilization and its biodegradation in contaminated environments.

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Implication of Rhizosphere Acidification in Nutrient Uptake by Plants: Cases of Potassium (K), Phosphorus (P), and Iron (Fe)

Hayet Houmani, Mokded Rabhi, Chedly Abdelly, and Ahmed Debez

Abstract The rhizosphere represents the interface between soil and roots. In this zone, many interactions between plant roots and the soil solution occur and result in important modifications of the physicochemical properties in this area. Plants require large amounts of nutrients to assure maximum growth and development. The absorption of excess nutrients by roots leads to many changes in the rhizosphere such as the acidification phenomenon which is known to be a continuous process in many soils through the world. It is due to the extrusion of protons at the root plasma membrane in favor of cation influx, a principal way used by plants to remove nutrients from the soil solution. Rhizosphere acidification plays a crucial role in nutrient acquisition by plants and is attributed to the activity of H^+ATPase pumps located at the plasmalemma. The implication of proton release in nutrient acquisition by plants was proved under low nutrient availability. Thus, an increase of the H^+ATPase activity was noted under a deficiency in many essential nutrients. Due to new advances in molecular biology, the role of H^+ATPases in nutrient uptake by plants is more elucidated and many genes encoding these pumps are identified. In the present chapter, we summarize information gained on the role of rhizosphere acidification in the uptake of two essential macronutrients and a key micronutrient, respectively, potassium (K), phosphorus (P), and iron (Fe), especially under deficiency conditions and we describe the recent findings related to H^+ATPases that drive the acidification process.

Keywords Acidification • H^+ATPase • Iron (Fe) • Nutrient uptake • Nutrient deficiency • Rhizosphere • Proton release • Potassium (K) • Phosphorus (P)

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1 Introduction

Plants require nutrients for their growth and development. These elements are classified into groups. The first, macronutrients, mainly consist of potassium, magnesium, nitrogen, calcium, and phosphorus. The second class is termed micronutrients and includes at least manganese, boron, copper, iron, molybdenum, and zinc. Plants have evolved different mechanisms to acquire such elements from the rhizosphere. The rhizosphere is defined as the critical zone of interaction among three components: plants, soils, and microorganisms (Zhang et al. 2010; Shen et al. 2011) and is considered a key interaction zone between plants and soils (Shen et al. 2013). Therefore many interactions occur between roots and the rhizosphere at the plasma membrane site because plant biological activity can affect the chemistry of the rhizosphere. Indeed, due to their activities, roots are able to modify notably the physicochemical properties of the rhizosphere via the exudation of organic compounds or the release of H^+ protons. Roots, the first organs in direct contact with the rhizosphere, are able to react with their environment and thus can alter the biogeochemistry of the rhizosphere (Schreiber et al. 2011; de Kroon et al. 2012; Postma and Lynch 2012; Hinsinger et al. 2003, 2005, 2009). This plays a key role in enhancing the bioavailability of nutrients such as P (Hinsinger 2001) via the release of proton into the external medium in order to acidify the rhizosphere (Neumann and Römheld 2002; Zhang et al. 2010; Hinsinger et al. 2009; Marschner 2012). As described previously by Marschner (1998), the processes that occur in the rhizosphere including the changes in pH or exudates released by roots play an important role in nutrient acquisition by plants. Rhizosphere acidification is a key mechanism for plant mineral nutrition (Palmgren 2001) because it is responsible for the plasma membrane proton motive force and leads to the solubility of nutrients. Recently, Fujii (2014) mentioned that soil acidification is considered an adaptive trait used by trees to uptake nutrients from the soil. Moreover, the form of nutrient taken up by roots significantly influences the rhizosphere properties. We can cite here the example of nitrogen. If this nutrient is supplied in ammonium form, an acidification of the rhizosphere occurs via the release of protons into the external medium (Taylor and Bloom 1998; Hinsinger et al. 2003). Generally, the uptake of an element is accompanied by the extrusion of a proton in the case of cations, or OH^- in the case of anions. It is known that dissolution of some minerals such as calcium (Ca), iron (Fe), and aluminum (Al) vary greatly with the size of particles and with the soil pH (Pierzynski et al. 2005; Oelkers and Valsami-Jones 2008). For nitrate (NO_3^-) uptake from the soil, an active transport coupled to an H^+ electrochemical gradient generated by the activity of PM H^+-ATPases across the root plasma membrane (Miller and Aldrich 1996; Forde 2000) takes place in the epidermal and cortical cells.

It was very well established that nutrient uptake from the soil is achieved by cation exchange, where protons (H^+) are pumped by root hairs into the soil. The proton release displaces cations attached to negatively charged soil particles and thereby makes the cations available for uptake by the roots. Because macronutrients are consumed in larger quantities and generally an excess uptake of cation over anion occurs, this leads to H^+ release into the external medium (Loss et al. 1993; Tang et al. 1997). In fact, when plants absorb high amounts of cations, this is positively correlated with H^+ excretion in each rooting zone. The continuous release of H^+ leads to a decrease of the pH around the roots and results in the acidification of the rhizosphere which is a determinant for cation driving and uptake by plants. Thus, the rhizosphere can be acidified directly under excess cation uptake over anion due to the release of protons from the roots (McLay et al. 1997). This process is related to the activity of hydrogen pumps, H^+-ATPases at the root plasmalemma, and plays an important role in cation acquisition by plants. It was suggested that the improvement of nutrient uptake and use was often ascribed to rhizosphere acidification.

Nutrients can also influence the uptake of each other via feedback and thus affect plant nutritional status and consequently, a modification of the rhizosphere properties is inevitable (Zhang et al. 2010). Depending on the form of N supply, the uptake of cations and anions is modulated and can affect the pH of the rhizosphere (Marschner 2012). In this context, Shen et al. (2013) showed that localized application of ammonium combined with a superphosphate notably enhanced the productivity of Chinese crops grown in calcareous soil and attributed this effect to the role of ammonium uptake in promoting proton release by roots resulting in a decrease of rhizosphere pH and leading to an increase in the bioavailability of phosphates as documented by Jing et al. (2010, 2012). Given the importance of rhizosphere acidification, many practices have been developed to increase such a process in order to improve nutrient uptake by plants via the manipulation of rhizosphere acidification (Zhang et al. 2010; Chen et al. 2011). Rhizosphere acidification, the principal engine of nutrient uptake for plants, can be stimulated using fertilization management or via screening genotypes with high rhizosphere acidification capacity (Shen et al. 2013). It has been suggested by Guo et al. (2010) that the excessive utilization of nitrogen fertilizer in Chinese intensive agriculture promotes soil acidification in the long term. Thus, a new practice used by agriculture to improve nutrient uptake is the intercropping system, which is defined as an association of genotype with high acidification capacity with other species less efficient in this process. In China, in intercropping systems, optimization of crop combination and nutrient management via a better understanding of the interactions that occur in the rhizosphere is necessary to improve sustainable crop production characterized by a high yield and high nutrient use efficiency (Zhang et al. 2010, 2012). It has been demonstrated by Li et al. (2004) that during the association of chickpea and wheat plants supplied with organic P, the first species improved P nutrition of the second one due to the increase of acid phosphatase activity and to the rhizosphere acidification. Such findings suggested that chickpea released high amounts of protons which are beneficial for both chickpea and wheat having a tangled roots (Li et al. 2007). According to Li et al. (2008a, b), the coculture of wheat and common bean was beneficial in terms of yield productivity and proton release rate which showed a significant increase by such kind of intercropping crops as compared to legumes cultivated individually.

The acidification process has received more attention in the last decade and a multitude of methods are used to study the processes of rhizosphere acidification.

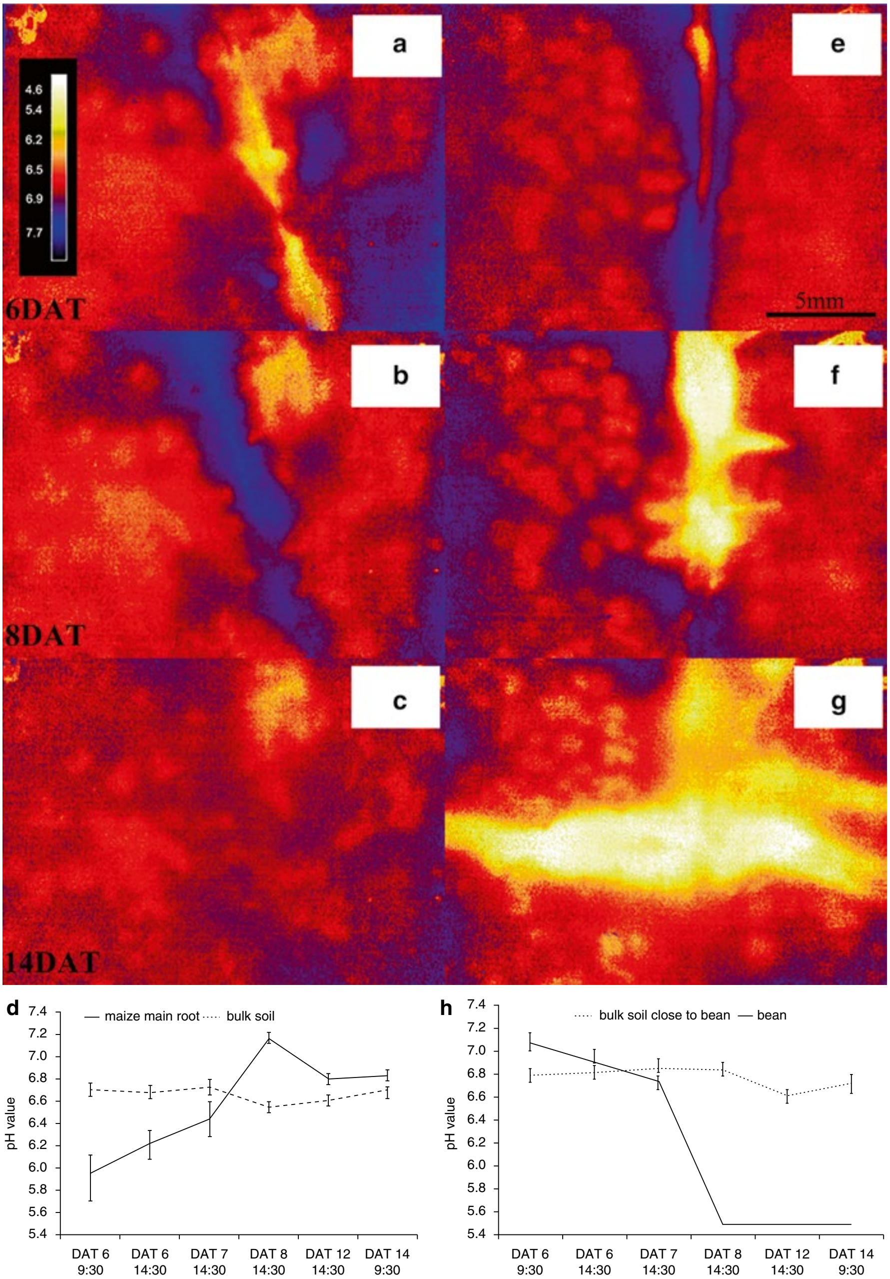

Fig. 1 Use of optodes to measure the dynamics overtime of pH for the rhizosphere and bulk soil of roots of maize (**a**–**d**) or bean (**e**–**h**) species (**a**–**c**, **e**–**g**) revealed the pH maps of the respective region of interaction rhizosphere root system (ROI) at a scale pH ranging from 4.6 to 7 at different plant replicates for each species (DAT), DAT6 (**a, e**), DAT 8 (**b, f**), and DAT 14 (**c, g**), respectively. (**d, h**) show the evolution of the mean pH value within the ROI at the root surface of maize (**d**) and bean (**h**) over time growing separately, in rhizotrons in a climate chamber. (Faget et al. 2013)

The pH evaluation can be performed using the newly developed planar optode techniques (Blossfeld and Gansert 2012; Blossfeld 2013). Recently, Faget et al. (2013) found by combination of fluorescence with optode techniques, clear dynamic changes in the pH of the rhizosphere of maize and bean (Fig. 1). A new technique developed by Rudolph et al. (2013) consisting of a spatiotemporal mapping of local soil pH changes induced by lupin and soft-rush was efficient in detecting the acidification of the rhizosphere by these two species.

The acidification process based on proton release into the rhizosphere, making nutrients more available for plants, was very well demonstrated under nutrient limiting conditions and showed a decrease in the soil pH. The ability of plants to acidify their medium is considered a good criterion of tolerance to nutrient deficiency stress especially in the case of iron (Fe). New insights into the role of the H^+-ATPases in rhizosphere acidification using genetic tools are available. In the present review, we summarize the implication of rhizosphere acidification in nutrient uptake, with a special focus on potassium and phosphorus as important macroelements and iron, a key micronutrient involved in many plant physiological and biochemical processes.

2 Rhizosphere Acidification and Nutrient Uptake: Role of the Pump H^+ATPases

According to Hinsinger (1998), plant nutrition is not only linked to plant physiology but includes all the processes that occur in the rhizosphere before the uptake of the required nutrient. Plants are able to change the pH of the rhizosphere during their growth and development. Such a property was well documented in the literature (Haynes 1983; Marschner et al. 1986; Nye 1981). When plants take up cations excessively from the soil solution, an increase of the proton extrusion is observed (Glass et al. 1981) leading to rhizosphere acidification. Indeed, the root hairs, the first organs that keep direct contact with the soil solution, are the site of noticeable proton flux detected by the use of microelectrode vibration (Palmgren 2001). According to Ruiz et al. (2002), the plasma membrane H^+-ATPase has a crucial role in ion transport and a positive correlation between H^+-ATPase activity and the concentrations of cation was found in roots (Ruiz et al. 2002). Such proton release is sustained by the activities of proton pumps located at the plasma membrane (Samuels et al. 1992; Jahn et al. 1998). It is well established that the major driving force for the cation and anion transport across the plasma membrane is the active extrusion of protons (H^+) due to the activity of proton pump ATPases located at the root plasmalemma. In fact, ions are taken from the soil solution and transported into the root cells prior to their distribution in the different plant tissues. During their transport across the plant plasma membrane, ions are driven by an electrochemical gradient of protons as a result of the activity of plasma membrane H/Cation-ATPases (Miller and Aldrich 1996; Sussman 1994). The latter are qualified as powerhouses for nutrient uptake (Palmgren 2001).

Due to the importance of soil acidification in nutrient acquisition, among the promising solutions to improve nutrient uptake by plants is raising the pH of the rhizosphere making the major nutrients such as K, Ca, Mg, P, S, and N more available for plant roots as suggested by Dakora and Phillips (2002).

2.1 Potassium (K^+)

Potassium uptake by roots requires an exchange with an ion that has the same equivalent positive charge. Generally, one proton is exchanged against one ion of potassium. In fact, the uptake of potassium via channels depends on the electrochemical potentials across the plasma membrane (Serrano 1989). A positive correlation between potassium uptake and proton release was noted in barley by Glass et al. (1981), suggesting the importance of this process in potassium acquisition by plants. Bucker et al. (2006) reported a simultaneous extrusion of protons and K^+ influx from the solution in rice, revealing a linear relationship between H^+ pumping and K^+ uptake by this species. It has been suggested that plants acquire potassium from soil through an active process called symport which depends on the gradient of proton via the plasma membrane as revealed by Sze et al. (1999). The occurrence of the H^+/K^+ symporter in the plasma membrane contributes to the K^+ accumulation under potassium shortage conditions (Maathuis and Sanders 1994; Schachtman and Schroeder 1994), provides strong evidence for exchange of the K^+ ion over a proton, and leads to rhizosphere acidification.

The establishment of this proton gradient creates a proton motive force responsible for the transport of cations (Rodriguez-Navarro 2000) such as monovalent ones, like potassium. Such a process is due to the activities of plasma membrane H^+-ATPases. The role of these proton pumps (H^+-ATPases) in K^+ absorption was well demonstrated in a previous work by Minjian et al. (2007). It was also proved that K^+ uptake by plants was correlated with high activity of plasma membrane H^+-ATPase (Briskin and Hanson 1992). According to these authors, the plasma membrane H^+-ATPase might conduct an antiport transport H^+/K^+ that exchanges H^+ over K^+, thus contributing to K^+ uptake. Moreover, the extracellular acidification based on H^+ pump activities was found to stimulate some transporters such as the symport K^+/H^+. This finding was later confirmed by the identification of genes encoding some potassium transporters in many species including LeHAK5 in tomato (Wang et al. 2002), HvHAK1 in barley (Santa-Maria et al. 1997), CaHAK1 in pepper (Martínez-Cordero et al. 2005), and OsHAK1 in rice (Bañuelos et al. 2002). Furthermore, the activation of the H^+-ATPase is necessary for K absorption by roots, as suggested by Minjian et al. (2007) who demonstrated that K^+ uptake by maize depends on the activity of proton pump H^+-ATPase and on a specific K^+ transporter located at the membrane. In fact, the activity of such pumps generated an electrochemical gradient established by the liberation of protons H^+, a determinant process in the K^+ acquisition by plants. These pumps were strongly stimulated when plants were subjected to limited K^+ supply and resulted in an acidification of the extracellular medium. In fact, the activity of such pumps increased under K^+ deficiency conditions leading to an increase of cation exchange capacity. A decrease of the pH surrounding the roots and an influx of K^+ into the roots occurred simultaneously (Chen and Gabelman 2000). Several studies showed that following a few minutes of reduction of the external K^+ concentrations, a hyperpolarization of the root membrane potential was noted (Maathuis and Sanders 1993; Nieves-Cordones et al. 2008). This phenomenon is considered as the first response to potassium deficiency which was accompanied by an important release of protons into the external medium and to an acidification of the rhizosphere (Behl and Raschke 1987). These two physiological responses are generated by the activity of the H^+-ATPase pump at the plasma membrane via pumping of H^+ from the cytoplasm to the apoplasm (Palmgren 2001). Such physiological responses are in favor of the activation of the K^+ channels and transporters resulting in an important influx of K^+ into the roots. Furthermore, the rate of proton excreted is considered as criteria to evaluate potassium deficiency tolerance in crops. Thus, one of the criteria of tolerance to K^+ deficiency is the capacity of the plant to expulse H^+. K^+ uptake efficiency in tomato was correlated with a high K^+ influx that was associated with low pH value (Chen and Gabelman 2000). Several proton pumps were identified in different plant species (Serrano 1989; Nardi et al. 2002). The role of these H^+-ATPases was studied well by the application of different pump inhibitors or stimulators such as vanadate and fusicoccin. The vendetta is known to block the activity of H^+-ATPases. For example, in rice, the addition of vanadate in the nutrient solution totally blocked the activity of the H^+-ATPases, and led to an inhibition of potassium uptake by the plants (Bucker et al. 2006).

2.2 *Phosphorus (P)*

The involvement of rhizosphere acidification on P mobilization was described in bacteria, fungi, and plants. The bacteria PSB or the fungi PSF can mobilize soil P by the release of some compounds and via the acidification of the soil (Jones and Oburger 2011). According to the literature, the excretion of H^+ into the rhizosphere improves phosphorus (P) availability in the soil (Neumann and Römheld 1999; Hinsinger et al. 2003, 2011). In fact, rhizosphere acidification led to both enhancement of P mobilization from soil and makes it available for plants (Hinsinger 2001; Hinsinger et al. 2011; Hinsinger et al. 2009; Zhang et al. 2010).

As for potassium, the uptake of P involves the H^+/Pi symport system as suggested by Ai et al. (2009) and is coupled to H^+ transport (Sakano 1990). Thus, under P deficiency conditions, this process increased notably. In rice, the mobilization of P is due to rhizosphere acidification via the liberation of H^+ from the roots. Such behavior occurred to maintain equilibrium between excessive uptake of cations against anions (Saleque and Kirk 1995). P starvation induced root H^+ release (Li et al. 2004) leading to rhizosphere acidification. This was very well documented (Neumann and Römheld 1999; Raghothama 1999; Hinsinger 2001; Richardson et al. 2001; Vance et al. 2003; Tang et al. 2004; Raghothama and Karthikeyan 2005).

In the case of white lupin and *Lupinus albus*, an acidification of the external medium occurred under P starvation (Racette et al. 1990). Shen et al. (2006) demonstrated that in soybean and *Arabidopsis* roots conducted under P deficiency conditions, an increase of the plasma membrane H^+-ATPase (PM H^+-ATPase) activity was noted. In rice, the increase of the PM H^+-ATPase contributed to the rhizosphere acidification (Shen et al. 2006; Zhang et al. 2011) and sustained the transport of this nutrient via the plasma membrane.

The ability of plants to acidify the rhizosphere is considered criteria to evaluate the P tolerance degree of plants inasmuch as species differ in their capacity to enhance PM H^+-ATPase under P limiting availability (Shen et al. 2006). P is present in the soil solution at low concentrations (μM). Thus, systems with high affinity are involved in its transport. Furthermore, Pi uptake occurred against a chemical potential gradient across the root plasma membrane (Shen et al. 2011) and it is mediated by a symporter Pi/H^+. Recently, this latter was characterized as a member of the PHT1 gene family because of the positive correlation found between PHT1 alteration and the decrease of P uptake (Ai et al. 2009).

According to Jing et al. (2010), the management of the rhizosphere through the optimization of N forms and the P input could be useful to stimulate both root proliferation and the acidification process. Calcareous soils are characterized by high pH. Thus, plants grown in such kind of soils suffered often from low nutrient availability. There, phosphorus can be present as hydroxyapatite (HAP), a stable form of dicalcium phosphate (DCP), which can be dissolved rapidly as the soil pH decreases (Wang and Nancollas 2008). Such a finding suggests the importance of the rhizosphere acidification process as an efficient strategy for mobilizing soil P from calcareous soils (Shen et al. 2011). Consequently, to improve the productivity of such areas, an application of ammonium could be effective inasmuch as NH^+_4 induces an acidification of the rhizosphere doing so, the nutrients ready for root uptake especially in the case of phosphorus. It was found that the positive effect of localized NH_4^+ and P on plant growth is related to its role in lowering the pH rhizosphere due to the presence of ammonium and in increasing the acquisition of P by roots (Bloom et al. 2003; Miller and Cramer 2004; Jing et al. 2010). In maize, application of ammonium decreased the rhizosphere pH by 3 pH units indicating that the localized application of P combined with ammonium improves nutrient uptake due to the stimulation of the rhizosphere acidification (Jing et al. 2010).

The coculture of cereals and legumes assumed that this association was beneficial for a cereal P status because of the high aptitude of legume species to release a larger amount of protons as revealed by Tang et al. (1997) and Hinsinger et al. (2003). In a P-deficient intercropping system, P can be mobilized by legumes because these plants are able to acidify the rhizosphere due to their capacity to release protons and this occurred during P deficiency and N fixation (Li et al. 2007; Zhang et al. 2010). Because cereals are not very efficient in lowering the pH of the rhizosphere, an intercropped cereal/legume resulted in an intermediate pH (Cu et al. 2005; Li et al. 2008a, b). In fact, the form of N, ammonium (NH_4^+), nitrate (NO_3^-), or dinitrogen (N_2), and its uptake are known to induce several changes in the pH of the rhizosphere and therefore affect P availability for plants as shown by Hinsinger et al. (2003).

In flooded soils, among the successful processes used by plants to mobilize phosphorus, we cited the acidification of the rhizosphere (Saleque and Kirk 1995) which involved the oxygen released from roots that oxidizes Fe^{2+} to release two protons according to the reaction:

$$4Fe^{2+} + O_2 + 10H_2O \rightarrow 4Fe(OH)_3 + 8H^+$$

The inequality of the uptake of cation over anion, especially in the presence of $NH4^+$ ions in reduced soil, was shown by Begg et al. (1994). In this case, an important release of protons into the rhizosphere was noted.

2.3 *Iron (Fe)*

The acidification process is among the important mechanisms involved in Fe uptake by plants and characterized the Strategy I plants, especially, under the iron (Fe) deficiency. According to Liang et al. (2013), Fe acquisition in plants adopting Strategy I, is achieved by the combined functions of two components: the ferric chelate reductase and the proton-extruding H^+-ATPase. In fact, this class of plants includes dicotyledonous and nongraminous monocotyledons known by their ability to induce an active proton extrusion via the increase of H^+-ATPase activity in root plasmalemma leading to an acidification of the rhizosphere (Zocchi and Cocucci 1990). The decrease of the rhizosphere pH is a typical root response of dicotyledonous species under Fe deficiency conditions (Zocchi and Cocucci 1990; Donnini et al. 2009). Such a physiological response is adopted by many plant species. Peanut increases the acidification of the rhizosphere via the release of protons from the roots (Zuo et al. 2000, 2003). Lowering the rhizosphere pH is considered the most important component conferring a good adaptive response to Fe-deficiency in Strategy I plants (Santi et al. 2005). As reported by Schmidt et al. (2003), the density of the plasma membrane ATPase (PM H^+-ATPase) was twofold higher in Fe-deficient roots of tomato leading to a very low pH of the rhizosphere.

As for K^+ and phosphorus, the ability of plants to lower the pH of the nutrient solution is used as an important criterion to screen tolerant genotypes to Fe deficiency (Dell'Orto et al. 2000). Such findings are very well documented in many species such as peach (Molassiotis et al. 2006), kiwifruit (Rombolà et al. 2002), pea (Jellali et al. 2010), and medicago (M'sehli et al. 2011), and was observed for both glycophyte and halophyte species. A recent comprehensive study in a perennial halophyte *Suaeda fruticosa* revealed that this species has a great ability to acidify the external medium (Houmani et al. 2012, 2015).

The release of protons into the rhizosphere occurred via the activation of a plasma membrane proton pump (H^+-ATPase) which is stimulated under such conditions (Schmidt 2003; Dell'Orto et al. 2000). In poor Fe soils, and in order to increase Fe availability, Strategy I plants activate a series of plasma membrane proton pumps (H^+-ATPases) (Zocchi 2006; Kim and Guerinot 2007) resulting in the establishment

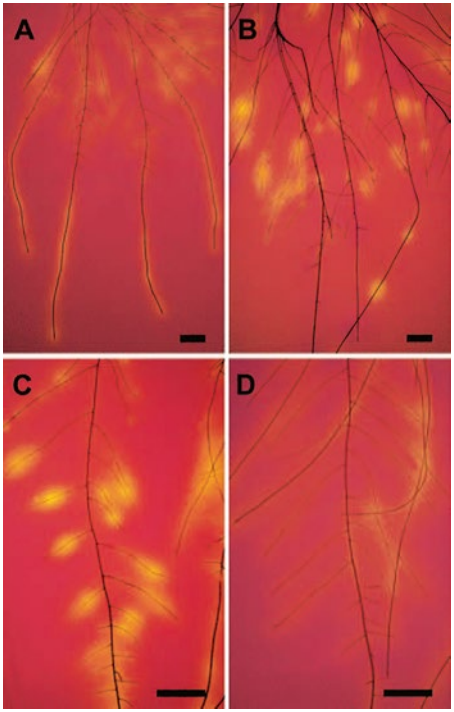

Fig. 2 Visualization of root medium acidification in Fe-sufficient (**a**), Fe-deficient (**b**) plants, and in roots using split-root system (plants grown in iron-containing medium) (**c**), or in Fe-free nutrient solution (**d**) using Bromcresol Purple as a pH indicator. The yellow color corresponds to high proton release (Schmidt et al. 2003)

of an electrochemical gradient (Palmgren 2001), and leading to an increase of ferric Fe solubility (Walker and Connolly 2008). Using immunolabeling methods, it was possible to detect the site of the H^+-ATPase enzyme at the deficient subapical root zones (Dell'Orto et al. 2002; Schmidt et al. 2003; Fig. 2). The activity of these pumps has been controlled genetically due to the transcriptional upregulation of a family of HA genes, which were identified by Dell'Orto et al. (2002) in Fe-deficient cucumber plants.

The H^+-ATPase activity is the key component of Strategy I plant responses to Fe shortage conditions. In fact, the differences in plant responses to Fe deficiency are particularly attributed to H^+ extrusion (Schmidt 1999) rather than to FC-R activity. Recently, Slatni et al. (2011) showed an increase of the H^+-ATPase activity under Fe starvation in nodules of common bean plants. The same authors have demonstrated that this H^+-ATPase protein was accumulated in Fe-deficient nodules of the *Flamingo common bean* variety and participated in the uptake of Fe by the nodules from the soil solution. It has been shown that high H^+ extrusion activity was positively correlated with a strong induction of PEPC activity in many plant species including *Phaseolus vulgaris* (Bienfait et al. 1989), *Capsicum annuum* (Landsberg 1986), and *Beta vulgaris* (Lopéz-Millán et al. 2000); by contrast, in plants with a low H^+-ATPase activity, PEPC activity was not induced under the same conditions (Zocchi et al. 2007; M'sehli et al. 2009).

3 New Advances in the Identification of H^+ATPases Using Molecular Tools

Plasma membrane H/Cation-ATPases are known as proton pumps localized in the plasma membrane of plants and are driven by the hydrolysis of ATP as a principal source of energy. H/C-ATPases play an important role in nutrient acquisition and translocation into the cell because they represent the major source of energy necessary for nutrient uptake and transport through the roots. This energy is generated by the extrusion of a positive charge across the plasma membrane. When protons are excreted into the external medium, an electrochemical gradient is established on either side of the membrane and cations can enter into the cell through the attraction due to the differences of charge and then are transported via different proteins.

Because of the recent progress in biotechnology, it is possible to provide new insights into the role of those H^+/Cation- ATPases using the plant model *Arabidopsis thaliana* and the new advances in genetic manipulation. In fact, by using reverse genetic methods, a complete H/Cation-ATPase gene family was identified in *Arabidopsis* giving us good information regarding genetic control of the activity of these pumps at the posttranslational level (Palmgren 2001). Several candidate H/Cation-ATPases localized at the root epidermal cells and root hairs were identified and were considered as the principal drivers for nutrient uptake from the soil to the roots (Palmgren 2001). Using the immunoblot technique, it was possible to detect high amounts of H/Cation-ATPase apart from the epidermal cells of roots (Parets-Soler et al. 1990; Jahn et al. 1998; Figs. 3 and 4). Such a localization suggests their role in the active loading of solutes into the xylem sap (Parets-Soler et al. 1990). As described by Oufattole et al. (2000), plant plasma membrane H^+-ATPases (PM H^+-ATPases) are encoded by a multigene family. Recently, 12 HC-ATPase genes were cloned in *Arabidopsis* (Palmgren 2001). In fact, it was shown that the activity of H^+-ATPase is upregulated by an H^+-ATPase AtAHA gene as pointed out by several biologists (Colangelo and Guerinot 2004; Walker and Connolly 2008; Buckhout et al. 2009; García et al. 2011). Recently, an H^+-ATPase (AHA) protein family was identified in *Arabidopsis* and was shown to be responsible for soil acidification (Ivanov et al. 2012). These data were confirmed using a mutant of AHA2 which lost its activity (Sussman 1994; Santi and Schmidt 2009). These authors demonstrated that the H^+-ATPase AHA_2 is responsible for the main acidification activity under iron deficiency conditions and the gene responsible for AHA_2 activity is regulated under these same conditions. A family of genes encoding H^+-ATPase proteins was also identified in cucumber H^+-ATPase [CsHA1; Santi et al. 2005; Santi and Schmidt 2008) and ($CsHA_2$ and $CsHA_3$; Młodzińska et al. 2010)], and are responsible for the rhizosphere acidification process. Using a semi-quantitative reverse transcriptase (RT)-PCR and quantitative real-time RT-PCR techniques, Santi et al. (2005) successfully identified two PM H+-ATPase cDNAs ($CsHA_1$ and $CsHA_2$) from Fe-deficient cucumber and found a high accumulation of CsHA1 gene transcripts in roots suggesting the genetic control of the pump proton activity under lowering Fe conditions. A new proteomic study identified a root V-ATPase implicated in the

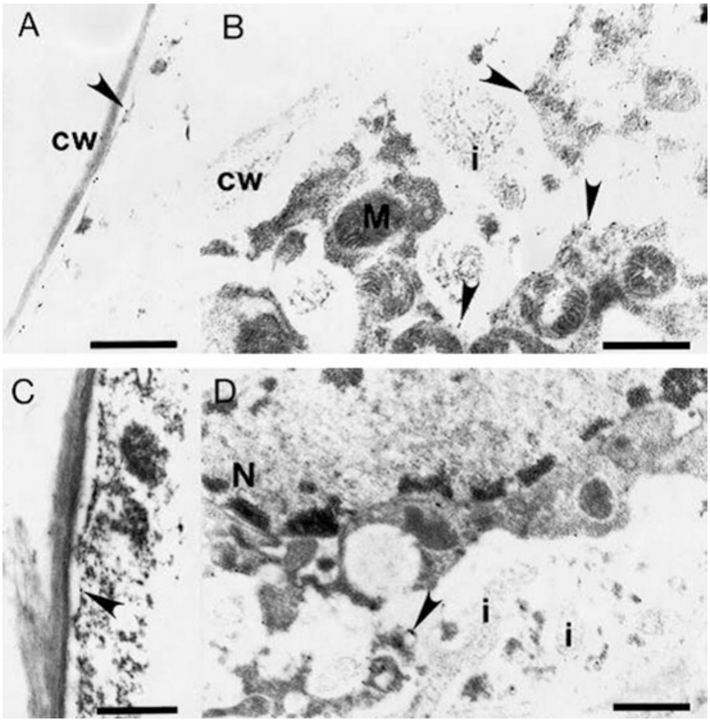

Fig. 3 Immunocytolocalization of plasma membrane H⁺-ATPase in epidermal cells of tomato roots. (**a**) Rhizodermal cell of Fe-sufficient tomato plant. (**b**) Wall ingrowths of Fe-deficient root transfer cell. (**c**) Control root section treated only with a secondary antibody: a goat antimouse IgG, dilution 1 :50. (**d**) Secondary wall ingrowths induced by exogenous application of 2,4-D. CW: cell wall; M: mitochondria; N: nucleus; I: invagination. (Schmidt et al. 2003)

responses of plants to Fe deficiency (Wang and Wu 2010; Lan et al. 2011). This protein was found to provide the necessary acidification for the induction of some physiological responses under Fe limitation conditions especially cell elongation and new root development.

4 Effect of Salinity on Rhizosphere Acidification

Salinity is a major constraint affecting plant growth and productivity (Hakeem et al. 2012, 2013). In general, saline soils are generally characterized by the predominance of salt toxic ions (mainly Na^+ and Cl^-) and by their low nutrient availability (Inal and Gunes 2008). This situation is probably attributed to the effect of salt ions on the H^+-ATPases and resulting in an inhibition of rhizosphere acidification. Rhizosphere acidification is a central mechanism by which plants can take mineral nutrients from the soil solution. Nevertheless, the activity of these pumps is

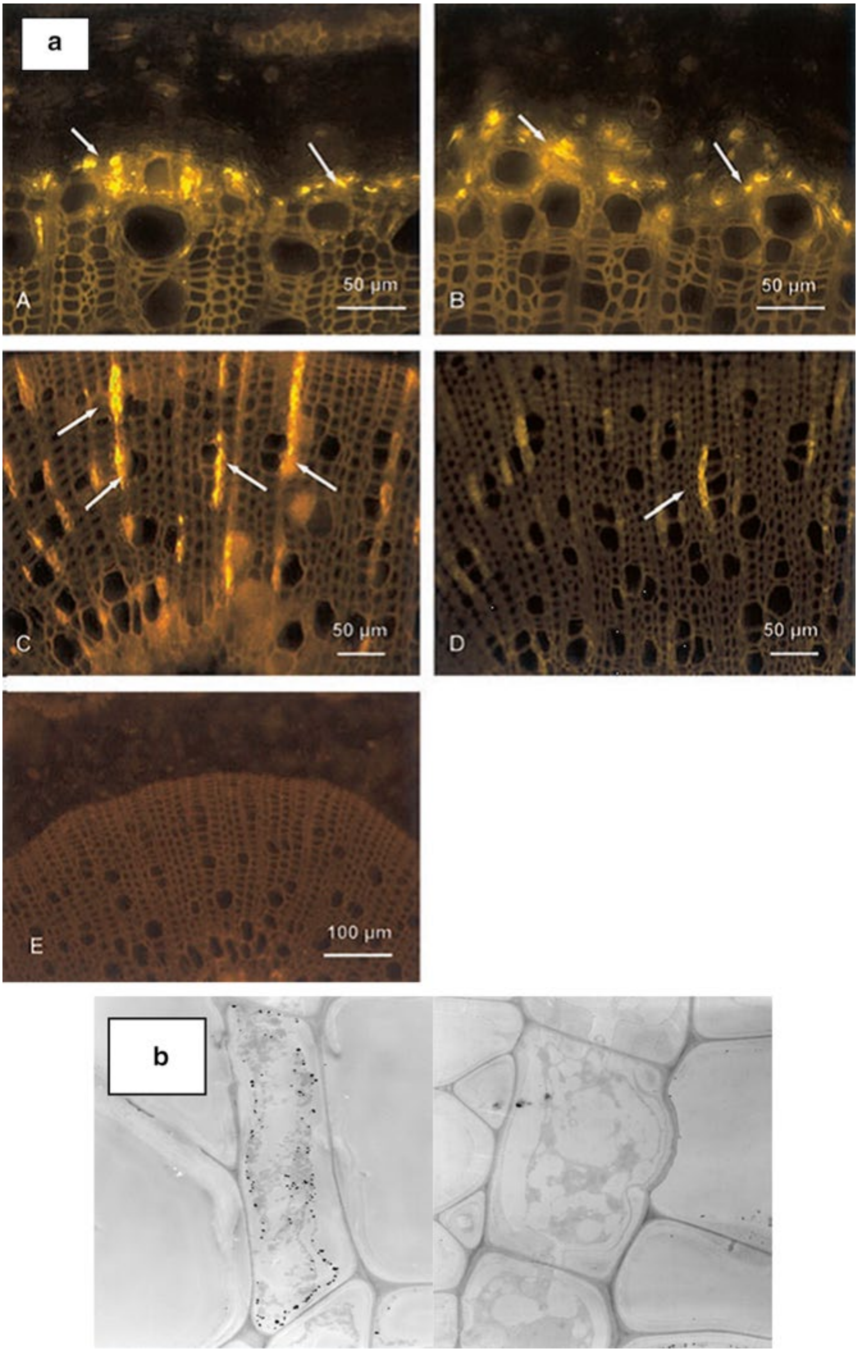

Fig. 4 (**A**) Localization of PM H⁺-ATPases in poplar stems using the monoclonal antibody 46 E5 B11 in plants. Similar labeling with low (**a**) or high K⁺ supply (**b**). (**B**) Cellular localization of PM H⁺-ATPases using the monoclonal antibody 46 E5 B11. (Arend et al. 2004)

dependent on the soil structure and properties. In fact, salinity can negatively affect the H^+ATPase function and lead to an inhibition of the proton release and consequently inhibit nutrient uptake by plants. It was demonstrated that a moderate salt stress inhibited the rhizosphere acidification of many glycophyte species. For *Medicago ciliaris*, the application of 75 mM NaCl reduced the activity of PM H^+-ATPase, resulting in a reduction of Fe uptake by this species (Rabhi et al. 2007; M'sehli et al. 2011). The study on some nutrient deficiency in halophytes, plants adapted to extreme environmental conditions, revealed that such kind of vegetation is able to maintain the uptake of nutrients from soil with high salinity levels. This behavior was proved under nutrient deficiency. A recent study (Houmani et al. 2015) of the halophyte *Suaeda fruticosa* under the combined effect of salt stress and iron deficiency showed that this species was able to maintain its acidification capacity under high salinity levels to maintain the uptake of this element of the external medium.

5 Conclusion

Rhizosphere acidification is an important natural process for nutrient uptake by plants. The liberation of the proton is in favor of the uptake of one cation. The proton release is essential for driving the transport of nutrients into the roots. This phenomenon is complex and is due to very consistent powerhouses, the H^+-ATPases that function to assure an adequate nutrient supply for plants. The use of the new advances in genetic research gives new insights in the role of such proton pumps in mineral uptake and translocation from the rhizosphere into the roots. The role of H^+-ATPases in higher plant nutrition was well demonstrated under limiting conditions of deficiency in several essential elements such as potassium, phosphorus, and iron.

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Effect of Industrial Pollution on Crop Productivity

Muhammad Ali Abbas, Hira Iftikhar, and Alvina Gul

Abstract Industrial effluents are a major health concern for all living matter on Earth. The components of these effluents are adversely affecting the environment, causing an imbalance in nature and as a result, in the natural processes going on in the ecosystems. When disturbed, the balance among these ecosystems causes the living organisms in it to adapt to these changes by acting out alternately at various metabolic and biochemical levels. Plants being the foundation of the food chain, and not being able to move, are the major concern at this point in as much as they uptake the harmful substances from the environment and accumulate them in their system, affecting their own health as well the health of all the consumers directly or indirectly depending on them for their food. Several crop plants cultivated as a major food source for humans worldwide need to be paid attention for adverse effects on developmental processes and yield as the agricultural soils are irrigated by water polluted with industrial wastes. As the title indicates, in this chapter we are concerned with the types of substances industrial wastes can contain, their uptake by the plant influencing the uptake, transfer, and movement of other nutrients, and the effect they cause on the growth and biomass of crop plants.

Keywords Industrial pollution • Crop productivity • Heavy metals • Ammonia

1 Introduction

Any product or by-product that is due to an industrial activity and is useless turns out to be industrial waste. It includes all the products that are useless and may harm the environment on an individual or global level. For example, burning of woods or coal for cooking purposes at restaurants may produce CO (carbon monoxide; Anne Elizabeth 2010). A few of the industrial wastes are paper products, sandpaper, metals, paints, chemical solvents, radioactive wastes, and other industrial by-products.

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Table 1 Permissible limits of various elements in industrial pollutants for soils of crop fields; typical concentrations of these elements in soil and crops under normal conditions (European Union 2002; Allaway 1968)

Element	Safe limit (μg/g)	Soil concentration (ppm d.wt)	Concentration in crops (ppm d.wt)
Cu	140	2–100	4–15 2.5 mg/kg (WHO/FAO)
Fe	—	7000–55,000	400–500 mg/kg (WHO/FAO)
Zn	300	10–300	15–200 20–100 mg/kg (WHO/FAO)
Mn	—	100–4000	15–100
Ni	75	10–00	1.0 0.02–50 (WHO/FAO)
Co	—	1–40	0.05–0.5
Pb	300	2–200	0.1–10 0.05–30 mg/kg (WHO/FAO)
Cd	3	0.01–0.7	0.2–0.8 <2.4 mg/kg (WHO/FAO)
Cr	150	5–3000	0.2–1.0

Carbonates, bicarbonates, municipal solid waste, industrial solid waste, toxic waste, chemical waste, heavy metals, and surfactants, all come under the umbrella of industrial wastes and contribute to environmental pollution and the hazards caused as a result. Now there are laws and authorities who regulate these laws to treat the wastewater that before dumping should be tested for the amount of harmful wastes. Certain limits have been defined for the pollutants having adverse effects on the environment. These limits, known as permissible limits (Table 1), define the safety range in which the pollutant isn't lethal or highly toxic to the environment and the living organisms residing in it.

Soil consists of various compositions of naturally occurring elements. These elements, including carbon, hydrogen, oxygen, nitrogen, phosphorus, potassium, calcium, and chlorine, among others, are the basis of the life form being the major constituents of the molecules that build up macromolecules including DNA and proteins. These are taken up by the plant from the soil it inhabits as vital nutrients for its growth, development, and flourishing. Since their identification, different studies have been carried out on the requirement and functions of these nutrients within the plant. As excess of everything is bad, similar is the case with mineral nutrients in the soil; excessive amounts of these nutrients pose danger to the survival and well-being of the plant. In excessive amounts, they can cause nutrient imbalance, disturbance in uptake by roots, altered translocation patterns, changes in enzymatic activity, affected growth rates and patterns, various visually noticeable symptoms, and reductions in overall yield of the plant. In this chapter, we are mostly concerned with the metals released into the environment in industrial wastes and their effects, mainly harmful, on the productivity of crops.

In nature, many metals exist in their different physicochemical forms. Metal ions with water molecules attached are believed to be very toxic. Metallic ions that are commonly presumed to be less toxic, are strong complexes and species associated with colloidal particles. Tin, mercury, and lead in their organometallic forms have higher toxicity compared to the imitating inorganic species.

The enrichment of soil with metals and heavy metals is a result of elevated industrial emission of pollutants and discharge, sewage wastewater, mining, and the heavy and uncontrolled use of fertilizers (Arora et al. 2008; Wuana and Okieimen 2011). In the case of enrichment of agricultural land, the food crops grown on it uptake and accumulate high levels of these pollutants in their tissues from where they are introduced into the food chain because plants form its base (Wuana and Okieimen 2011). Although some of these elements are helpful in plant growth, they become toxic at higher levels and have a negative impact on plant growth and yield. From plants, they are easily transferred to any animals or humans that consume them as food and hence they start to accumulate in the food chain, rendering an imbalance and causing unexpected circumstances.

2 Industrial Pollutants

Industrial waste, containing toxic material, released into the environment is a major concern for plant growth and health. This waste contains several different types of elements and compounds that may affect the crops in different ways. Depending upon the type of crop and its characteristics, the effect may either be harmful or beneficial. Either way, these elements start accumulating in the plant with a definite impact on its metabolic pathways and processes, leading to differential growth and development. The pollutants may vary in the nature of their effect depending on their type; these include inorganic as well as organic compounds, nonmetals, metals, metalloids as well as heavy metals, and nanoparticles, among others. Some of the elements discussed in this chapter are essential nutrients, macro and micro, and trace elements at optimal level; however, as their concentration in the soil rises to a certain level, the same elements become toxic to the plant.

Industries may discharge their waste as effluents into water bodies or into the atmosphere while several industrial processes are carried out. Thus these pollutants might get into the plant by uptake from soil affecting the plant or the atmospheric pollutants may have a foliar effect on various crop plants. In this chapter, we adhere to the inorganic pollutant uptake from the soil by the plant.

The release of various types of pollutants from different industries is interlinked and some of the common industries and the kind of pollutants they discharge into the environment are shown in Fig. 1. These include the dyes and pigment industry releasing arsenic, aluminum, iron, cadmium, copper, and lead; the textile industry releasing aluminum, arsenic, iron, nickel, copper, mercury, and cadmium; the chemical industry releasing arsenic, silver, gold, zinc, chloride, aluminum, chromium, lead, cadmium, copper, mercury, and iron; tanneries releasing zinc, arsenic, aluminum,

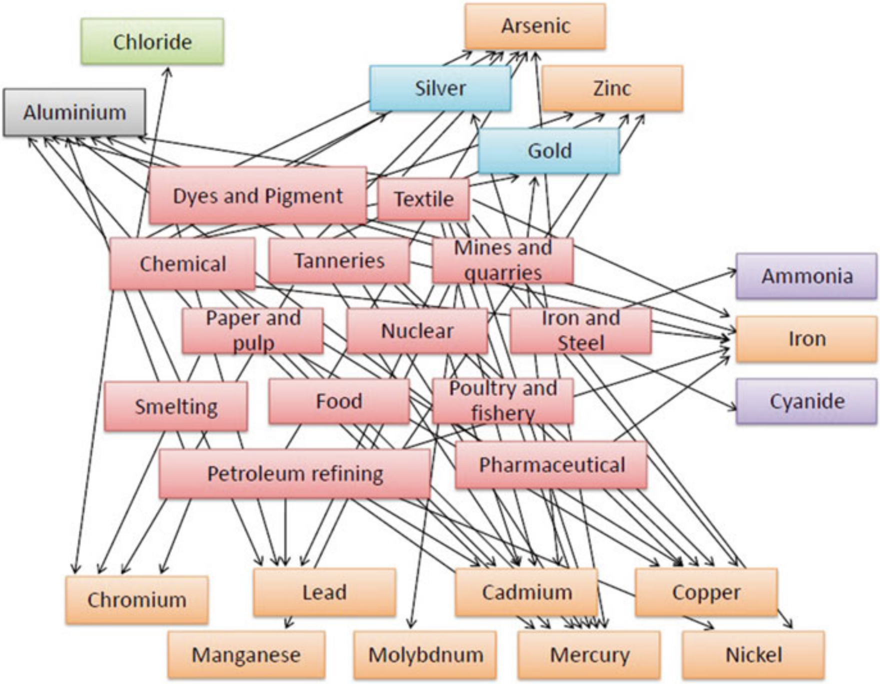

Fig. 1 Types of industries and most common elements released by them as pollutants. *Pink*, industries; *orange*, heavy metals; *purple*, inorganic compounds; *cyan*, metals/nanoparticles; *grey*, metals; *green*, nonmetals

iron, chromium, copper, and mercury; mines and quarries releasing aluminum, silver, gold, zinc, arsenic, mercury, cadmium, molybdenum, lead, and manganese; the paper and pulp industry releasing aluminum, chromium, copper, and mercury; the nuclear industry releasing cadmium; the iron and steel industry releasing ammonia and cyanide; the petroleum refining industry releasing aluminum, arsenic, zinc, iron, chromium, lead, mercury, cadmium, and nickel; and the pharmaceutical industry releasing aluminum, iron, and copper.

The effect of these pollutants in crop plants is described here with some examples focusing more on the harm caused by them.

3 Effect on Crop Productivity of Various Pollutants

Crop productivity is the growth of the cultivated crop plant achieved after it has reached its full grown state. In addition to the seed quality and genetic characteristics of the crop, its productivity depends on several environmental factors. The soil

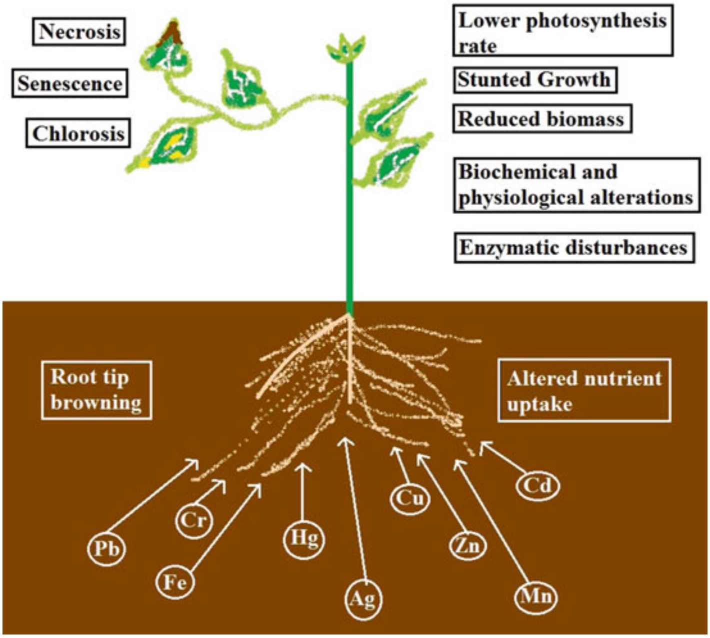

Fig. 2 Major types of effects on plants caused by industrial pollutant uptake from soil

composition of the field in which the crop is cultivated contributes a great deal to the proper growth of the plant. This composition varies from field to field and changes with natural processes, ecosystem composition, crop cultivation, and so on. The dumping of industrial waste near agricultural land contributes to drastic shifts in soil composition and balance from the original.

As described earlier in the chapter, the composition of industrial pollutants varies widely and ranges from simple elements such as metals and heavy metals to inorganic compounds to complex organic compounds. These cause a wide range of effects on the plants and are overviewed in Fig. 2. These effects include, but are not limited to, reduced growth, lowered levels of photosynthetic rates, biomass reductions, altered biochemical and metabolic pathways, different enzymatic compositions, silencing of some genes and overexpression of some others, reduced chlorophyll levels, visual symptoms including chlorosis, necrosis, root browning, wilting, senescence, and plant death.

Various crops follow different nutrient uptake patterns according to their needs and genetic makeup. Disturbances in the soil composition also cause adverse alterations in these patterns. Once taken up from the roots, the nutrients are stored there, according to the requirements, and then translocated farther upwards to various plant parts as per need. Roots release various exudates and other secretions to create charges and attract the required nutrients near roots. The uptake occurs at the exchange sites, however, the rise in levels of certain nutrients that are more reactive than others make them able to replace the less reactive ones from the exchange sites. These elements are then taken up by the plant in larger amounts, despite being needed just as trace elements. Increase in uptake rates leads to accumulation and alterations in the normal processes in the plant.

Various nutrients under the categories of inorganic compounds, metals, metalloids, and heavy metals are described here with the effect of their toxicity in crop plants and their production patterns.

3.1 Inorganic Compounds

Inorganic compounds, naturally occurring in the environment as well as synthesized or released due to industrial activities, are a main cause of nutrition imbalance for plants growing in soil affected by the wastes. This group ranges from simple compounds such as oxides of carbon in the air with foliar effects on plants to more complex inorganic compounds, even toxins in the soil causing toxicity in the rhizosphere of the plant and accumulating in the plant parts, adversely affecting its growth and development.

Salt pollution caused as a result of higher salt concentrations in agricultural soil causes salinity which is a major addressed problem for crop productivity. High salt concentrations in the soil cause salinity and sodicity leading to a harmful impact on plant growth as well as yield, such as in wheat (Nuttall et al. 2003). However, we do not discuss the effects of salinity in this chapter as there is vast information on it and there are plenty of examples from which a whole new chapter can be formulated on the consequences of salinity on crop productivity. Ammonia and cyanide are the major concern from industrial pollutants, but we just stick to ammonia in this chapter.

3.1.1 Ammonia

Ammonium and nitrate, as nitrogen sources together, help in improving the growth of the plants; however, independently neither can cause this growth enhancement effect (Haynes and Goh 1978; Cox and Reisenauer 1973). Nitrogen being among the most important mineral nutrients for the plant, small quantities of ammonia as basic sources of nitrogen availability to the plant are beneficial for its growth and have a positive impact on the health of the plant; yield and flavor are known to be enhanced in fruits by relatively small amounts of ammonia (Siddiqi et al. 2002). In the presence of ammonia, the growth of tomato seedlings becomes restricted and limited. Ammonia disturbs ion uptake balance by the roots leading to retarded root and shoot growth eventually leading to growth inhibition due to the acidity of the external environment as cation uptake rises (Raven and Smith 1976; Magalhäes and Huber 1989).

The uptake pattern of certain essential nutrients is known to be affected by the presence of ammonia, and with increases in its concentration, this pattern appears to have drastic effects on mineral nutrient uptake of the plants grown in that contaminated soil. Ca, Mg, and K uptake decrease significantly in tomatoes when ammonia is the only N source (Siddiqi et al. 2002).

Ammonia concentrations higher than normal cause ammonia accumulation in certain crop plants without affecting growth and development, for example, rice and spruce (Wang et al. 1993; Kronzucker et al. 1998). However, it is reported to accumulate more in tomato which is known to be a lot more sensitive to ammonia and hence is affected by higher ammonia concentrations (Britto et al. 2001). High ammonia levels are also known to result in Ca deficiency leading to a significant yield reduction (Siddiqi et al. 2002).

High ammonia levels in constructing wetlands threaten and inhibit plant growth (Surrency 1993). Many types of plants have been studied and are known to be affected by ammonia toxicity caused as a result of various concentrations (Hageman 1984; Wang 1991; Dijk and Eck 1995; Magalhães et al. 1995)

Growth of common cattail and Indian potato noticeably reduces along with a significant reduction in total biomass at ammonia levels higher than 200 mg per liter (Clarke and Baldwin 2002).

3.2 Metalloids

Metalloids are a group of elements that can act both as metals as well as nonmetals depending upon their properties and associations. Among metalloids, arsenic is the most important element affecting various plant activities, most importantly nutrient uptake.

3.2.1 Arsenic

Arsenic is a metalloid that, when discharged into the environment, produces toxicity of utmost concern (American Agency for Toxic substances and Disease Registry (ATSDR), 2007; Tu and Ma 2003; Hasanuzzaman et al. 2014). In some environments, it is present in high values that can be very toxic to all levels of life. As (V) and As (III) are found to be a predominant inorganic form of the arsenic.(Tripathi et al. 2007). As III and AsV, depending on the redox conditions, are known to interconvert. They also exert numerous toxicity effects on plant health. (Carbonell-Barrachina et al. 1998; Marin et al. 1992).

As can enter aquatic as well as terrestrial environments via anthropogenic activities alongside natural formations (Tu and Ma 2003). Plants mainly take up arsenic in the former form, that is, AS (V), which causes a lot of stress including growth suppression (Stoeva et al. 2003) and deformed body (Stoeva et al. 2005) and can be fatal. Under greenhouse conditions phytotoxicity of As has also been reported; As when in excess produces stresses such as reduction in plant height, stem length, suppression of seed germination, decrease in shoot growth, wilting of leaf, necrosis of leaf blades, and lower fruit and grain yield (Liu et al. 2005; Abedin and Meharg 2002; Burló et al. 1999). This is because of the similarity of the phosphorus to the arsenic, and the system flaws due to which it is taken up by the plant (Meharg and Macnair 1992). Research has shown that it resembles the phosphorus analogues which are transported by the phosphorus transporters to the cell plasma. (Stoeva and Bineva 2003). As and P have analogous activities exhibiting comparable physicochemical behavior in soil and they tend to compete in soil particle surfaces for the sorption sites (Hingston et al. 1971). Research has shown the evidence for P nutrition to be closely related to As sensitivity in plants, and P fertilizers, when applied, raise soil availability of As and enrich As uptake in plants (Pigna et al. 2010; Wang and Duan 2009; Geng et al. 2006). On the other hand, availability of P can also be affected by AS concentration in different soil. It is a big concern that when P is applied at a normal pace the effects of different As concentrations in the ground for the increase of plants is investigated. After getting into the cell plasma, it interferes with the metabolic pathways; moreover, it is rarely seen that the As (v) reduces to As (III). (Stoeva et al. 2003; Meharg and Hartley-Whitaker 2002;). As (III) inhibits cellular function even causing death by inhibiting, combining with sulfhydryl groups and inhibiting cellular enzyme and tissue proteins. (Ullrich-Eberius et al. 1989). Also, there is sufficient evidence that plants, when exposed to an inorganic form of As, although As is not a redox metal, result in the generation of reactive oxygen.

Most importantly the potential uptake by food crop plants and transfer of soil As into them is hazardous to not only humans, but to other consumers too. Many cases have shown clear evidence of arsenic-related toxicity that can be related to the uptake of As by the food crop and later by the humans who mainly consume them. The nature of As in water stored underground from Asian countries is essentially inorganic and several investigators have shown the presence of equal quantities of As III and AsV species (Samanta et al. 1999). The presence of As in soil and the effects of toxicity to plants and animals are major concerns. It can cause skin, bladder, lung, and prostate cancer if exposed to long term at low concentrations. Other than cancer, it can cause cardiovascular disease, diabetes, and anemia at low-level exposure (Zhang et al. 2002).

Many developing countries such as China are now taking steps and have great concern controlling environmentally hazardous compounds. There was an epidemic that caused 40 ha of agricultural soil polluted in Hunan province due to irrigation of As-contaminated water by local farmers (Liao et al. 2004). Now there are standards by which the government regulates agricultural activity in the areas where they suspect As in soil. For instance, if soil arsenic concentrations exceed the limit of 40 mg/kg, the area is banned for agriculture purposes. The Chinese government, in 2005, constituted the maximum limitations of inorganic arsenic in some crop products as less than 0.2 mg/kg, although some heavy metals concentrations in soil exceeded the limitations.

The main winter crops in Asian countries are winter wheat and rape. In the grains of these two crops or the stalk which is employed as cattle feed, high arsenic concentrations in land or water may contribute to elevated As accumulation. The permissible level of the inorganic form of As intake from all external sources, including water and food is 15 μg/kg body mass (WHO 1989). Therefore the evaluation of the potential health hazard to humans or animals through the consumption of crop plants that have been grown under high As levels in soils is urgently called for.

3.3 Metals

Metals play an important role as part of the nutrients required by the plant for normal biochemical functioning of the metabolic pathways. Some, in their ionic form, play roles in ion flux and maintaining the balance of nutrients across the membranes. Imbalance of nutrients is caused by improper functioning as a result of disturbed levels in the plants.

3.3.1 Aluminum

Being among the most abundant metals on earth, Al comprises approximately 7 % of the Earth's crust. It is highly toxic for plants and causes considerable harmful effects on plant growth and yield. However, its presence in the form of precipitates or complexes with silicates or aluminosilicates isn't toxic to the plants. Under acidic conditions, it gets solubilized and hence crop growth depends on soil acidity as it's a limiting factor. That is why it is commonly linked to higher grades of aluminum.

Soil pH is maintained by the balance among cations and anions. This balance, however, can be disturbed as a result of various natural factors, including acid rain that can bring down acidic molecules from the atmosphere to the soil and leaching down of basic cations that proceeds steadily and can be enhanced depending upon various farming procedures in the crop fields (Kennedy 1986).

Root growth in maize gets completely inhibited as its apex comes in contact with the Al toxic region in soil (Ryan et al. 1993). Initially, root growth is inhibited by aluminum concentration, which results in lower consumption of water and nutrients and lower exploration of bulk soil. Nitrogen fixing may be seriously affected by Al toxic in the subsoil mainly for leguminous plants. At toxic levels, Al is known to alter other minerals' uptake and translocation in plants such as that of calcium by significantly lowering its uptake from soil (Huang et al. 1992; Rengel 1992). In a nutshell, these results may decrease carbon separation, biomass formation, and erosion and protect soil against elevated temperature, nitrogen incorporation (Debarba and Amado 1997), and weed control, and the addition of organic carbon to the soil.

3.4 Heavy Metals

Heavy metal refers to a group of elements that may be metallic in nature with a high density. These are naturally found in the environment but industrial activities have resulted in an increase in the levels of these heavy metals. As a result of higher levels, they are disturbing the natural processes in the ecosystem. For plants, some of these are essential micronutrients and trace elements as part of vital molecules whereas others are nonessential. The nonessential ones are more toxic to the plants especially in higher concentrations causing toxicity conditions. These include lead (Pb), mercury (Hg), and silver (Ag) (Nieboer and Richardson 1980).

The essential elements among the heavy metals, necessary for the plant in trace amounts as micronutrients, include copper (Cu), iron (Fe), zinc (Zn), manganese (Mn), nickel (Ni), cobalt (Co), and molybdenum (Mo) (Wintz et al. 2002; Reeves and Baker 2000). The effect of these on crop productivity is discussed here in detail.

3.4.1 Copper (Cu)

An essential micronutrient for the plant, Cu functions in assimilating carbon dioxide, being a part of proteins involved in the electron transport chain of respiration as well as photosynthesis and in turn ATP synthesis (Demirevska-kepova et al. 2004).

Mining and smelting of Cu ores results in excessive Cu in soil, affecting plant growth and productivity. High Cu concentrations represent stress conditions for the plant causing chlorosis on leaves and a decrease in plant growth (Lewis et al. 2001). Cu toxicity has been reported to have a highly negative impact on the growth of cauliflower, accompanied by severe chlorosis in young leaves of the plant (Chatterjee and Chatterjee 2000). Reductions in chlorophyll content are a result of disturbed electron transport during photosynthesis and degradation of the thylakoid membranes under high Cu concentrations (Bohner et al. 1980; Sandmann and Boger 1980).

The plant roots take up Cu in ionic as well as chelated forms from the soil. Due to its high reactivity and bonding with the exchange sites at roots, it is known to displace a variety of ions occupying the free spaces in the root regions. As a result of this activity, its concentration in the root regions rises up significantly as compared to other parts (Mengel and Kirkby 1987).

Oxidative stress in plants resulting in the formation of reactive oxygen species occurs as a result of Cd toxicity (Stadtman and Oliver 1991) causing alteration in metabolic pathways (Hegedus et al. 2001). Higher Cu concentrations affect plant growth by altering the Cd movement and levels in cucumber (Moreno-Caselles et al. 2000) and Indian mustard (Singh and Tewari 2003). Cu toxicity causes harmful effects on plant growth starting from germination of seed, length of the seedling, and amount of lateral roots, for example, in aubergine (Neelima and Reddy 2002). Higher Cu concentrations cause significant biomass reduction in cauliflower along with disturbances in the metabolism of nitrogen within the plant (Chatterjee and Chatterjee 2000). At enzymatic levels, Cu toxicity has inhibitory effects on the activity of catalase in barley and cauliflower (Chatterjee and Chatterjee 2000; Agarwala et al. 1977).

3.4.2 Iron (Fe)

Iron is a vital constituent of many important proteins in the plant involved in some crucial processes such as photosynthesis, which is responsible for all food produced, and the major constituents of the photosynthetic system such as the chlorophyll and the chloroplast (Marschner 1995). For optimum growth of the plant, it requires an adequate amount of Fe being available to the plant constantly at all times (Wiersma 2005).

Its presence and availability in the soil is due to the presence of its ionic as well as chelated forms, however, higher concentrations sometimes lead to stressful circumstances leading to phytotoxicity in the plants grown in that soil. A large amount of Fe^{2+} is absorbed and taken up via plant roots when its concentration in the soil rises to toxic levels, causing Fe toxicity, mainly translocating it to leaves and causing damage to various plant parts at the cellular and genomic level (de Dorlodot et al. 2005; Arora et al. 2002).

Reduction in photosynthesis rates leading to a huge reduction in crop yield as a result of Fe toxicity is known to occur in several crops including soybean and canola. This is because of the inhibitory effects of the toxic conditions on chlorophyll. Induction of oxidative stress is also a common cause of Fe toxicity leading to production of several reactive oxygen species and other responses in the plant body (Sinha et al. 1997).

Fe accumulates in leaves of rice plants and causes disturbances in the normal occurrences leading to toxic conditions; this follows as a result of higher concentrations of Fe(II) in the field (Ponnamperuma et al. 1955). Higher Fe concentration leads to unbalanced nutrient uptake, especially affecting macronutrients such as potassium and phosphorus (Olaleye et al. 2001; Yoshida 1981).

Browning of leaves and roots occurs under such conditions, leaves dry out, and root growth is stunted (Sarwani et al. 1995; Jugsujinda and Patrick 1993; Yoshida 1981; Ponnamperuma et al. 1955). With a rise in the toxicity level and based on the resistance ability, yield of the rice crop reduces to about 12–100 % (Sahrawat et al. 2000; Abifarin 1988). Cultivars of rice that can resist Fe toxicity conditions have also been reported which can be grown under such conditions to avoid the adverse effects caused by the toxic conditions (Sahrawat and Sika 2002; Abifarin 1988).

3.4.3 Zinc (Zn)

Various metabolic pathways are dependent on different nutrients that the plant uptakes from various sources; zinc is one of the essential micronutrients required in the normal functioning of various metabolic processes in plants. It is a structural part of several enzymes and transcription factors, and also acts as a cofactor for enzymes such as peroxidase, dehydrogenase, oxidase, and anhydrase. It's very well known to regulate nitrogen as well as photosynthesis (Swietlik 1999; Marschner 1995).

However, an increase in its concentration up to 150–300 mg/kg (Warne et al. 2008; Devries et al. 2002) and uptake by the plant results in phytotoxicity events that can be overviewed due to the physical effects. This results in noticeably lowered or inhibited metabolism resulting in reduced growth and development in several species including the common bean (Cakmak and Marshner 1993) and mustard (Prasad et al. 1999), along with oxidative damage triggered by an increase in zinc or cadmium concentration. Senescence may also result depending upon metal concentration in the contaminated soil.

In abnormal concentrations, Zn and Cd can cause abrupt changes in enzymatic activities and their efficiency to catalyze associated pathways in bean (Somasekharaiah et al. 1992; Van Assche et al. 1988) and pea plants (Romero-Puertas et al. 2004).

Root growth as well as shoot growth has been shown in various studies to be limited in higher Zn concentrations (Fontes and Cox 1998; Ebbs and Kochian 1997; Choi et al. 1996). Leaf chlorosis may result in young leaves and extend to the older ones in the case of long-term exposure to excessive Zn (Ebbs and Kochian 1997).

High Zn concentration also results in a competitive micronutrient transfer to upper plant parts; a high Zn level causes difficulty for Mn and Cu in moving from the roots towards the shoots causing their deficiency in the shoot region and accumulation in the root region (Ebbs and Kochian 1997), disturbing the metabolic processes. Apart from the micronutrients Mn and Cu, the macronutrient P's transport has also been shown to be hindered producing reddish-purple leaf color representing a P deficiency in the plant leaf (Lee et al. 1996).

3.4.4 Manganese (Mn)

Mn has an important role in functionality of several enzymes. It also has an important role in photosynthesis and as part of the chloroplasts. Mn is basically an important nutrient for better growth of the plant (Marschner 1995; Burnell 1988). Despite its essentiality, higher concentrations of Mn compromise plant health and growth.

Photosynthesis has been observed to slow down as a result of high Mn concentrations (Kitao et al. 1997a, b). Chlorophyll synthesis gets affected due to alterations in certain vital processes (Clarimont et al. 1986). Rice accumulates Mn in its chloroplasts (Lidon et al. 2004; González and Lynch 1999) and common bean shows decreased chlorophyll levels and activity (González and Lynch 1997, 1999; Gonzalez et al. 1998). Tobacco and wheat have also been known for these effects under Mn toxicity; chlorophyll decreases significantly in wheat and its activity falls down in tobacco under such conditions (Moroni et al. 1991; Houtz et al. 1988; Nable et al. 1988).

Mn toxicity may block the availability of certain nutrients such as Fe due to its antagonistic effects on it, which is also a cause of chlorosis in such plants as a result of insufficient uptake of Fe by the plants (Lidon 2002; Horst 1988a, b). This is because Fe and Mn share the same exchange or translocation sites and thus compete for these sites. At higher Mn concentrations, it is able to occupy these sites to enhance its uptake inhibiting Fe uptake by the plant (Alam et al. 2000).

Higher Mn concentrations than normal cause necrosis in the aerial parts of the plants (Wu 1994) leading to browning of the leaves and ultimately the leaf dies (Elamin and Wilcox 1986a, b), such as in cucumber (Crawford et al. 1989). Browning of roots and leaves may also be caused during Mn toxicity: in leaves it causes chlorosis, whereas in roots it causes cracking (Foy et al. 1995; Le Bot et al. 1990; Bachman and Miller 1995; Wu 1994). Chlorosis and necrosis of leaves is also an effect of toxicity caused at higher Mn concentrations in cowpea and common bean, due to its oxidation in the epidermal cell wall (Wissemeier and Horst 1992; Horst and Marschner 1987; Horst 1982).

Enzymatically, the plant generates peroxidase as a result of induction of oxidative stress in response to Mn toxicity (Fecht-Christoffers et al. 2003).

3.4.5 Nickel (Ni)

Ni is another micronutrient acting as a structural part of enzymes such as urease helping in normal functionality. It plays a redundant role as cofactor in some enzymes replacing Zn and Fe. Ni is a trace element; however, its concentration has been rising because of industrial activities releasing pollutants into the ecosystems, that include but aren't limited to mining, smelting, and even fertilizers (Gimeno-Garcia et al. 1996).

Toxic levels of Ni in the soil can lead to severe alterations in metabolic activity of the plant, stunted growth, and ultimately reduced yield. Chlorosis is an aftereffect of high Ni concentrations and uptake by the plant (Yang et al. 1996b). Certain vegetables are known to uptake and accumulate Ni in their leaves (Sharma and Kansal 1986).

Ni toxicity caused by abnormally high levels of Ni^{2+} causes a wide variety of physiological changes that lead to abnormal physical appearances such as chlorosis and necrosis in crops such as rice (Rahman et al. 2005; Pandey and Sharma 2002; Zornoza et al. 1999; Das et al. 1997; Sabir et al. 2014). Ni toxicity is also known to affect nutrient uptake activities of the plants. With an increase in concentrations of Ni, Fe has a direct relation and increases in shoots and roots of fenugreek, whereas the opposite occurs for Zn and Cu at both sites (Parida et al. 2003) due to the competition among them for exchange sites at the roots for uptake by the plant (Narwal et al. 1994; Cataldo et al. 1978). The direct uptake relation of Ni with Fe is also known for maize plant.

Under high concentrations, Ni gets accumulated in the roots as well as shoots of the plants, for example, fenugreek (Parida et al. 2003), spinach, mustard, and chickpea (Gupta et al. 1996; Wadhawan 1995).

Shoots of crops are affected at the enzymatic levels, for example, H-ATPase in the plasma membrane of rice (Ros et al. 1992). Ni toxicity can be observed as lowered water uptake in the plants which has been studied in angiospermic species, both monocots and dicots (Gajewska et al. 2006; Pandey and Sharma 2002).

Ni toxicity is also known to cause metabolic disturbances in wheat (Pandolfini et al. 1992) and other plants depending on their sensitivity to stress and the conditions (Gonnelli et al. 2001).

3.4.6 Cobalt (Co)

Higher concentrations of Co are found in many types of soils including calcareous and acidic soils. Industrial areas including industries set up for refining metal have higher Co concentrations than normal in their surrounding regions due to their effluents being released into the environment (Freedman and Hutchinson 1981; Barceloux 1999).

Co is important as part of the vitamin B12 complex. It has an important role in the symbiosis of leguminous plants with nitrogen-fixing bacteria. It is known to influence various enzymes as well as coenzymes by making various associations with them (Marschner 1995). At higher concentrations and affected by the mineral composition of the soil, its uptake by the plant increases (Kubota 1965). However, even at higher concentrations, with a rise in the pH of soil, significant reduction in its uptake occurs (Adriano 1987). Co toxicity is known to cause alterations in the uptake and translocation of various nutrients important for plant growth and development. Chlorophyll content in the chloroplasts also is affected under such conditions and the process and rate of photosynthesis reduces to a significantly lower level in addition to affected enzymatic activity (Vanselow 1965). Iron chlorosis gets induced in barley under Co toxicity due to its inhibitory effects on the activity of catalase and decreased chlorophyll content (Agarwala et al. 1977).

Co toxicity in plants hasn't been studied much in detail, however, shoot growth is known to be retarded and adversely effected in tomato, barley, and rapeseed, along with biomass reduction of the plants (Li et al. 2009). The effects of higher Co concentration on cauliflower have also been studied and are shown to disturb the normal uptake and transport of other nutrients including P, Mn, Cu, Zn, and S from the roots of this plant. Photosynthetic activities are affected because of reduced Fe and chlorophyll amount in the leaves due to Co toxicity. On the enzymatic level, certain proteins such as the enzyme catalase become limited. The water content in leaves, however, is known to rise under higher Co concentrations than usual (Chatterjee and Chatterjee 2000).

Plant metabolism has been reported to be negatively affected by Co concentrations as low as 0.1 ppm in the medium. Retarded leaf growth accompanied by chlorosis is an effect of Co toxicity in citrus (Vanselow 1965). Concentrations of Co as much as 50 ppm cause Co toxicity and adverse effects on the leaf of oats (Vergnano and Hunter 1952).

3.4.7 Lead (Pb)

Pb has been found to be the most abundant element in soil with highly toxic effects on life especially for plants growing in the contaminated soil which are affected in terms of growth and development by alterations in their vital metabolic pathways such as photosynthesis (such as cause of chlorosis). Due to its effects on enzymes, it can cause reduction and loss of germination in some plants (Morzck and Funicclli 1982). Effects on the enzymatic levels include activity reductions of amylase and protease to about half in the endosperm of rice (Mukherji and Maitra 1976). Photosynthetic processes are affected because of enzyme inhibition (Sinha et al. 1988a, b), for example, the enzymes involved in fixing carbon dioxide, carboxylating enzymes (Stiborova et al. 1987), and also unbalancing the mineral nutrition of the plant (Sharma and Dubey 2005).

Hazardous effects of Pb on crops have been an interest for scientists since long ago. They have been studied to reduce and even completely abolish growth of seedlings in important crops such as rice, tomato, maize, soybean, barley, and some leguminous plants (Huang et al. 1974; Miller et al. 1975; Mukherji and Maitra 1976; Stiborova et al. 1987; Sudhakar et al. 1992). Pb is known to affect radish, barley, and onion at all parts of the plant, including leaves, stem, and underground roots by interfering with the process of elongation (Juwarkar and Shende 1986; Gruenhage and Jager 1985). Negative effects on root growth increase with rising Pb levels, for example, in sesame (Kumar et al. 1992). The degree of damage by Pb toxicity also depends upon the pH and the ionic composition (Goldbold and Hutterman 1986).

The morphological effects of Pb on pea and sugar beet have also been studied extensively at anatomical levels (Paivoke 1983). It has also been reported in vascular plants to interfere with the process of repair (Kaji et al. 1995). However, it's interesting how alfalfa doesn't show any apparent effects on its morphology even under Pb concentrations as high as 100 mg/mL (Porter and Cheridan 1981). But in the case of lettuce and carrot roots, a considerable effect occurs on growth patterns and rate (Baker 1972). Pb^{+2} toxicity altering metabolic pathways highly reduces plant growth and hence its overall biomass (Van Assche and Clijsters 1990). The effects are also known to induce reactive oxygen species (ROS) under Pb toxicity (Reddy et al. 2005).

3.4.8 Cadmium (Cd)

Cd gained attention due to being the most abundant and severely toxic heavy metal; its uptake by the plants has raised concerns (Arora et al. 2008). Cd concentrations higher than 100 mg per kilogram in soil (Salt et al. 1995) can cause phytotoxicity in crop plants resulting in retarded growth, necrosis, chlorosis, root tip browning, and senescence (Guo et al. 2008; Mohanpuria et al. 2007; Wojcik and Tukiendorf 2004; Sanita di Toppi and Gabbrielli 1999). Altered nutrient uptake, for example, reduction in uptake, is known to be a cause of Cd toxicity for important mineral macronutrients and micronutrients (Mohamed et al. 2012; Yang et al. 1996a).

Cd is known to have a highly negative effect on the process of photosynthesis (Mohamed et al. 2012). In some plants, the process of photosynthesis is disturbed due to deficiency of Fe(II) caused as a result of high Cd concentrations (Alcantara et al. 1994). Gaseous exchange through stomata is known to be affected under Cd toxicity (López-Climent et al. 2011). Higher Cd concentrations have also been known to be a cause of closed stomata in soybean and clover, resulting in reduced or no transpirational activity at all (Barcelo and Poschenrieder 1990). Alterations in the uptake and transportation of macronutrients such as K, P, and Ca, the micronutrient Mg, and even water occur as a result of higher Cd concentration (Das et al. 1997).

Cd has also been identified to inhibit nitrate assimilation in the shoots of some plants by affecting the enzyme nitrate reductase failing root-to-shoot transport of nitrates (Hernandez et al. 1996). Higher Cd concentrations cause a reduction in the assimilation of ammonia and fixing nitrogen in plant nodules, for example, in soybean (Balestrasse et al. 2003).

Permeability of the plasma membrane is altered by high Cd concentrations toxic to the plant resulting in reduced water content (Costa and Morel 1994) and ATPase activity, for example, in roots of sunflower as well as wheat (Fodor et al. 1995). Lipid peroxidation has also resulted because of higher Cd levels (Fodor et al. 1995). Some other consequences include effects on those enzymes responsible for carbon dioxide fixation and inhibition of chlorophyll synthesis in the chloroplast affecting metabolism (De Filippis and Ziegler 1993). Cd toxicity induces oxidative stress in plants with a huge reduction in concentrations of superoxide dismutase, catalase, and peroxidase (Mohamed et al. 2012; Milone et al. 2003; Hendy et al. 1992).

Growth and as a result yield of crop plants such as chickpea, maize, and soybean reduce to significantly lower levels at toxic Cd levels (Hasan et al. 2008; Krantev et al. 2008; Dewdy and Ham 1997). Reduced vegetative growth under such conditions has been reported in maize and mung bean (Ekmekci et al. 2008; Wahid and Ghani 2007).

3.4.9 Chromium (Cr)

Cr is known to hold the seventeenth place on the list of most abundant elements found in nature (Avudainayagam et al. 2003). Over the past years, an increase in chromium levels in the environment due to industrial activities has raised concerns regarding the risks it causes in contaminated environments (Zayed and Terry 2003).

Concentrations above 100 μ kg^{-1} dry weight cause toxicity to plants growing in contaminated soil (Davies et al. 2002). Large quantities of Cr cause disturbances in the physiological processes of the plant and hence affect the initial seed germination negatively (Peralta et al. 2001), for example, germination of common bean reduces to half its original rate during Cr (VI) toxicity (Parr and Taylor 1982), germination of alfalfa reduces to around one fourth in Cr (VI) toxic medium (Peralta et al. 2001), and sugarcane bud germination decreases by one third to about half the percentage (Jain et al. 2000). Wheat germination has been known to be markedly reduced in high Cr(III) conditions, in contrast to oat, which is not affected at levels under 4000 mg per kilogram of soil (Lopez-Luna et al. 2009). On the enzymatic level, this reduction in germination rate is a result of the effect on the activity of protease, which is enhanced by high Cr levels, or reduced amylase activity which involves sugar transport (Zeid 2001).

A variety of crops and trees has been shown to be affected by diminished root growth due to the occurrence of heavy metals (Tang et al. 2001). Cr is one of the heavy metals with the most hazardous effects on the root length of plants (Prasad et al. 2001). It may be a result of the fact that a large portion of the chromium taken up by the plant remains in the root region and only a fraction of it moves towards the upper parts (Paiva et al. 2009; Sundaramoorthy et al. 2010). Cr (VI) has been known to cause significant reductions in root number as well as growth and later root formation in mung bean (Rout et al. 1997; Samantary 2002). Similarly, in maize, it causes reductions in size and root hair (Mallick et al. 2010).

Plant height has been reported to reduce as a negative effect of Cr(VI) on shoot growth in oat, maize, wheat, and mung bean (Mallick et al. 2010; Rout et al. 2000; Lopez-Luna et al. 2009). Leaf growth in cauliflower is affected by Cr(III) toxicity (Chatterjee and Chatterjee 2000; Pandey et al. 2007, 2009).

Photosynthesis is largely affected by Cr toxicity at various enzymatic as well as metabolic levels, such as carbon fixation and the electron transport chain (Clijsters and Van Assche 1985). Again in this case, Cr (VI) has been studied well to affect both photosystems in the chloroplasts, for example, in peas (Bishnoi et al. 1993a, b). Cr toxicity causes an imbalance in the uptake and translocation of various mineral nutrients in crops such as maize, rice, watermelon, and spinach (Mallick et al. 2010; Sundaramoorthy et al. 2010; Dube et al. 2003; Gopal et al. 2009).

Heavy metal stress is known to induce antioxidant activity as a stress response when levels rise from the normal tolerable level (Shanker et al. 2003a). This includes activation of antioxidant enzymes such as catalases and SODs (superoxide dismutases) until the concentration rises to a certain point after which the activity of SOD does not rise and that of catalase lowers(Gwozdz et al. 1997).

3.4.10 Mercury (Hg)

Living beings have been endangered by yet another pollutant, mercury, with a very high risk factor (Boening 2000). Hg toxicity in agricultural lands results from an increase in Hg^{+2}levels (Han et al. 2006). More importantly, the toxicity caused by it and the aftereffects are far more severe and worrisome than several other metals and heavy metals, including but not limited to zinc, cadmium, copper, and lead (Munzuroglu and Geckil 2002).

Hg toxicity causes adverse changes in physiological processes in various species (Zhou et al. 2007), accumulating in higher plants as well as aquatic ones (Israr et al. 2006; Wang and Greger 2004; Kamal et al. 2004). In higher plants, toxicity resulting from this heavy metal can trigger various responses, based on biochemical as well as physicochemical changes, leading to visual and noticeable changes in normal plant life (Gupta and Chandra 1998).

As the concentration of mercury increases in the medium, biomass begins to decrease as shown by many plant species (Patra and Sharma 2000); however, with rising nutrient concentrations in the medium, the amount of mercury uptake by the plant starts to fall down considerably (Göthberg et al. 2004). It has also been reported that the mercury, when present, can cause noticeable changes in the translocation pattern and uptake amount of various nutrients required for normal functioning of the plant (Gupta and Chandra 1998).

Hg has been reported to be a cause of decreased levels of chlorophyll in higher plants as a result of the high inhibitory effects on the enzymes involved in its biosynthesis, thus affecting photosynthesis (Cho and Park 2000; Prasad and Prasad 1987). Another effect is a change in flow of water by a physical blockage due to closure of stomata (Zhang and Tyerman 1999). The ROS level is elevated as an active response to oxidative stress induced in response to high Hg levels, which also influence the mitochondrial activity leading to disrupted metabolic activities (Cargnelutti et al. 2006; Messer et al. 2005). At the enzymatic level, during oxidative stress induced as a result of Hg toxicity, an increase in the activity of peroxidase, catalase, and superoxide dismutatse, as well as malondi-aldehyde and hydrogen peroxide at the molecular level have been observed (Cho and Park 2000).

As a response to toxicity caused by mercury, the plant cell wall can retain mercury as a strategic measure for its defense (Cavallini et al. 1999).

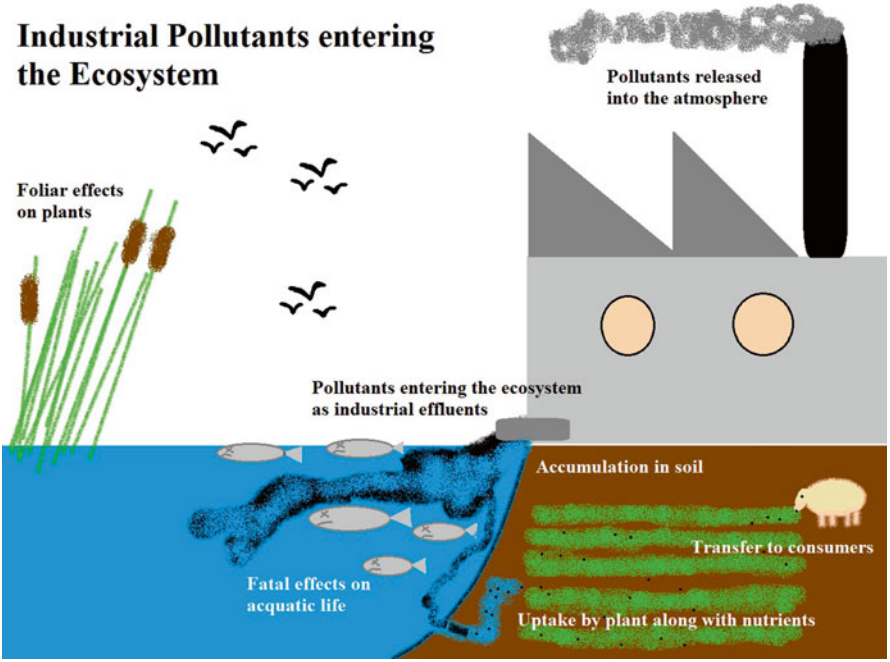

Fig. 3 Overview of industrial pollutants being released into the environment and entering the food chain

4 Long-Term Ecosystem Effects: Why Consider Pollutant Treatment before Discharging into the Environment

As a result of toxicity and accumulation in the plant, these pollutants enter the food chain as plants are at the bottom of the food chain and are a primary source of food for most living species. The end-user for crops is a human who cultivates this crop on quite large scales as a food source and its effect on them needs to be detailed to get a better understanding of how these pollutants are adversely affecting the ecosystem and all the living organisms in it. The entrance of these pollutants into the environment and the effect on the food chain is briefly represented in Fig. 3.

5 Conclusion

Industrial pollutants containing organic and inorganic compounds, metals, and heavy metals, need to be pretreated before their discharge and entrance into the ecosystem as they adversely affect plant life at all levels, including seed germination, seedling and plant growth at roots, shoots, leaves, fruit, and total biomass of the crops. Although beneficial for the plant at optimal levels causing improvement in growth and development at various stages, the same elements that act as nutrients for the plant can cause toxicity leading to harsh environmental conditions which harm plant growth considerably and raise concerns regarding the safety and balance of nature. The accumulation of these pollutants in the atmosphere and the environment as a whole disturbs the balance among various levels of the ecosystem as plant yield decreases which is the basic source of food in the ecosystem. As these elements accumulate in the soil, plants, being unable to move, having no choice but to grow and survive under these phytotoxic conditions, uptake these harmful elements, and accumulate them in various parts depending upon their translocation patterns. When these plants are consumed by various animals and humans, the toxic elements, including the heavy metals are transferred to them and can cause serious health issues. The accumulation of these industrial pollutants in agricultural soils is thus quite dangerous as the crops grown over them are affected adversely and transfer these adverse effects to humans, being the ultimate food consumer of those crops. Another aspect of the harm caused by these pollutants is the huge economic losses caused by them as a result of considerable yield reduction due to the crops being unable to cope with the polluted soil resulting initially in either lower biomass production or worse, no germination at all. Although the plants have evolved certain ways to survive these stressed conditions, including changes in translocation pattern, nutrient uptake, or altered gene expression to counteract the effect of these elements, certain crop plants are sensitive to them and are not able to keep up with the changing harsh conditions. As a result, they may be affected which is sometimes seen as visual symptoms of chlorophyll loss, chlorosis, necrosis, abnormal growth, wilting, and ultimate death of the plant. The balance of nature thus needs to be maintained to avoid unprecedentedly adverse conditions severely affecting plant growth leading to poor human health as the final consumer level is the human for whose well-being all the research carried out is directly or indirectly focused. As these pollutants have raised concerns and endangered all life forms, there should be strict policies applied for the industrial pollutants entering the environment in any form and action should be taken to preserve the balance of nature.

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Role of Seed Quality in Improving Crop Yields

Rinukshi Wimalasekera

Abstract Despite being an important source of food and feed, seeds are essentially an important delivery system of genetic information. Seed quality is a crucial determining factor of yield and quality of crop production. Good quality seed is superior to other standard seed in genetic and physiological purity and is free from seedborne diseases and disorders. The quality of the seeds is determined by the interaction of a number of genetic and environmental factors and climatic changes significantly affect seed characteristics. Production of better quality seeds in an effective and efficient manner is a challenge for increasing food demand. Seed quality is a complex trait and novel research approaches to improve seed quality involve a combination of seed technologies, genetics, and molecular biology. Some of the classical methods of seed improvement include coating, pelleting, priming, and production of artificial seed. Development of hybrid seed varieties that adapt to unfavourable climatic conditions and are resistant to a range of pests and diseases are at the forefront of the seed industry in improving crop yield. Hybrid seed varieties of rice, wheat, corn, barley, soybean, and diverse field crops are commonly used in various regions of the world for enhanced crop yield. Modern gene technology methods are being used to modify (GM) crops/seeds genetically to carry one or more beneficial traits such as herbicide and insect resistance, better resistance to drought/waterlogging, and modified nutritional profiles. Research on genetics of seed development and chemistry of seed reserves is an essential need in developing new technologies for crop improvement. The key challenge ahead is the identification and incorporation of beneficial genes and traits into elite cultivars, and development of new approaches to producing GM crops to minimise regulatory constraints and increase consumer acceptance.

Keywords Seed quality • Climate change • Seed improvement • Hybrid seeds • Genetic modification

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1 Introduction

Seed is a unique and fundamental entity that stores genetic information for the consequent life cycle of a plant. As vital propagating units, seeds play a very important role in crop production and human sustenance. Irrespective of the crop species, agricultural region, and growth season, use of good quality seeds ensures a good yield (Bradford and Bewley 2002). Good quality seed is superior to other standard seed in characteristics such as genetic purity, which include high and even germination rates, uniform growth pattern, physiological purity illustrated by viability and vigour and good health that ensures seeds are free from seedborne diseases and disorders. Other aspects include uniform size, shape, colour, texture, weight, freedom from other crop and weed seeds, insects, and devoid of other undesirable substances (Basra 1995; Seeds (2014) http://www.agriquest.info/; Seed Enhancement (2014) http://www.seedquest.com/keyword/seedenhancement).

In nature, numerous genetic and physical factors are responsible for determining the quality of seeds. Genetic factors that influence quality include genetic makeup and age and nutritional status of the mother plant. Environmental features such as temperature, water status, photoperiod and light quality, soil nutrition at seed setting and development, and physical factors such as injury and damage during planting, establishment, and storage as well as moisture and temperature during storage contribute to a large extent to seed quality. Interaction of genotype and environment ultimately determine the status of the seeds (Bradford and Bewley 2002; Nambara and Nonogaki 2012; Finch-Savage and Leubner-Metzger 2006; Seeds (2014) http://www.agriquest.info; Seed Technology (2014) http://www.seedbiology.de).

There are many advantages to using good quality seeds in agriculture, the utmost advantage being the full exploitation of the genetic potential of the crop providing high return per unit area. The other benefits include the ability of adapting to extreme growth and climatic conditions, higher degree of resistance to pests, diseases, and weeds, uniformity in plant growth, and maturation allowing easy harvesting and postharvest handling and high market value (Bradford and Bewley 2002; Nambara and Nonogaki 2012; Seeds (2014) http://www.agriquest.info; Seed Technology (2014) http://www.seedbiology.de). In brief, good quality seeds are the basic source of a secure food supply.

In many regions, especially in developing countries, famers do not have access to good quality seeds for a number of reasons, including insufficient seed production, the unavailability of quality-checked seeds, inefficient distribution, lack of seed certification methods, and higher seed prices (Seeds (2014) http://www.agriquest.info; Seed Testing International (2014) http://seedtest.org/en/seed-testing-international). The Food and Agriculture Organization (FAO) plays an active role in determining guidelines in seed quality assurance that guarantee the quality of seed from production, harvesting, and postharvest handling until delivery to the farmer (Seeds (2014) www.fao.org/seeds).

With the understanding of seeds as basic and crucial input for increased productivity and profitability, considerable effort has been made to improve seed quality and develop new varieties and hybrids by plant breeding and biotechnology methods.

Over the past years, seed companies contributed to enhancing crop production by utilising seed genetic traits such as insect and pest resistance, water-use efficiency, and higher yields in genetic engineering and breeding programmes.

This chapter encompasses the factors affecting seed quality, methods of seed enhancement, and recent advancements in breeding and biotechnological approaches in improving seed quality for better yield.

2 Impact of Climate Change on Seed Production

Climate change is one of the key problems in agriculture and hence global food security. The major challenges to crop production are global warming, severe and frequent drought and floods, pollution of air and soil, and higher pressure from pathogens. Devastating effects of climate change in agricultural production over a range of crop species have been reported from all over the world (Seeds (2014) http://www.agriquest.info; Seeds (2014) www.fao.org/seeds). Seed quality is significantly affected by climatic changes. Aspects ranging from flower characteristics, pollen viability and pollination, seed setting, length of the seed-filling duration, seed size, dormancy and nutritional profiles, and ultimately the seed quality are considerably influenced by climatic factors. The other climatic change impacts on quality seed production include the changing crop–weed interactions, altered population dynamics of pests, including evolution of new races of pests, changing the status of disease development, diminishing pollinator biodiversity and genetic diversity (Walck et al. 2011; Singh et al. 2013).

The world's food consumption mainly relies upon the seeds of wheat, rice, maize (corn), barley, and sorghum. These grain crops are largely vulnerable to climatic changes, especially global warming and prolonged dry periods. The major impacts on climate change will be on rain-fed farming, especially in Asia and Africa and drought conditions are predicted to affect cereal production dramatically, risking a loss of about 280 million tons of production (Singh et al. 2013).

Warming in terrestrial ecosystems has a pronounced effect on agriculture in every region of the world. In many plant species, increase in temperature results in a decline in the seed number per fruit, reduced seed size, and altered seed physiological conditions (Martínez-Andújarl et al. 2012; Singh et al. 2013). According to the present predictions of rising temperatures, by 2030, rice and maize production in South Asia will have declined up to 10 % and maize production in Southern Africa will have dropped by 30 % (Lobell et al. 2008). Research findings of the International Rice Research Institute (IRRI) indicate that temperatures above 35 °C for more than one hour during flowering cause sterile flowers and consequently produce no grain. According to IRRI forecasts, increased temperature leads to a 20 % reduction in rice yield and a higher night-temperature also causes a decline in production by 10 %. This yield loss has a significant effect on food security in the world, especially in Asia where rice is the staple food (Hybrid rice (2014) www.irri.org/our-work/research/rice-and-the-environment).

Wheat is an essential source of food for a large population of people and it is grown over a wide range of environments. Rise in temperature during the growing season considerably lowers the yields (Asseng et al. 2011). For example, in a study in main wheat-growing regions of Australia, up to 50 % reduction in yield was observed by temperature elevation of ±2 °C during the grain-filling stage. Warmer temperatures prevailing in several regions of the United States during the past few years resulted in faster growth of wheat and corn, reducing the time for the seeds to mature, and subsequently causing reduced yields (Karl et al. 2009). Using a number of crop simulation models, it has been predicted that future climatic projections have a remarkable effect on wheat yield in many agro-ecological zones of the world (Kang et al. 2009).

Maize (corn) species are grown in diverse agro-ecological regions and are a very important staple food in sub-Saharan Africa (SSA) and in many countries in Latin America. Maize production in Africa is badly affected by occasional droughts and increased temperature during flowering and grain-filling time (Maize (2014) http://www.iita.org/maize). Cowpea is an important food crop in many African and Asian countries. Although it is considered as a drought-resistant crop, farmers of SSA face substantial yield losses due to frequent drought conditions (Cowpea (2014) http://www.iita.org/cowpea).

Apart from grain production, much of the other important crop productions are affected by increasing atmospheric temperature, prolonged drought periods and variation in rainfall pattern, and increasing CO_2 concentration (Reddy and Hodges 2000; IPCC 2007). For example, coconut, one of the very important crops in many Asian regions is adversely affected by climatic changes. Long dry spells associated with high temperature result in low nut setting and fruit components. The Coconut Research Institute of Sri Lanka has reported that climatic change is especially sensitive in coconut inflorescence development from primordial initiation to button nut formation (Ranasinghe 2011).

3 Seed Technology and Development of Improved Seeds

Seed technology is described as the methods through which the genetic and physical characteristics of seeds could be improved. It is a multidisciplinary science that includes the processes of variety development, seed production, processing, storage, certification evaluation, and release (Feistritzer 1975). A great deal of attention has been paid to seed improvement by exploring diverse and emerging new technologies ranging from physical seed enhancement, classical and modern breeding, molecular biology, proteomics, metabolomics, and translational biology. Seeds are invaluable carriers of favourable traits from generation to generation and in seed production stringent attention is given to maintain genetic purity and exploit its potentiality in the next generation. Climatic change is a key concern in the seed improvement process and emphasis is paid in integrating stress-adaptive traits by breeding programmes and genetic modifications. Today, seed companies play a leading role in research on producing high-quality seeds of high-yielding varieties. Almost every important crop species in the world today is produced through improved seed varieties.

4 Seed Enhancement

Seed quality enhancement processes comprise the use of physical methods such as seed priming, seed coating, and artificial seed development, classical and modern breeding, and gene technology. These technologies enhance physiology, quality, vigour, and synchronicity of seed establishment and growth under diverse environmental conditions (Halmer 2004; Seed Technology (2014) http://www.seedbiology.de). Environmental parameters as well as plant hormones and growth regulators essentially control seed germination and subsequent growth. In certain seed improvement processes, manipulation of gibberellins, abscisic acid, ethylene, auxin, cytokinins, and brassinosteroids is done.

4.1 Mechanical Seed Enhancement

Rubbing off the seed/fruit coat and polishing followed by sorting of seeds into size classes or densities are some mechanical techniques that improve seed quality. For example, in sugar beet fruits polishing removes projections and hairs that enhance germination (Seed Technology (2014) http://www.seedbiology.de).

4.2 Seed Coating and Pelleting

Seed coating is a method of improvement of seed quality and seedling performance through treatment with plant protection products such as fungicides, pesticides, insecticides, growth stimulants, and nutrients followed by coating with synthetic polymer often with a colour (Ehsanfar and Modarres-Sanavy 2005; Mastouri et al. 2010). This technology offers many benefits including protection from pathogens and pests by precise and even distribution of agrochemicals, and increased shelf life; polymers adhere tightly to the seed and prevent loss of coated material and reduce exposure to dust and other substances, with ease of handling because of increased seed size, higher visibility in the field, and product identification (Ehsanfar and Modarres-Sanavy 2005; Seed Technology (2014) http://www.seedbiology.de). Some film coating techniques are used to modify imbibitions and germination. In seed pelleting, a thick covering is added to seeds to cover irregular seed shapes and to fix plant protection agents/hormones to the pellet matrix. The increased size of the pelleted seeds has the advantage in planting features such as use of machines for sowing seeds, precise placement, and visibility on soil. This method is especially important in small horticultural seeds such as sugar beet and vegetable seeds (Seed Technology (2014) http://www.seedbiology.de; Seed Enhancement (2014) http://www.seedquest.com). Today, a variety of crop seeds improved with the method has been released to the market. A few examples are namaticide-treated corn, cotton, and soybean; systemic insecticide coated wheat and corn seeds; aphid control of vegetable seeds; and controlled release of plant-protecting materials from smart seeds of wheat, corn, and canola (Ehsanfar and Modarres-Sanavy 2005; Seed Testing International (2014) https://www.seedtest.org).

4.3 Seed Priming

Seed priming is a seed quality enhancement method used to increase the rate of germination and uniformity and overcome seed dormancy. It is the most important physiological seed enhancement method by allowing controlled imbibitions and induction of the pregerminative metabolism (Jisha et al. 2013; Seed Technology (2014) http://www.seedbiology.de). Priming solutions can be supplemented with plant hormones or beneficial microorganisms. The standard method is osmopriming in which seeds are incubated in a well-aerated solution of low water potential and subsequently washed, dried, and planted in the regular manner (Seed Technology (2014) http://www.seedbiology.de). Use of primed seeds has a great advantage in adverse conditions in the field such as cold or warm soils and high temperature. There are several examples describing the beneficial effect of seed priming on germination and establishment of a variety of crop species (Jisha et al. 2013). Rice cultivars primed with water and polyethylene glycol (PEG) show significant impact on germination indices, seedling quality, and better tolerance to drought stress (Sun et al. 2010). On-farm seed priming practised for wheat, rice, maize, sorghum, millet, and cowpea in the dry zones of many Asian countries has facilitated fast and vigorous seedling growth subsequently leading to increased crop yields (Harris 2001; Chivasa et al. 2001). For legume crops inoculation of seeds with Rhizobia bacteria is done to increase the process of nitrogen fixation (Seed Enhancement (2014) www.seedquest.com).

4.4 Synthetic Seeds

Synthetic seeds comprise artificially encapsulated somatic embryos, shoot buds, cell aggregates, or any other tissue that has the ability to produce a complete plant (Gray and Purohit 1991; Redenbaugh 1993). Important features of synthetic seeds are large-scale propagation method, genetic uniformity of plants, direct delivery of propagules that eliminate transplanting, and relatively higher multiplication of plants (Seed Technology (2014) http://www.seedbiology.de; Synthetic Seeds (2014) http://www.agriquest.info/index.php/synthetic-seeds). This technique is especially beneficial when seed propagation is not successful, no seeds are formed, or when a certain species produces only a reduced endosperm (Ravi and Anand 2012). There are a number of other advantages such as germplasm conservation, product uniformity, and easy handling during storage, transportation, and planting (Ravi and Anand 2012). However, the exact application of synthetic seeds will vary from species to species. Synthetic seeds are commonly produced in coniferous forest species, cotton, soybean, vegetables including tomato, forage grasses, and in autogamous species such as wheat, barley, and oat in which hybrid seed production is costlier (Ravi and Anand 2012; Synthetic Seeds (2014) http://www.agriquest.info/index.php/synthetic-seeds).

5 Plant Breeding and Hybrid Seed Production

During crop domestication over a long period of time, seed traits have been modified through selection. Most of these selections led to favourable seed traits for agricultural benefits (Martínez-Andújarl et al. 2012). Breeding for improved seeds is a foremost approach in agriculture. Drought, heat tolerance, and pest/pathogen-resistance are the major traits in focus in breeding programmes of crops, vegetables, and fruits. Some of the new methods integrated into breeding programmes include marker-assisted selection methods and quantitative trait loci (QTL) analysis (Birch et al. 2011).

A hybrid is produced by crossing two genetically dissimilar parents. Pollen from the male parent will pollinate, fertilise, and set seeds in the female to produce F1 hybrid seeds. The improved qualities of the F_1 generation are referred to as “hybrid vigour” or “heterosis” and are often superior in yield, disease resistance, and more efficient in use of soil nutrients and weed control. It is of prime importance to ensure that parent lines have high genetic and physical purity to obtain the best quality F_1 seeds. Different methods are being employed in producing hybrid seeds in different crops (Dale 1994; Heffner et al. 2009).

Significant efforts in breeding conventional varieties and hybrids in rice have been made. Today, world rice production mainly relies on hybrid rice. In the past, hybrid rice production was limited because of the self-pollination character of rice. In 1974, a group of Chinese researchers transferred the male sterility gene from wild rice to create the cytoplasmic genetic male-sterile (CMS) line and hybrid combination (FAO 2004). Use of hybrid rice cultivation significantly increased and in China, the area under hybrid rice was 50 % of the total rice area in 1995 (FAO 2004). FAO statistics show that hybrid rice significantly increased yields by 15–20 % more than the improved varieties and also it performed well in unfavourable soil and climatic conditions (FAO 2004). In Egypt, hybrid rice produced higher yields than conventional rice varieties in saline soils (FAO 2004). To date, a large number of hybrids have been released to different countries (Rice and the Environment (2014) www.irri.org). Over the past years, FAO, IRRI, the United Nations Development

Programme (UNDP), and the Asian Development Bank (ADB) have provided strong and consistent support to improving hybrid rice breeding (Rice and the Environment (2014) www.irri.org).

Wheat is a critical crop for much of the world's population and the demand for wheat production increases with population growth. Increasing wheat yields is a major concern to meet the food challenge. World wheat production is also heavily dependent on the hybrids that have heterosis in grain productivity, grain-filling rate, increased plant height, well-developed root system, greater tolerance to a variety of stress conditions, and increased straw mass (Hybrid Wheat (2013) http://www.hybridwheat.net). Yield consistency is a major advantage apart from the yield potential from which farmers of some regions benefit. Some hybrid wheat varieties have 15 % increases in yields compared to conventional wheat even in more stress conditions (Hybrid Wheat (2013) http://www.hybridwheat.net). Hybrid wheat production programmes need a series of tedious technological processes that change floral development and architecture such as male sterility to impose out-crossing (Whitford et al. 2013). To block self-pollination and maintain male-sterile parent by a recessive system is recently being described as an improved method of producing hybrid wheat (Kempe et al. 2014). Several new hybrids were created and a great deal of research into wheat hybridisation was initiated in the 1970s–1990s throughout the world, mainly in the United States, Australia, and Europe. However, at present only a few companies are pioneers in hybrid wheat production (Hybrid Wheat (2013) http://www.hybridwheat.net). Today hybrid wheat is grown on 600,000 acres across Europe, and most commonly grown across whole farms in France (Hybrid Wheat (2014) www.bcwagric.co.uk). Wheat farmers in India profited by the introduction of hybrid wheat varieties that have high adaptability to grow in semi-arid zones of India (Matuschke and Qaim 2006).

Corn is an important crop worldwide next to wheat. In many African and Latin American countries, it is an important food source whereas in other countries most of the corn production is used in livestock and poultry feed. Corn seed is a cross-pollinating variety and pollinated by wind. One of the greatest concerns in hybrid corn seed production is genetic purity. Commonly, hybrid seed production is done by creating male sterility. In general, hybrid corn produces up to 30 % increase in yields per acre compared with conventional varieties. In the United States 95 % of the corn acreage is under hybrid corn, producing 20 % or more corn on 25 % fewer acres than in the 1930s. Some other beneficial aspects of the hybrid strains are consistently larger and better formed ears than those produced by ordinary methods, stronger stalks and roots, allowing the plant better to resist toppling by the wind, and the plants are more adapted to conditions such as drought, dampness, or cold. Most of the hybrid corn types are designed to mitigate yield loss in drought conditions (Corn Seeds (2014) http://www.monsanto.com).

In the world cereal crops, barley was ranked fourth both in terms of quantity produced and area under cultivation (FAOSTAT 2007). Barley is a widely adaptable crop, especially to drought conditions, and has a short growing season. Commercialisation of barley seeds came relatively later than other crop species and today farmers benefit from hybrid barley which has important characteristics such as higher yield combined with yield stability and improved grain quality and adaptation to severe winter conditions (Ullrich 2010). Rye, which is closely related to wheat and barley, is grown extensively as a grain and as a fodder. Hybrid rye is drought tolerant and absorbs soil nutrients more efficiently and therefore has a tremendous value in drought-prone regions and wider range of soil types. Hybrid rye also has good foliar disease resistance and vigorous growth (Forage Rye (2014) http://www.elsoms.com). Cowpea is an important food legume in the tropics. There are several cowpea varieties and a considerable amount of effort has been made on producing hybrid cowpea strains in order to get higher yields from water-limited regions. However, the breeding programme carried out under controlled conditions has proved to be less successful in developed cowpea intraspecific F1 hybrids (Lelou and Van Damme 2006). Sorghum is a grain species used as a food source in some countries especially in Africa, and it is widely grown for animal feed in other countries. Seed industries have developed several sorghum hybrids that are drought tolerant and tailored to localised high yields (Sorghum Hybrids from DuPont Pioneer Can Boost Your Yields (2014) https://www.pioneer.com; Sorghum (2014) http://www.monsanto.com). Soybean is a legume grown as a food or for livestock. Hybrid soybeans have been developed that are able to adapt to various climate conditions and are now grown largely in many states of the United States and in South America (Soybean seeds (2014) http://www.monsanto.com).

Apart from main crop species, hybrid seeds are used widely in potato, canola (rap), sugar beet, and many vegetable and fruit species that have better characteristics mainly in terms of enhanced yields.

6 Genetic Modification

Modern gene technology methods are being used to enhance crops/seeds genetically to carry one or more beneficial genes and traits. The first genetically modified (GM) crop developed through the use of transgenic methods and approved for cultivation was the ‘Flavr Savr’ tomato in 1994 in the United States(Krieger et al. 2008). The major commercially grown GM crops have the traits of herbicide and insect resistance, better resistance to drought environment, modified nutritional profiles such as improved amino acid composition of maize, improved fatty acid composition of maize and soybean, and modified starch in maize and potato (http://www.worldseed.org).

This technology is developing much faster today and many of the seed companies are producing and marketing GM seeds of a variety of crops, vegetables, fruits, and flower species. In the year 2012 an unprecedented hundredfold increase in biotech crop hectarage from 1.7 million hectares in 1996 to 170 million hectares was observed indicating biotech crops as the fastest adopted crop technology in recent history (ISAAA Brief 44 2012). From 1996 to 2011, biotech crops contributed to food security by increasing crop production valued at US$98.2 billion (ISAAA Brief 44-2012). For GM crops, certain strict scrutiny and biosafety regulations apply before releasing and growing in mass scale to prevent any potential hazardous effects to the consumers and environment.

Genetic engineering has been used successfully mostly to create transgenic rice for better biotic and abiotic stress tolerance and enhance the nutritional quality thereby to overcome the limitations of conventional rice breeding (FAO 2004; FAO Factsheet (2004) http://www.fao.org/rice2004). Advances in genomics and DNA marker-assisted selection processes have been used to improve yields. However, biosafety issues and public perceptions play key roles in further progress of the use of biotechnology in GM rice production. In the past few years IRRI has developed and distributed rice varieties with better tolerance to drought, submergence, cold, and salinity. Several QTLs that give drought tolerance in rice have been identified and introduced into high-yielding varieties (Hybrid rice (2014) http://irri.org/our-work/research/better-rice-varieties). Three QTLs that link to cold tolerance have been identified and introduced into desirable spikelet fertility and early maturity traits that finally resulted in promising cold tolerant lines (Hybrid rice (2014) http://irri.org/our-work/research/better-rice-varieties). These varieties are valuable resources for China and Korea where a considerable yield loss due to low temperature is recorded. A region of rice genome responsible for salt tolerance ‘Saltol’ has been used to develop salt tolerant varieties during the seedling and reproductive stages of the plant. Submergence tolerance varieties were developed with overexpression of the SUB1 gene which confers resistance to submergence up to 14 days. IRRI has shown that the SUB1 and Saltol can be combined in a high-yielding variety to increase tolerance to salinity and submergence. Development of some improved varieties that tolerate a high concentration of iron in the soil is an achievement in the use of biotechnology and breeding. In addition, considerable research efforts have been made to develop disease, insect, and herbicide resistant rice. Genetic engineering of rice varieties with Bt toxin genes is one of the most commonly known and firstly developed type of insect-resistant rice. Herbicide-resistant rice varieties have been developed by the chemical mutagenesis method. This variety ‘Clearfield rice’ is resistant to acetolactate synthase-inhibiting herbicides such as imidazolinone. LibertyLink rice has resistance to phosphinic acids such as glufosinate, and Roundup Ready rice, with transgenic resistance to glyphosate (Rong and Snow 2005). Enhancing nutritional quality of rice seed by biotechnological methods is an important theme of ongoing research. Golden Rice, which produces provitamine A (beta carotene), is a good example of a commercially available nutritional quality enhanced variety (Burkhardt et al. 1997; http://irri.org/golden-rice). Golden rice plants were developed by transferring two daffodil genes and one bacterial gene that carried out the four steps required for the production of beta-carotene in rice endosperm. Biofortified crops, such as Golden Rice are an important source of vitamin A in many rice-consuming countries (Burkhardt et al. 1997; Golden Rice (2014) http://irri.org/golden-rice). Transgenic rice has been produced to have increased levels of iron and zinc in the grain by expression of the soybean ferritin gene (Vasconcelos et al. 2003; Borrill et al. 2014).

Genetically modified wheat has been produced mainly for improved drought and salt tolerance, herbicide tolerance, and pest resistance. These innovations are expected to enhance the productivity, sustainability, and profitability of wheat farmers. The first herbicide tolerant wheat 'Roundup Ready™' was produced through introducing a gene from *Agrobacterium tumefaciens* coding for the enzyme 5-enolpyruvylshikimate-3-phosphate synthase (EPSPS) to produce a glyphosate tolerant wheat line (Pocket K No. 38: Biotech Wheat (2014) http://www.isaaa.org; Monsanto and GM Wheat (2014) http://www.monsanto.com). This wheat is still not introduced to the market and is in the phase of field trial evaluation. 'Clearfield wheat' which is tolerant to the imidazolinone herbicide is a product of mutation breeding and not a genetically modified variety. Clearfield® wheat varieties are now grown in many regions across Canada (Monsanto and GM Wheat (2014) www.monsanto.com). Wheat is affected by a number of fungal diseases among which *Fusarium* is the worst, resulting in small and stunted grains or sometimes no grains and producing mycotoxins. Leading seed companies and other research institutions have launched programmes on producing fungal resistant wheat, specifically *Fusarium-resistance* and stem rust resistance varieties (USDA 2010; Pocket K No. 38: Biotech Wheat (2014) http://www.isaaa.org). In addition, a wide range of traits such as resistance to yellow mosaic virus, head scab, powdery mildew, and insects are under investigation (Pocket K No. 38: Biotech Wheat (2014) www.isaaa.org). Producing drought tolerant wheat is also under consideration and the International Maize and Wheat Improvement Center (CIMMYT) used a drought tolerance gene (DREB1A) from *Arabidopsis thaliana* to enhance this trait in wheat (CIMMYT 2004). Promising approaches have been made to increase iron and zinc content in wheat by biotech methods (Borrill et al. 2014). Wheat containing more lysine and with an improved baking quality trait has been developed by identification and genetic modification of candidate genes responsible for β-glucan synthesis in the starchy endosperm (Nemeth et al. 2010).

Certain maize varieties are being genetically modified for agriculturally desirable traits such as drought resistance and pest and herbicide resistance. Glyphosate and imidazoline herbicide resistant varieties have been commercially available since 1996 and farmers of many countries are reported to be benefitted substantially by use of these maize (Genuity DroughtGard Hybrids (2013) http://www.monsanto.com; http://www.bayercropscience). Bt corn is a very popular genetically modified corn variety. One or more proteins from *Bacillus thuringiensis* bacteria are expressed in the corn plant toxic to certain insects and pests such as corn borer, corn ear worms, and root worms. There are different variants of Bt corn depending on the type of Bt gene expressed. These GM corn minimised pest damage and today are grown widely across the world (Bohnenblust et al. 2014; Petzold-Maxwell et al. 2014). To minimise the yield loss from drought stress, GM corn has been developed with improved water-use efficiency. DroughtGard® corn hybrids and other varieties selected for drought-tolerant characteristics are commercially grown (Genuity DroughtGard Hybrids (2013) www.monsanto.com). Allele, ZmDREB2.7 identified in the drought-tolerant maize varieties, was effective in imparting plant tolerance to drought stress (Liu et al. 2013). In a study, overexpression of phytase (*Aspergillus niger phy*A2) in maize seeds led to improved phosphorus availability (Chen et al. 2008).

Genetically modified sorghum has been produced for herbicide resistance (glyphosate and glufosinate), fungal resistance, and improved food and feed quality. All of the GM varieties are still under field trial conditions.

Several different varieties of GM soybean are cultivated in large scale. Transgenic 'Roundup Ready Soybean' is resistant to herbicide Roundup (Soybean seeds (2014) http://www.monsanto.com). Soybean expressing Cry1Ac protein from *Bacillus thuringiensis* and glyphosate resistance is an economically important variety that produces high yield (ISAAA Brief 44-2012: Highlights. Global Status of Commercialized Biotech/GM Crops (2012) http://www.isaaa.org). Importantly, soybean has been genetically modified to improve the quality of oil. The amount of oleic acid and stearic acid has been increased by silencing or knocking out delta 9 and delta 12 desaturases and increased oil stability (Clemente and Cahoon 2009; Sorghum Hybrids from DuPont Pioneer Can Boost Your Yields (2014) www.pioneer.com).

Potato plants resistant to Potato Virus X (PVX) and Potato Virus Y (PVY) have been developed by expressing coat proteins of PVX and RNA silencing, respectively (Huisman et al. 1992; Missiou et al. 2004; http://cipotato.org). Potatoes transformed with a resistance gene for late blight, RB, showed increased resistance to *P. Infestans* (Kuhl et al. 2007; http://cipotato.org). Improvement of amino acid composition of potatoes has been made by expressing *AmA1* from *Amaranthus hypochondriacus* (Chakraborty et al. 2000) and 'Amflora' developed by BASF, produces pure amylopectin starch (www.agro.basf.com). Some of the GM potatoes were grown for a period of time and today none of the GM potatoes are grown commercially.

Research has been done to modify several kinds of fruits and vegetables genetically for characteristics such as pest resistance, herbicide tolerance, improved nutritional quality, flavour, and postharvest storage. GM tomato is the pioneer product available in the market. However, most of these GM products are not released into the market or are being suspended after some time of commercialising. Due to the controversial issues regarding the potential risks of the GM crops to consumers and the environment, introducing them to the market is a question. It is not intended in this chapter to discuss the controversies and issues of GM crop production.

Conclusions and Future Perspective

Seeds are fundamental to agriculture and seed quality has a major impact on crop yield. Seeds as vital propagating entities are greatly affected by the climatic change leading to declining yield and quality. During the last few decades, dramatic advancements in technology led to production of improved seeds as a delivery system leading to increased crop productivity worldwide. Introduction of seed enhancement methods such as seed coating, pelleting, priming, and production of synthetic seeds contributed to enhancement of seed quality. Hybrid seed production at commercial scale using advanced techniques is a significant achievement in the seed industry. Hybrid seeds are developed for features such as increased disease resistance, drought/cold tolerance, and improved nutritional quality. However, hybrid seed development is limited in some crop species due to high cost and the time taken for the process. Research is being continued to overcome these problems and produce hybrid seeds for multiple advantages in the field and evaluate the yield with farmer participatory trials. Farmers in some parts of the world do not have access to improved varieties due to improper distribution, high cost, or lack of knowledge. Efficient distribution of improved seed varieties and knowledge transfer should be considered as a central goal for future food security. Production of transgenic/GMO crop plants in order to better resist certain diseases that cause enormous crop losses, better combat against particular pests, and withstand herbicides, and with increased/modified nutritive values is a major development in agriculture. In brief, seeds are the delivery systems for agricultural biotechnology. However, key issues concerning the GMO on safety of the consumer and the environment should be addressed seriously before they are commercialised. It is of prime importance to develop safer seeds to maximise the yield potential by combining methods of breeding, biotechnology, and agronomy. Ultimately, sustainable agriculture is the answer that attempts to sustain biodiversity through a blending of innovation and traditional local knowledge.

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Sustaining Cocoa Production on Oxisols in Malaysia

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Abstract Oxisols are dominated by variable charge minerals in their clay fraction, containing an insufficient amount of Ca and Mg in their soil solutions. Under natural conditions, cocoa grown on the soils is subjected to the stress of low pH and Al and/or Mn toxicity, which eventually produces low yields. This chapter discusses the chemical properties of Oxisols in Malaysia and explains how the productivity of the soils is enhanced using lime or basalt, which increases soil pH. When the pH goes up above 5, Al in the soil solutions is precipitated as inert Al-hydroxides, with the concomitant elimination of toxic Mn. The increase in pH would result in the increase of the CEC, attributed to the reaction of the variable charge minerals present in the soils. Basalt application would also lower pH of the soils, which further increases the CEC. On dissolution, lime supplies Ca and Mg into the soils, and basalt not only releases these metals, but also K, P, and S. Ca, by itself, is able to reduce Al toxicity. One of the best methods of alleviating the infertility of Oxisols for cocoa cultivation is to apply basalt in combination with organic materials. Growing cocoa on Oxisols requires heavy application of NPK fertilizers, usually in the form of ammonium sulfate, rock phosphate, and muriate of potash, respectively. Occasionally, kieserite is applied to increase Mg reserve in the soils. Application of a high amount of N fertilizer will in the end acidify the soils, but it will be offset by the production of hydroxyl ions due to the specific adsorption of phosphate and sulfate ions on the surfaces of the oxides of Fe present in the soils. In that way, the production of cocoa on the Oxisols of Malaysia is sustained.

Keywords Amelioration • Application • Cultivation • Management • Mineral charge • Toxicity

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1 Introduction

Cocoa (*Theobroma cacao*) is an important agricultural commodity in the export market of Southeast Asia and West Africa. In Malaysia, the crop was first planted in Jerangau, Terengganu (Peninsular Malaysia) in the 1950s and was later spread to Tawau, Sabah (East Malaysia). To support the continued growth of the cocoa industry in Malaysia, a research station with state-of-the-art facilities was set up by the government in Temerloh, Pahang. The three cocoa-planting areas have something in common: they have similar soil type which, according to soil taxonomy (Soil Survey Staff 2010) can be classified as Oxisols, considered to be among the most weathered soils in the tropics. However, the yield of cocoa planted in the soils in terms of its bean is reasonably high considering their low productivity. This is because of the proper soil/agronomic management practices being put into place during the course of cocoa production on the infertile soils.

Currently, the national average of cocoa production in Malaysia is about 0.8 t ha^{-1} $year^{-1}$ (Shamshuddin and Noordin 2011). This is far too low compared to those in African countries, such as the Ivory Coast. For Malaysia, the target rate of cocoa bean production is 1.5 t ha^{-1}, which is still way below the potential yield of 10 t ha^{-1} $year^{-1}$. However, in Tawau, Sabah, a yield of >2 t ha^{-1} $year^{-1}$ is achievable following good soil management practices.

2 Chemical Properties of Oxisols

In order to know how and why cocoa is able to grow sustainably on Oxisols, we need to understand the chemical properties of the soils and their responses to the application of soil amendments and fertilizers. We know that Oxisols occurring in Malaysia are acidic in nature, with pHo ranging from 4.5 to 5.0 (Tessens and Shamshuddin 1983; Shamshuddin and Fauziah 2010a). They are also known to contain toxic amounts of Al and/or Mn in the soil solutions (Shamshuddin et al. 2011) that affect cocoa growth as well as its taste (Shamshuddin and Noordin 2011). Oxisols are defined by the presence of an oxic diagnostic horizon (Soil Survey Staff 2010). The soils are extremely weathered, dominated by the presence of kaolinite and sesquioxides in the clay fraction (Anda et al. 2008a; Shamshuddin and Anda 2008). Under natural conditions, the CEC of Oxisols is very low, with value <16 $cmol_c kg^{-1}$ clay. As such, basic cations are mostly lost via leaching under the environment prevailing in the tropics, further lowering the productivity of the soils.

We know for sure that soil materials are both negatively and/or positively charged. The negative charge is derived via a process called isomorphic substitution. For instance, the replacement of Si by Al in mica present in soils would result in an excess of negative charges, termed negative permanent charges (Shamshuddin 2011, 2012). Positive permanent charges also exist in the soils, being produced by the isomorphic substitution of Fe by Ti in soils containing a high amount of oxides of Fe (Tessens and Zauyah 1982).

Fe oxides have another kind of charge known as variable charge. As the pH of the ambient solution changes, the charge on the surfaces of these minerals also changes. When the pH is low, protons are chemisorbed onto the minerals to become net positively charged (Shamshuddin 2011, 2012). On the contrary, the minerals are net negatively charged at high pH. The pH at which the net charge of the variable-charge mineral is zero is termed pHo (Van Ranst et al. 1998; Anda et al. 2008a).

The value of pHo for silicate is low (close to 4 or lower), whereas that of oxides is higher (mostly >5). Oxisols are composed of many variable-charged minerals, such as goethite and hematite. The pHo reported in the literature is actually the resultant pHo value for all the minerals in the soils. As oxides are abundant in Oxisols (Tessens and Shamshuddin 1983; Anda et al. 2008a; Shamshuddin and Fauziah 2010a), their pHo are high, with values 5 or higher.

In reality, the mineralogical composition of soils varies according to their stage of weathering. As the soils weather, more oxides are formed, leading to an increase in their pHo (Tessens and Shamshuddin 1983). It is expected that at the last stage of soil weathering, the soils become less productive and hence need special soil management practices to sustain cocoa production.

Basically, the total charge in the soils can be subdivided into permanent and variable charge components. The amount of total charge in the soils can be manipulated by changing their variable charge component. The variable negative charge (CEC) in the soils is related to the difference between pHo and pH (pHo–pH) (Shamshuddin and Fauziah 2010a; Shamshuddin 2012). Hence, the CEC of the soils can be increased by increasing the difference between their pHo and pH. This can be done either by lowering pHo, increasing pH, or both. The former can be done by incorporating basalt into the soils (Anda et al. 2009, 2013; Shamshuddin and Kapok 2010; Shamshuddin and Fauziah 2010b), whereas the latter is easily accomplished by lime application (Shamshuddin et al. 1991, 1998) or by applying basalt (Shamshuddin and Kapok 2010; Anda et al. 2013).

A soil system is stable when the charge in it is low, meaning that soil potential decreases as the charge decreases. Therefore, the potential in the soil is low when soil pH is near its pHo. So, under natural conditions, soil pH tries to move to its pHo in order to achieve maximal stability. As soil pH increases with weathering, its pHo increases. This phenomenon has been shown clearly by the study of Tessens and Shamshuddin (1983). These researchers found that soil pH increased linearly with increasing pHo.

Primary minerals in soils disintegrate during the course of soil weathering and new minerals are formed thereafter, meaning that the silicates in the soil change to oxides of Fe and/or Al, and consequently the pHo of the soils is increased. In the end, soil pH is increased in tandem with the pHo increase. This is why the pH of Oxisols is higher than that of the Ultisols as observed in the Malaysian study (Tessens and Shamshuddin 1983; Shamshuddin and Fauziah 2010a).

Tessens and Shamshuddin (1983) had analyzed the pH of many Oxisol samples from all over Peninsular Malaysia and found that the values were mostly in the range of 4.5 to 5.0. Under normal circumstances, soils will be at their greatest stability when the potential in them is zero, that is, at the $\text{pH} = \text{pHo}$; hence, the pH of the Oxisols tries to approach 4.5–5.0 in order to remain under stable condition.

As the soil pH of highly weathered Oxisols is low (<5), Al on their exchange complex is readily dissolved and goes into the soil solution. In many cases, the Al in the soil solution is present at toxic levels for crop growth (Shamshuddin et al. 1991, 1998). Naturally, Al concentration in the soil solution increases as the pH is lowered. Likewise, Mn may exist at toxic levels under low pH condition. Low soil solution pH and high Al concentration have little consequence on the growth of either oil palm or rubber, but they are expected to affect the growth and yield of cocoa significantly (Shamshuddin and Noordin 2011).

3 Lime Application to Improve Soil Productivity for Growing Cocoa

One of the most common agronomic practices to alleviate soil acidity is lime application, using ground magnesium limestone (GML). However, the ameliorative effects of GML are only observed in the zone of its application (Shamshuddin and Ismail 1995). When GML is added into an Oxisol, its pH increases with value depending on the rate applied. Because of the presence of variable-charged minerals in the soil, the CEC is consequently increased. Under this situation, the cations in the Oxisol are held by the negatively charged soil surfaces. This means that a GML application only helps alleviate the subsoil acidity. Therefore, a deep rooting crop such as cocoa still suffers from Al and/or toxicity (Shamshuddin et al. 1997). Shamshuddin and Ismail (1995) found that Ca and Mg in the topsoil could be partially brought to the subsoil by applying GML in combination with gypsum at the appropriate rate. When this agronomic practice is done and over with, the excess Ca from the dissolution of the gypsum present in the topsoil can subsequently move down the soil profile.

To grow cocoa on Oxisols, their pH needs to be raised to a value above 5. At this pH level, Al in the soil solution starts to precipitate as inert Al-hydroxides, rendering it unavailable to the growing cocoa in the field, with concomitant elimination of Mn. Soil solution pH can be increased effectively by GML application (Shamshuddin et al. 1991, 2009, 2010). For this reason, it is a standard practice to apply GML in the planting hole at least 4 t ha^{-1} (Rosilawati et al. 2014). According to MARDI (1990), 159 kg of GML should be applied in order to raise soil pH to the required level and subsequently eliminate Al and/Mn from the soil solution so that cocoa seedlings will not be under the stress of H^+, Al^{3+}, and/or Mn^{2+}.

4 Basalt Application to Improve Soil Productivity for Growing Cocoa

Basalt is sporadically distributed throughout the Malay Peninsula (Hutchison and Tan 2009) where pockets of basalt outcrops are found in Segamat, Johor, and Beserah, Pahang. There is a quarry in Segamat that produces basalt dust of the size about 5 mm or less. The best ground basalt for agricultural use is the one with the size of <1 mm; anything bigger will take a long time to disintegrate and dissolve completely under field conditions (Shamshuddin et al. 2011; Anda et al. 2013). We now know that basalt is also found in Quiun Hills, Tawau, Sabah. Soils at this site are currently being used for growing cocoa.

It has been found that soil pH can be increased by ground basalt application (Anda et al. 2009, 2013; Shamshuddin and Kapok 2010). On dissolution, basalt not only increases soil pH, but also supplies a significant amount of Ca, Mg, K, P, and S into the soil system (Gillman et al. 2002). The best agronomic practice is to apply basalt in combination with organic fertilizer (compost) that supplies some N to the growing cocoa in the field. Although basalt takes a long time to disintegrate and dissolve completely in soils (Shamshuddin et al. 2011; Anda et al. 2013), it gives a long-term ameliorative benefit to the cocoa plant. As soil pH increases, negative charges on the exchange complex of the variable-charged minerals increases (Shamshuddin and Ismail 1995). This helps retain most of the basic cations in the topsoil and hence, the productivity of Oxisols is further enhanced.

To prove that what has been said above is in order and defensible, a study has recently been conducted. The main objective of the study was to alleviate the infertility of an Oxisol from the Malaysian Cocoa Board Experimental Station, Temerloh, Malaysia, for cocoa cultivation using basalt in combination with compost. Other experimental plots in the research station have been limed adequately before planting cocoa. The research was conducted in a glasshouse at Universiti Putra Malaysia, Serdang. Thereafter, a field trial was conducted at the experimental station in Temerloh.

Basalt is an igneous rock containing mainly olivine, feldspars, pyroxenes, and amphiboles. In the presence of a sufficient amount of water, basalt disintegrates and dissolves, releasing Ca, Mg, K, P, and S into the soil system (Gillman et al. 2001, 2002). As such, basalt is a complete slow-released fertilizer without nitrogen. Of the minerals present in basalt, olivine is the most soluble in soils. The best basalt for the amelioration of Oxisols is the one that contains Mg-olivine, called forsterite (Mg_2SiO_4). Forsterite dissolves in soil solution, releasing SiO_4^{4-} according to the following reaction:

$$4\mathrm{Mg}^{2+} + 4\mathrm{SiO}_4{}^{4-} + 4\mathrm{H}_2\mathrm{O} \rightarrow 4\mathrm{Mg}^{2+} + \mathrm{Si(OH)}_4 + 4\mathrm{OH}^-$$

This reaction shows that a large amount of hydroxyl ions is released into the soil solution when SiO_4^{4-} undergoes hydrolysis. In this reaction, silicic acid [$Si(OH)_4$] is concomitantly made available for uptake by the cocoa plant. It was found by Anda et al. (2013) that basalt application in the field increased soil solution Si significantly. The presence of a sufficient amount of Si in the plant system may possibly prevent the outbreak of certain cocoa diseases. Si is classified as a “beneficial nutrient” that can alleviate the problems of plants exposed to multiple stresses (Heckmam 2013). However, ground basalt takes a long time to dissolve completely even though under the condition of low pH (Shamshuddin et al. 2011; Anda et al. 2013). Nevertheless, basalt application is a good agronomic practice for the long-term ameliorative effects on the low productive Oxisols.

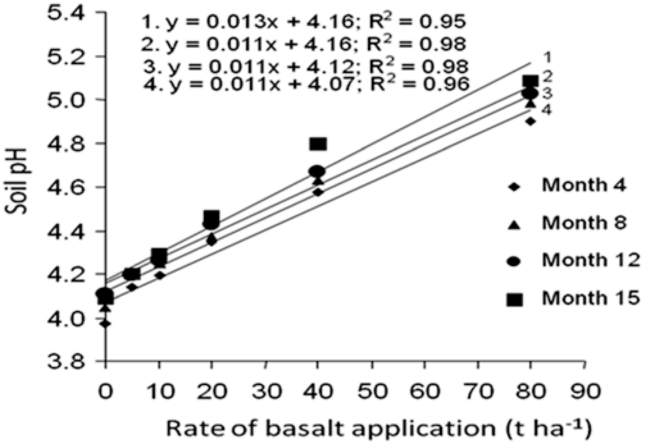


Fig. 1 Effect of basalt application on the pH of the topsoil of an Oxisol. *Source*: Shamshuddin and Anda (2008)

The result showed that soil pH increased linearly as basalt rate increased (Fig. 1). The basalt used in this glasshouse experiment was obtained from Australia, which had been studied in detail by Gillman et al. (2001) and (2002). In the current study, it was shown that soil pH increased after 15 months of basalt application (Anda et al. 2009), which is consistent with the study of Shamshuddin et al. (2011) and Anda et al. (2013).

Under the glasshouse condition, basalt application onto an Oxisol had lowered its pHo (Fig. 2). Likewise, in the field study, it was found that basalt application decreased pHo from 3.8 to 3.5 (Anda et al. 2013). It was also found that basalt applied in combination with compost had lowered the pHo of the soil even further. The lowering of pHo and increase in soil pH would have increased the CEC of the soil (Shamshuddin and Fauziah 2010a; Shamshuddin 2012). Increase in soil pH due to basalt application had reduced the soil solution Al and Mn concentration significantly and resulted in the healthy growth of cocoa plants in the field (Anda et al. 2013). These researchers concluded that after 24 months of basalt application in combination with compost, the growth of cocoa in terms of its height and girth diameter had increased significantly, which resulted in the early production of cocoa pods.

In a glasshouse experiment using cocoa as the test crop, soil solutions were extracted after 15 months of its growth (Table 1). The results showed that Ca, Mg, and K increased with increasing rate of basalt application. On the other hand, Al and Mn decreased, which means that basalt applied at the suitable rate was able to reduce the toxicity caused by the two acidic metals.

In the same experiment, it was observed that cocoa responded well to basalt application. For the control treatment, the dry matter weight was 709 g pot^{-1} (Table 2). When basalt was applied at 10 t ha^{-1}, the dry matter weight was increased

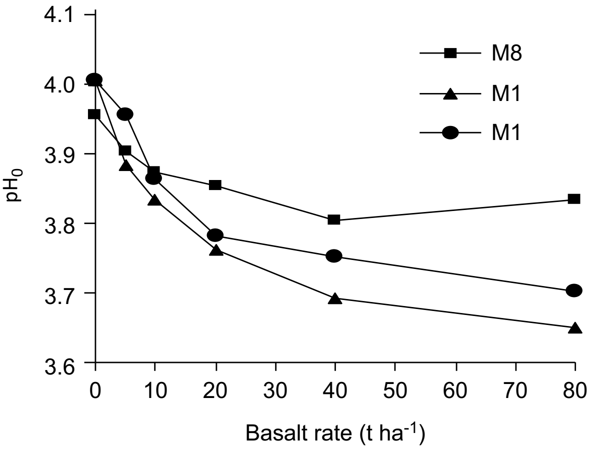


Fig. 2 Effect of basalt application on the pHo of the topsoil of an Oxisol. *Source*: Anda et al. (2009)

Table 1 The elemental composition of the soil solutions

	Element				
	Ca	Mg	K	Al	Mn
Basalt rate (t ha^{-1})	(μM)				
0	153b	66c	41c	16a	29a
5	145b	139c	36c	13b	12b
10	171b	153c	39c	6c	9c
20	175b	317b	43c	3cd	3d
40	222a	515a	65b	2d	3d
80	266a	610a	82a	2d	1d

Source: Shamshuddin et al. (2011)

Table 2 Dry matter weight (DMW) of cocoa as affected by basalt application

Rate (t ha^{-1})	0	5	10	20	40	80
DMW (g pot^{-1})	709c	742c	846b	873b	899ab	960a

Source: Shamshuddin et al. (2011)

to 846 g pot^{-1}. This clearly shows that basalt is a good soil amendment worth considering for application in cocoa plantations in Malaysia.

Data from the soil solution analyses of the field trial using the same soil as that of the glasshouse experiment were then studied in detail. Relative dry matter weight was plotted against Al concentration in the soil solution. The relationship between dry matter weight and soil solution Al is given in Fig. 3. The Al concentration corresponding to 90 % relative dry matter weight is considered the critical level. From this figure, the critical Al level for cocoa of 4.7 μM was then determined. Based on data presented in Table 1, it required about 20 t basalt ha^{-1} to decrease the Al to this level of concentration.

Fig. 3 Relationship between relative dry weight and soil solution Al concentration. *Source*: Shamshuddin et al. (2011)

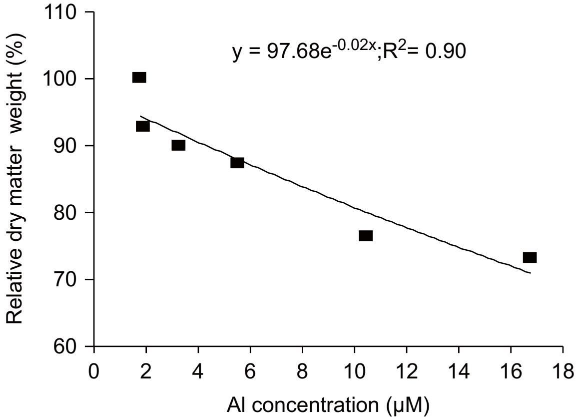
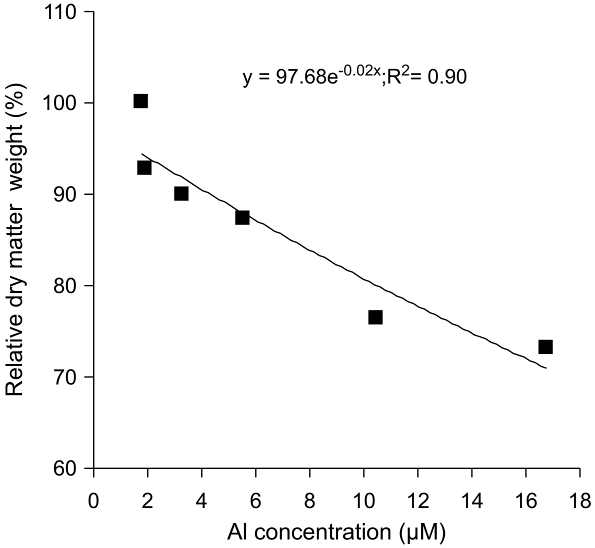


Fig. 4 Relationship between dry matter weight and Mn concentration



A similar graph was then plotted for Mn data and the graph obtained is given in Fig. 4. The critical Mn concentration estimated from this plot was 5.8 μM. It shows that about 20 t basalt ha^{-1} are needed to reduce Mn concentration to the level suitable for cocoa growth in the field. From glasshouse and field trials, it can be concluded that cocoa is indeed very sensitive to the presence of high Al and Mn concentration in the soil solution. For this reason, Oxisols can only be utilized for cocoa cultivation after they have been adequately limed. Alternatively, the soils can be ameliorated using ground basalt applied at the appropriate rate.

In rice, the uptake of Si in the form of silicic acid prevents the outbreak of rice blast disease (Abed-Ashtiani et al. 2012). It is likely that cocoa can also benefit from the presence of Si in its biomass (Heckmam 2013). A study in Indonesia by Wijaya et al. (2009) indicated that the pods on cocoa trees treated with Si were not attacked by pod borers, and may be attributed to their having Si, resulting in being harder than they otherwise were and therefore difficult to penetrate. The uptake of Si had improved cocoa growth significantly. Hence, it can be assumed that basalt application alleviates the problem of low fertility Oxisols, which finally provides the long-term benefits to growing cocoa in the plantations.

5 Maintaining Organic Matter Level in Oxisols

Organic matter in the Oxisols on which cocoa is planted should be maintained at the sufficient level of 2–3 %. When organic matter mineralizes, the NPK released from it are added into the soil system and are eventually available for the uptake by cocoa. This would, to some extent, reduce fertilizer application and therefore cut down the cost of production. In the glasshouse experiment using an Oxisols taken from the Malaysian Cocoa Board Experimental Station, Malaysia, compost was applied as a treatment either alone or in combination with basalt. It was found that application of compost in combination with basalt had improved cocoa growth by 37 % (Anda et al. 2008b). This result is similar to that found by the field trial at the MCB Experimental Station (Anda et al. 2013). Compost being recalcitrant in nature due to the presence of a high amount of cellulose will have a long residence time in Oxisols and therefore has the potential to sustain C reserve in the soils.

6 Effects of Fertilizer and/or Amendment Application on Soil Productivity

In the planting hole, phosphate rock at the rate of 150 kg is usually applied to boost the growth of cocoa seedlings (MARDI 1990). For the mature cocoa in the field, the common fertilizers applied to supply the necessary nutrients (NPK) so as to sustain its growth are ammonium sulfate, phosphate rock, and muriate of potash, respectively. Occasionally, kieserite ($MgSO_4$) is applied to supply sufficient Mg to the cocoa plants.

It has been found in the long run that ammonium sulfate application on the soils of the tropics can result in the decrease of soil pH. This phenomenon has been observed in the rubber plantations in India by Joseph (2012), which can also occur in the soils cropped to cocoa in Malaysia. However, the increase in soil acidity can be somewhat offset by the action of phosphate (Tessens and Zaharah 1983) and sulfate ions (Shamshuddin and Ismail 1995); the specific adsorption of the two anions on the surfaces of the oxides of Fe can, to a certain extent, increase soil pH.

Another long-term effect of soil management for cocoa cultivation is the increase in pH due to GML or basalt application. The pH increase would result in the increase of CEC, attributed to the presence of a high amount of variable-charged minerals in

Oxisols (Shamshuddin 2011, 2012). Basalt application also lowers pHo with the subsequent pH and CEC increase (Shamshuddin and Fauziah 2010b), further improving the productivity of the soils. The presence of extra Ca released by the dissolving GML or basalt can reduce the effects of Al stress (Alva et al. 1986). Cocoa is expected to perform better in the presence of high-solution Ca concentration than it otherwise is.

Adding gypsum into soils with a high amount of sesquioxides is good in itself. The SO_4^{2-} thus released from the dissolution of gypsum is specifically adsorbed by the oxides, resulting in the release of hydroxyl ions that help increase the negative charge slightly (Shamshuddin and Ismail 1995). As mentioned above, the presence of extra Ca in the Oxisols due to gypsum application is able to reduce Al toxicity a bit (Alva et al. 1986). Under this condition cocoa is able to grow better than it otherwise is. It was found that by applying 4 t gypsum ha^{-1} on Oxisol, soil pH significantly increased from 4.18 to 4.54 (Shamshuddin and Ismail 1995). Thus, application of gypsum will further improve the productivity of the soil.

7 Summary and Future Prospective

In spite of their low fertility, Oxisols in Malaysia have been utilized for cocoa production in a big way. The acidity occurring in the Oxisols and the presence of toxic amounts of Al and Mn in the soil solution as well as the insufficient level of Ca and Mg can be alleviated by the application of ground magnesium limestone, basalt, and/or organic materials. Ca released by the dissolving lime or basalt can, to a certain extent, reduce Al toxicity. Cocoa is a fertilizer-demanding crop; hence, NPK fertilizers need to be adequately applied regularly. Long-term application of N fertilizer would increase soil acidity, but this will be offset by the release of hydroxyl ions as a result of phosphate and sulfate ions adsorption on the surfaces of the oxides of Fe present in the soils. The agronomic practices mentioned above should be adopted so as to sustain cocoa production on the Oxisols in Malaysia.

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Plant Mutagenesis and Crop Improvement

Ambash Riaz and Alvina Gul

Abstract To increase the production of food by a minimum of 70 % for the next decades is a big challenge. There is an urgent need to eradicate the hunger of an increasing human population, which is becoming disturbing because of climate change, decreasing water resources, a decline of arable land, and by the serious health and environmental hazard due to the use of agrochemicals. Increased production of quality food with low input is deemed to be a very fascinating option. On the other hand, the limitation of variations in plant crops, especially staple crops, limits the options of uncovering new alleles of genes. Hence, new variations among plant crops with new gene combinations and induced mutation is the better option thus far. Induced mutation uncovers the new combination of genes that result in a new breed with superior traits to the parents. In addition to that, cell and molecular biology methods are increasing the effectiveness and efficiency of mutation induction and detection of novel alleles of genes. Different mutagens mainly include physical and chemical mutagens and are now being applied by researchers for plant mutagenesis. This chapter reviews the methodology of mutation induction, mutagens that are being used for this purpose, and how they help us to improve the crop.

Keywords Agrochemical • Induced mutation • Physical and chemical mutagens • Mutagenesis

1 Introduction

Mainly in developing countries, the most important challenge is to attain increased productivity in a farmer's field for crop production. The Food and Agriculture Organization of the United Nations (FAO) reported that 70 % more food than today is required to feed the over nine billion human population estimated to live on Earth

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by 2050 (FAO). To meet this target, it is important to produce 37 % increased annual incremental rates (Tester and Langridge 2010). These difficulties are complex because of the finite nature of land and water resources for agriculture. In fact, in most parts of the world, counting the developing countries which are considered as serious food insecure regions (Tester and Langridge 2010; Hertel et al. 2010; Ringler et al. 2000; Nelson et al. 2009), these resources are either inactive or are decreasing because of the extra demands by economic and demographic pressures of urbanization and the need for the formation of bioenergy, livestock feeds, and many other industries (FAO). Climate changes and variations are also affecting the important land areas which then tend to become unsuitable land for crop production (FAO Beddington et al. 2011) causing major issues for food insecurity.

Therefore, it is clear that an important part of the required increase in the production of food cannot be achieved by further consumption of water resources and additional land. Because of harmful and unhealthy effects of agrochemicals to both humans and the environment, their use is not a sustainable option. Simply, more food must be produced with as much less input as possible to meet the world's demand (Mba 2013).

Cells of all living creations have similar genetic information yet they are different from each other. It is because mutation may occur in their genetic makeup resulting in the vast range of variations in them. Mutation is defined as the naturally occurring heritable change in genetic information of an individual and is considered the single most significant factor in account to the evolutionary prospectus which is passed on generation to generation for the development of new individuals, genera, and species (Mba et al. 2010). Furthermore, mutations can be used to study functions and nature of genes, and building blocks of plant development and growth, thus producing new beneficial genetic variation for the improvement of agriculture and economic crops (Adamu and Aliyu 2007).

It has been shown that variations in desired characteristics can be introduced into plants successfully through mutation and their practical value in plant improvement is well demonstrated. The major benefit of mutation is to improve one or two properties of a plant without changing the rest of its characteristics. Induced mutation has great ability and serves as an alternative technique in genetic improvement of agriculture crops (Mahandjiev et al. 2001). Induced mutation is used as a tool for major crop improvement such as in wheat, cotton, rice, barley, cowpea, and peanut. Many mutagens are used to induce mutations in crops; the mutagens include both physical and chemical mutagens (Ahloowalia and Maluszynski 2001).

2 Artificially Induced Mutation

Induced mutations offer a major increase in the production of crops (Kharkwal and Shu 2009) and the opportunity to induce desired characteristics in the plant that either have been lost during evolution or not found in nature. Mutagen treatment either breaks the chromosomes or alters the gene. Mutation occurs due to the error in DNA; this error is sometimes repaired or sometimes passed to the next generation and established in the organism genome as spontaneous mutations. Without phenotype appearance, a mutation cannot be detected. As a result, genetic variation appears limited and breeders only have the option to induce mutation (Adamu and Aliyu 2007). For more than several decades, mutagens have been used to induce useful mutations in plants (Vasline et al. 2005). During the past 70 years, from 175 plant species, including fruits, vegetables, pulses, oilseeds, cereals, fibers, and ornamentals, more than 2543 mutant cultivars have been released in 50 countries from all over the world (Chopra 2005; Maluszynski et al. 2000).

In the 1920s, the first-ever cases of artificial induced mutation, which is genomic lesion creation above the threshold in wild-types, in drosophila, barley, and maize were reported. Induced mutation became widespread in biological sciences after these activities. In artificially induced mutation, the increase in genetic variation is done through the effectiveness of the mutagen. Many traits such as resistance to disease, culm length, yield, maturity, and lodging resistance have been subjected to mutation. It was first evaluated that the use of artificial induced mutation by mutagen to achieve genetic variation in plant crops could be useful. Mutation is induced in plants by exposing their propagules such as meristematic cells, seeds, organs, or tissues to either physical or chemical mutagens having the mutagenic characteristic (IAEA 1977). In some cases the whole plant is exposed to the mutagen. Physical mutagens exist, such as electromagnetic radiations such as UV light, gamma rays, X-rays, and particle radiations such as alpha and beta particles, and thermal and fast neutrons. In the past, irradiation was carried out by either chronic or acute ways. Farmers, on the other hand, prefer to expose plants at relatively low doses for an extended period of time of a week or sometimes even for a month; the second way is to expose plants at high doses over relatively very small periods of time such as seconds or minutes. The existing view then was that acute irradiation caused greater mutation frequencies. At present, such differences have had no apparent effect on the output of induced mutagenesis as most induction in practice is of the acute type. Chemical mutagens are mostly base analogues such as bromouracil that during DNA replication, incorporate in DNA and stand as alternates to normal bases, intercalating agents such as ethidium bromide, and alkylating agents such as commonly used ethyl methane sulfonate (EMS). The United Nations Organization (1982) and Mba et al. (2007) listed the chemical and physical mutagens that are commonly used and also their mode of action. In common, these mutagens bring changes in the DNA of the plant, changing its characteristics, traits, and appearance. Some of the examples of induced mutagenesis in plants are given in Table 1.

Table 1 Induced mutagenesis in different plants

Facilitated mutation	Plant examples
Ability of self-compatible hermaphroditism	Grapes and papaya
Failure of the hard seed coat and other germination inhibitors	Peas, wheat, and barley
Elimination of toxicity and bitterness	Lima beans, potatoes, cabbages, nuts, almonds, watermelons, eggplants
Failure of natural seed dispersal mechanism	Barley, wheat, peas
Elimination of sexual reproduction need, i.e., parthenocarpy or seedlessness	Grapes, pineapples, bananas, oranges

2.1 Mutagenesis in Plants by Physical Methods

From the discoveries of radioactivity by Becquerel in 1896, radioactive elements by Pierre and Marie Curie in 1898 and X-rays by Roentgen in 1895, man's aptitude to artificially induced mutations in plants had been started. For these inventions, the Nobel Prize in physics was awarded to Pierre and Marie Curie, Becquerel in 1903, and to Roentgen in 1901 (Mba et al. 2012a, b). Soon after these discoveries, the demonstrations of X-rays causing alteration in the genetic makeup of crops such as maize and barley (Stadler 1928, 1930, 1931, 1932) and in fruit flies (Muller 1927) were released.

Among the most commonly used physical mutagens, ionizing radiation is one of them (Mba and Shu 2012). These radiations are the part of the electromagnetic radiation (EM) spectrum having the ability to dislodge their electron from the nuclear orbits of the atom on which they act and they also have relatively high energy. The victim atom then converts into ions, thus the term ionization radiation. These ionizing components of EM consist of X-rays, cosmic, and gamma rays (γ). As far as the nonionizing radiations are concerned, such as ultraviolet (UV) light, they are able to penetrate tissue to some extent and are also used for induced mutation.

UV light is considered as a mutagen because of its capability to interlink with DNA and other biological molecules as the wavelength of UV light is absorbed by the base pairs of DNA and by amino acids in protein which are aromatic in nature. Most commonly used physical mutagens are X-rays and gamma rays (Mba and Shu 2012). Gamma rays are produced in the procedure radioisotope decay such as cesium-137 (137Cs), cobalt-60 (60Co), and to a small extent, plutonium-239 (239Pu). Gamma sources having these kinds of isotopes are typically known as gamma cell irradiators. A gamma cell is used to induce irradiation for short periods known as acute irradiation. In the exposure of the plant to irradiation for a long period of time, known as chronic irradiation, the procedure is installed in a specially designed gamma chamber or room, field, or greenhouse (Mba 2013). On the whole, the irradiations are preserved sources usually encased in stainless steel for safety measures against unintended radiations. In all ways, only an effectively trained (which depends on national statutory requirements) and certified individual operates the irradiation source. In addition to that, special precautions such as controlled access to the irradiation sources are forced on everyone to avoid any kind of mishap (Mba 2013).

The work on induced physical mutation in China and Japan in the early and mid-1990s, respectively, resulted in applications of ion beams as a useful technique in the induced mutation in plant crops (Mei et al. 1994). Ion beam irradiation is different from the above-mentioned physical mutagens and in addition to that, mass deposition, energy transfer, and charge exchange of ion beams play an important part in their mutagenecity. It is assumed that these additional properties of ion beams give additional properties and different spectra of variations to plants when exposed under it inasmuch as compared to other mutagens ion beams are generally produced by particle accelerators, for example, cyclotrons using 14N, 56F, 7Li, 20Ne, 40Ar, or 12C as radioisotope sources (Mba 2013).

Cosmic radiations, usually known as high-energy molecules, originate from space; mainly protons have also appeared to create mutagenesis in crops (Mei et al. 1998). Mainly in China, cosmic rays in combination with microgravity and vacuum, in the general outer space environment, have been used to create useful mutations in different crops such as maize (Mei et al. 1998), tomato, cotton, sesame, sweet pepper, wheat, and rice sources (Mba 2013).

The purpose of mutagenesis is to create the highest variability in the genome with less reduction in feasibility. Of the technologies based on physical method, that is, radiation bombardment with fast neutrons and gamma rays, are now becoming most successful technologies. Among these, bombardment with fast neutrons creates large deletions, loss in chromosomes, and translocation, and irradiation with gamma rays induces small deletions and point mutations in contrast to chemical mutagens. These kinds of physical methods create damage on a large scale and badly decrease plant feasibility (Wu et al. 2005).

2.1.1 Physical Mutagenesis for the Improvement of Quality and Yield Traits

Crops propagated through vegetative propagation in combination radiation have demonstrated to be a very useful method to induce desired characteristics in plants. By inducing mutation, it is possible to induce a specific trait in the plant and make them upgraded clones (Xu et al. 2012). After soybean and palm, oilseed rapes, mainly *B. juncea*, *B. campestris* or *B. rapa* and *B. napus*, are considered the third essential supply of vegetable oil over all the world. Thus, changing fatty acid composition to improve the quality is an essential objective in improving the crop plant. But, on the other hand, they also reduce the development of the embryo and microspore embryogenesis of *Brassica napus*. Thus, choosing suitable physical mutagens is very essential for induced mutation. Analysis of the erucic acid and glucosinolate content in the mutant is done by immersing the root in 0.05 % colchicine solution for 3 h for chromosome doubling and exposure of the microspores to UV radiations. By this method, 270 double haploid line populations exhibit a high level of erucic acid and low and high levels of glucosinolate content were identified in three groups of doubled haploid lines (Barro et al. 2003).

Microspore mutagenesis use can produce mutant lines with reduced glucosinolate as compared to parents. After the UV treatment of microspores of *B. napus*, 16 mM of reduced glucosinolate content were found in contrast to 99.6 mM content in parents. The average glucosinolate in *Brassica carinata* was 80.6 mM without any physical mutagen treatment but after the exposure of its microspores under UV, the normal glucosinolate content was 37.5 mM in the mutant which is, as obvious, half of the parental (Barro et al. 2003). Barro and coworkers also demonstrated the optimization of UV treatment from the survival curve of the embryo yield after the exposure of microspores of *B. carinata*. In the doubled haploid homozygous plant seeds, analyses of fatty acid and glucosinolate content were done with the aim of selecting lines having changed erucic acid and glucosinolate content.

As mentioned earlier, 270 double haploid line populations identified with a high level of erucic acid and low and high levels of glucosinolate content were identified in three groups of doubled haploid lines. In eight lines, the glucosinolate contents were decreased with the average of 80.6 m mol g^{-1}, however, in four lines, glucosinolate contents were enhanced up to 99.2 m mol g^{-1} per seed. The erucic acid was enhanced from 42.8 % in control lines to 49.5 % of the total fatty acid composition in some lines of additional six mutant lines. In two generations, all lines exhibited stable contents of erucic acid (Xu et al. 2012).

He et al. (2007) explained the use of physical mutagen UV for microspore isolation and embryos derived from microspores of *Brassica napus* genotypes, that is, M9, h28, h57, and h58. He also demonstrated that the treatment of UV on genotype h57 for 10 s can induce highest plant generation (55.56 %) and induction of callus (77.78 %). In cassava, cyclic somatic embryogenesis was used to induce mutation (Joseph et al. 2004). To select the appropriate experimental embryo, 50 Gy of gamma radiations is a good dose for creating mutations. It is reported that over 50 % of mutant lines were morphological varieties from the wild-type line. As a result, through this method, new cassava lines with wide morphological variations were produced.

Li et al. (2005) demonstrated the effect of gamma ray irradiation on quality, yield, and development of microtubers of *Solanum tuberosum* in vitro. Explants (propagated plantlets) of two varieties of potato, Atlanti and shepody, were exposed to five doses, that is, 0, 2, 4, 6, and 8 Gy of gamma rays, to analyze the effects of low radiation on the quality and production of microtubers in vitro.

Microtubers of both varieties were exposed to gamma rays for an extra 5 days tan control (nonirradiated). For the Atlantic cultivar, the irradiation period was extended by 10–15 days with 4, 6, 8 Gy radiations. This irradiation treatment of plantlets gave major enhancement in the number of microtubers, that is, 34.5 % and 116.7 more than wild; also it gave enhancement in fresh mass, that is, 23.2 % in the Atlantic cultivar and 77.6 % in the Shepody cultivar. Low radiation, 2–4 Gy, exposure gave enhancement in microtuber starch contents and high dose, 6–8 Gy, treatment gave increased ascorbic acid and decreased amount of sugar. Medium range 4–6 Gy exposure also caused enhanced protein contents in microtubers. explained the positive effect of gamma rays on the first generation Sudan grass. They also explained the variations in Rhodes grass with enhanced gamma rays. The exposure of Rhodes grass to gamma rays demonstrates alteration in leaf, plant height, morphology of reproductive organs, habit, and stem. Sharma et al. (1989) reported changes in many commercial traits such as green matter yield.

In rapeseed, reduction of the saturated fatty acid from normal 5.7 % to 5 %, a decrease of the linolenic acid content from 11.4 % to <8 %, and increase of oleic acid level from 47.1 % to >50 % were obtained via irradiation mutation (Ferrie 1999). The fatty acid compounds and their components have greatly affected rapeseed quality, including oleic acid, linolenic acid, unsaturated fatty acid, oil contents, and so on. Kott (1996) explained that the increase of oleic acid content from 60 %

to 85 % and reduction of linolenic acid from 10 % to 3 % were obtained by chemical mutagens. These mutagens have also proved to be the main tools to create mutations in ornamental plants and fruits. It has been reported that the in vitro shoots of Pyrus communis (pear) cultivar were exposed to 3.5 Gy gamma rays and of the selected 97 variants, only two them showed chemical behavior (Predieri and Zimmerman 2001). Microcuttings from the radiated shoot and from some nonirradiated shoots, after three subcultures, were rooted to produce plants to analyze orchard shoots. Trees with improved traits, related to their production such as consistent productivity and early bearing, were produced. In Chrysanthemum morifolium Ramat cv. Lalima, mutation in its shape and color of flower were developed by gamma rays. Ray florets were inoculated on 8.87 mM BAP and 1.07 mM NAA MS media and then exposed to 0.5 and 1 Gy gamma radiations. From 0.5 Gy, two mutants were produced and vegetatively propagated to produce true-to-type flowers. Many mutants of different fruits were produced such as increased flavor banana mutant with an early ripening in Malaysia, deep red juice and flesh in seedless grapefruit mutant in Novaria and the United States, resistant to different diseases, Japanese pear in Japan, and altered skin color of apple in Austria. On the other hand, this method yet needs improvements of clonally propagated crops including sweet potato, plantain, date palm, potato, yams, and strawberry (Ahloowalia and Maluszynski 2001).

2.1.2 Physical Mutagenesis Example

Mutational Effects of Ion Beams on Plant Crops

The ion beam effect has been analyzed not only in animals but also in plants; for example, research on *Nicotiana tabacum* and *Arabidopsis thaliana* demonstrated that in comparison to low LET radiations, ion beams are more effective in reducing the survival rate and germination rate (Tanaka et al. 1997; Hase et al. 1999). Also, analysis on glabrous (gl) loci and transparent testa (tt) showed that carbon ions (113 keV mm^{-1} produced twentyfold more mutations per dose as compared to 0.2 keV mm^{-1} electrons, hence proving the ion beam's power as a mutagen (Shikazono et al. 2003, 2005). More analysis of ion beams demonstrated that it can cause a large change in DNA such as translocation, inversion, and deletion, as well as small intergenic mutations. In comparison to electrons, ion beams usually (although not every time) create deletions with different sizes ranging from 1 bp to 230 kbp (Shikazono et al. 2005). Mutants created through ion beam can be measured as nulls or destroyed in several cases as deletion through ion beams led to total gene loss or frame-shift. It is an important difference from chemical mutagens such as EME, which usually induce point mutation by transition of AT-GC.

The major mutational ion beams effect is because of high double strand breakup (DSB) due to ions. The analysis on tobacco BY-2 protoplast as a model demonstrated that early DSB yeils were positively linked with LET and the high LET neon, carbon, and helium ions more efficient in creating DSBs in comparison to

C-rays (Yokota et al. 2007). In addition to that, it was shown that neon and carbon ions produced short fragments of DNA more consistently compared to C-rays, showing that ions can take action locally and densely on the genome to be targeted (Yokota et al. 2007).

It might be possible that ion beams induce a high rate of mutation because it is more complicated for a cell to repair DBS than single strand breakage. On the other hand, the molecular mechanism of mutation induced by an ion-mediated mechanism is yet to be explored. To resolve the issue, the breakpoints of DNA flanking sequences, generated by ion beams were analyzed and demonstrated that several analyzed sequences have 1–29 bp deletions whereas many breakpoints produced by electrons were flanked by 107 bp duplications (Shikazono et al. 2005). Based on this research, it is hypothesized that high LET ions produce DSBs as well as cause great damage to broken ends unlike electrons and these damaged ends may be removed during the natural process of repairing, hence, causing the deletion mutation (Shikazono et al. 2005).

Even though more research is necessary to clarify its accurate mode of action, ion beams can be considered an effective alternative to other mutagens such as low LET radiations and EMS that can induce high mutation and a mutational spectrum. Thus far, ion beam is used as a mutagen to a large number of plant varieties such as *Lotus japonicas*, chrysanthemums, *Arabidopsis thaliana*, carnations, and so on. It is important to analyze that this method has been thriving in the isolation of new mutant lines, doing a great job in plant breeding and genetics.

Ion Beams for Forward Genetics

Mutant isolation is only a first step in forward genetics but it is a very vital process that helps in analyzing any related gene function and giving a new vision to any physiological or developmental event. The technique of mutagenesis through ion beams has a great role in plant research, for example, by screening of M2 generation *Arabidopsis* seeds irradiated by carbon ions to produce plant lines resistant to a chemical named *p*-chlorophenoxyisobutyric acid that disturbs the auxin signaling pathway; a new mutant antiauxin resistant1-1 (aar1-1) was recognized (Rahman et al. 2006). Further analysis of this new mutant showed that the mutant displayed a satisfying response specifically to 2,4-dichlorophenoxyacetic acid (2,4D), a synthetic auxin, but did not show any response to indole-3-acetic acid (IAA), natural auxin (Rahman et al. 2006). As it has been known that both IAA and 2,4D have the same effect on the signaling pathway of auxin in spite of their stability differences, this result was very surprising. It was shown that the mutation aar1-1 is the deletion of 44 kb around eight annotated genes (Rahman et al. 2006). From them, a gene code for acidic protein, SMAP1, was revealed to be singly responsible for the phenotype of aar1-1 (Rahman et al. 2006). In addition to that, SMAP1 protein molecular analysis is important to reveal the 2,4D specific signaling pathway of auxin.

A model of legume *Lotus japonicas* has also been exposed to ion beams. Leguminous plants create a symbiotic relationship with bacteria living in soil called rhizobia, which supply ammonia to the host plant through nitrogen fixation. As organogenesis is relatively costly, the host plants firmly control the nodule number and its growth. For this reason, legumes developed a long signaling pathway that reduces adverse extra production of nodules. A CLAVATA1-like receptor kinase gene is needed for this regulatory system and the mutations in this gene create the hypernodulation phenotype (Krusell et al. 2002; Nishimura et al. 2002; Searle et al. 2003; Elise et al. 2005). But a defined molecular mechanism has not been clarified because of the absence of other mutants of hypernodulation despite several efforts of isolating such plant lines from *N. Suganuma* and *L. japonicus* using T-DNA or EMS mutagenesis (Nishimura et al. 2002; Schauser et al. 1998; Szczyglowski et al. 1998). To avoid this problem, use of helium ions as an alternative mutagen was experimented with and a new mutant line of Lotus hyperrnodulating, clavier (klv), was released (Oka-Kira et al. 2005). Using the klv mutant for the grafting experiment demonstrated that klv is essential in shoots as compared to the root, showing that klv in combination with CLV1-like receptor kinase gene, make an extended signaling pathway that maintains the nodule number (Oka-Kira et al. 2005). This successful recognition of the klv mutant showed high mutagenic efficiency of ion beams and also demonstrated a different spectrum of mutation in comparison to T-DNA and EMS.

Ion Beam Limitations

Ion beam mutagenesis methods have been practiced with many plant varieties in the research field; as mentioned before, it has been considered a successful method to produce novel mutants. Because of its high LET properties, it effectiveness can be justified which eventually results in creating a unique spectrum of mutations, strong mutational effect, and high DSB yield as compared to other physical as well as chemical mutagens. On the other hand, ion beams have some limitations that should be considered before any experiment related to ion beams commences; for example, mutations induced by ion beams are mostly deletions that can result in total loss of gene or frame-shifting, hence, ion beams are not good for isolation of hypomorphic mutants. Furthermore, ion beam irradiation creates many other kinds of mutations such as translocation, abnormalities in chromosomes, large deletions up to 100 kb, small intergenic deletions, and inversions. Even though this large mutation by ion beams is advantageous for the induction of new mutants, the randomness of mutation patterns can effectively create problems of molecular cloning of the gene in many cases (Magori et al. 2010).

2.2 *Mutagenesis in Plants by Chemical Methods*

About two decades after the use of physical mutagens on crops, nitrogen mustard, and poisonous mustard gas used during World Wars 1 and 2, were shown to have the potential to cause mutations in cells (Auerbach and Robson 1946a, b, 1947)

Chemical mutagenesis is a technique to create useful mutations in plants for the improvement in their traits such as their germination ability and other related agronomic traits. Proper selection of efficient and effective mutagens is very important in any mutation program so they can produce a high frequency of desirable and useful mutations in plants. In many crop species, various chemical mutagens have been applied to obtain desirable mutations (Roychowdhury and Tah 2011a, b). On the other hand, many scientists highlighted that artificially induced mutation by sodium azide (SA), ethyl methanesulphonate (EMS), and colchicine (Col) give better access to overcome the limited variability in plants, especially carnation that produce the specific mutation without disturbing the other traits of plants (Roychowdhury and Tah 2011a, b). It might be assumed that growth abnormalities which develop in plants after chemically induced mutation are due to suppression of mitosis and cell death at different exposures to chemicals. Colchicine is a chemical known for its chromosome doubling ability, and also possesses antimicrotublar action. Sodium azide is a chemical agent responsible for creating point mutation in the DNA level and EMS is a common alkylating agent, but on the other hand, these chemicals have been shown to have great potential to produce useful mutations in the plant genome thus creating variations among a plant species. Hence, they become important techniques to increase the agronomic characteristics of crop plants (Roychowdhury and Tah 2011a, b).

Chemical mutagens are widely used because of their characteristics such as ease in handling; they do not need extra equipment and can induce maximum mutation frequency. As compared to physical mutagens, chemical mutagens alter the single base pair (bp), or single nucleotide polymorphism (SNPs). Ethyl methanesulfonate is widely used among all the chemical mutagens. During DNA replication, it creates the alkylation selectively on guanine bases resulting in the DNA polymerase replacing the cytosine residue with thymine residue opposite the *O*-6-ethyl guanine causing the random point mutation. Most transitions (70–99 %) that EMS causes are the change of GC base pairs to AT base pairs (Till et al. 2004, 2007). Mutation in coding regions of DNA can also be silent, that is, nonsense or mis-sense. In the noncoding region of DNA, mutation can cause up- or downregulation of gene transcription by altering its promoter or other regulatory regions, in the result of mutagenesis, abnormal mRNA splicing. Changed stability of RNA and alteration in protein translation may also occur.

Other chemical mutagens such as methylnitosourea (MNU) and sodium azide (Az) are also being used with the combination of Az-MNU solution. Generally, Az-MNU causes the shifting of base pairs specifically AT to GC and GC to AT. Hence, compared to EMS, the shift can go either way (18). All three chemical mutagens mentioned above can be extremely carcinogenic and must be handled with extra care. Unlike EMS, the MNU mutagen is unstable above 20 °C temperature and it is also sensitive to shock, creating difficulties to work with it. Compared to MNU and EMS which are both in liquid form in their ground state, Az is a solid dust, making it less attractive because of the additional step of dissolving the volatile substances and acute toxicity (Sikora et al. 2011).

For many years, mutagens have created a large amount of genetic variations in plants and have played a significant role in plant breeding programs all over the world. It was reported by the FAO/IAEA division in Vienna that with the help of induced mutation, 2965 crops with one or more useful traits were created during the last 40 years and released all over the world (FAO-IAEA 2011). There are many examples of crops such as barley including malting barley, cotton, grapefruit, wheat (e.g., durum wheat), rice, and sunflower that ultimately resulted in a positive economic impact (Sikora et al. 2011).

A number of scientists have reported the use of mutations to create useful characteristics and genetic variations in crop plants (Tah 2006; Khan and Goyal 2009; Mostafa 2011). In any mutagenesis program, it is important to consider the dose of chemical mutagen. In general, a higher concentration of mutagen causes greater biological damage. To increase pollen sterility, lethality, metrical traits, and germination of seed, great knowledge is required about pH value, seed soaking, chemical concentrations, and the effects of time and temperature (Khan et al. 2009). Carnation offers many chances of utilization of increasing genetic variability, recombination, and mutations in quantitatively inherited agronomic characteristics. Induced mutations are the ideal technique when it comes to improve identifiable traits. Present research has proven that genetic variability is connected with the metrical traits and germination behavior in the Dianthus crop. Hence, induced genetic variations can be effectively utilized for developing mutant strains having desirable properties (Roychowdhury and Tah 2011a, b).

2.2.1 Chemical Mutagenesis for Improving Quality and Yield Traits

EMS is a strong chemical mutagen that can alter chromosome structure. Barro et al. (2001) explained that with the treatment of EMS doubled haploid mutants with altered erucic acid were produced in *Brassica carinata*. It was done to identify the modified erucic acid level in mutant lines of *Brassica carinata*.

Nine lines were isolated from a nearly 400 doubled haploid recovered plant population that showed useful alteration in erucic acid level in the seed oil. Among these, three mutant lines exhibited below 25 %, minimum of 17 %, of erucic acid and this fatty acid concentration was more than 25 % in three lines. By microspore mutation, some very good characters related to agriculture can also be identified. In *Brassica napus*, the mutant lines with dwarf stem and long pod were attained through chemical mutagenesis using 0.2 % and 0.25 % EMS (Shi et al. 1995).

To create the new varieties of chrysanthemum (*Dendranthema grandiflora Tzvelev*), mutation through EMS in immature floral pedicels were reported by Latado et al. (2004). Pedicels of chrysanthemum cultivar Ingrid were inoculated in the 0.77 % solution of EMS for 1 h and 45 min, then washed with water for 15 min and inoculated in MS media with vitamin and salts in combination with 2 mg L^{-1} IAA, 1 mg L^{-1} BAP, and 1 g L^{-1} of hydrolyzed casein. From the population of 910 plants treated with EMS, 48 mutants were identified as having different petal color: light pink, yellow bronze, salmon pink, and pink salmon. Many of them, 89.6 % of the total, were phenotypically uniform. Many chlorophyll mutants of *Nicotiana tabacum* anthers were identified by the treatment of EMS (Medrano et al. 1986). Stable mutants of rice anthers were also obtained by EMS treatment (Lee and Lee 2002). It has been found that the anthers treated with 0.5 % solution of EMS for 10 days after culture showed the frequencies of stable mutants, green plant regeneration, and induction of callus. EMS treated at 10 and 20 days showed stable mutant frequencies of 20.7 % and 12.0 %, respectively. Hence, it is assumed that the good timing of EMS treatment after inoculation of anther on the medium can enhance the stable mutant frequency of rice cultured anthers. Hofmann et al. (2004) reported that soybean embryonic cultures were also treated with EMS for mutation induction. It is complicated to get haploid plants in *Solanum* species through in vitro androgenesis, however; the efficiency of androgenic progeny can be enhanced by the use of EMS in *Solanum nigrum* (Kopecky and Vagera 2005).

A protocol was developed for production of physiological or agronomical mutants of two varieties of barley, Cobra and Igri, and also the production of low androgenic responding cultivar of barley by the treatment of a chemical mutagen sodium azide (NaN3) to isolate the culture of microspores in vitro (Castillo et al. 2001). The treatment of mutagen NaN3 with different concentrations was used during anther induction pretreatment right after the process of microscope isolation which makes them produce double haploid plants.

Different concentrations of mutagen EMS (i.e., 0.001, 0.01, 0.1 %) and NaN3 (i.e., 1, 10, 100 mM) were used for the isolation of microspores and embryos, at the early cotyledon stage of oilseed rape at different time intervals of 1, 5, and15 h (He et al. 2007). It was demonstrated that with a low concentration of chemical mutagen, a high yield of embryos was obtained, however, with the increase of mutagen concentrations and prolonged time period, the embryo yield gradually reduced. With the increase in EME concentrations and extended time period, the germination and survival of embryos were reduced. But, when 0.01 % EMS concentration was applied on embryos for 5 h, better results were obtained as embryo survival, high germination rate of embryos, and plant regeneration were achieved. The treatment of a low concentration of NaN3 was an encouraging effect on plant regeneration and embryogenesis in most studies of the genotype. Plant regeneration rates of genotype M9, h57, and h58 were obtained of 11.11, 15.79, and 22.22 %, respectively, when microspores were treated with NaN3 with the concentration of 10 mM for 1 h. Twenty-eight genotypes gave the highest plant regeneration rate, 19.05 %, when their embryos, developed from microspores, were treated with NaN3 with the concentration of 10 mM for 1 h. On the other hand, when NaN3 concentration was increased to 100 mM, no plant regeneration was found in all genotypes. Hence, it is indicated that use of the proper concentration of NaN3is an important step in in vitro mutagenesis.

An efficient procedure for the development of double haploids, derived from microspores of *B. juncea*, was developed with high frequency of embryo and embryogenic conversion applied to the investigation of reduced glucosinolate trait from a canola quality *B. juncea* line named Heera to a famous variety Varuna of India by backcrossing (Mukhopadhyay et al. 2007). Microspore culture showed

65–70 % production of double haploid when treated with colchicine and these microspores, when transferred to the field, exhibited a reduced mortality rate of 10 %. Freshly isolated microspores of rapeseed in the induction medium treated with colchicine for 3 days resulted in improved embryogenesis without any side effect on the embryo development (Iqbal et al. 1994; Zaki and Dickinson 1991). Isolated microspores short-term treated with colchicine enhanced the embryogenesis frequency and cell division number in *Brassica napus* (Zhang et al. 2003). After isolation of microspores, 12–15 h seems to be the optimal time for such treatments. Many approaches are being experimented with, including the other antimicrotubule compounds such as oryzalin, pronamide, trifle uraline, and amiprophose-methyle (APM) usage for doubling of chromosomes and embryogenesis during the early steps of microspore culture. The right combination of time duration for the treatment and concentration of colchicine is very important for diploidization and embryogenesis. Zhou et al. (2002a, b) reported that immediate treatment of colchicine on haploid microspores of winter and spring *Brassica napus* exhibited better diploidization and embryogenesis. Treatment of colchicine with the concentration of 500 mg L^{-1} for 15 h gave hg doubling frequency of 83–91 %. Furthermore, at this stage, very few chimeric and polyploid plants developed.

2.2.2 Chemical Mutagenesis Example

Mutational Effect of Sodium Azide on Plant Crops

Sodium azide (NaN3) is a chemical mutagen and is considered an important mutagen for crop plants. It has been shown that sodium azide is effective for physiology of plants and reduces cyanide-resistant respiration in tobacco callus (Al-Qurainy and Khan 2009). In many organisms including animals and plants, it is identified as a powerful mutagenic (Rines 1985; Owais and Kleinhofs 1988; Raicu and Mixich 1992; Grant and Salamone 1994) and it is also described in many screening assays. In different organisms, sodium azide is slightly mutagenic (Jones et al. 1980; Arenaz et al. 1989). The mutagenicity is interceded through the production of an organic metabolite of sodium azide (Owais and Kleinhofs 1988). This metabolite of azide compound first enters in the cell nucleus, makes connection with DNA, and induces point mutation in the host genome. To understand the mechanism of its mutagenicity, much research has been performed on bacteria and barley in recent years (Kleinhofs et al. 1978; Nilan and Pearson 1975). As it is a strong mutagen, it makes strong contact with plant parts and effects its growth by disturbing the plant metabolic mechanism.

Mutagenic Effects of NaN3 on Plant Parts

As mentioned above, sodium azide is a powerful mutagen and strongly inhibits the growth of parts of the plant with the increase of its concentration and treatment time period. The effect of sodium azide is explained on tomato and it is observed that it is very effective in inducing mutation which ultimately alters root length, seedling survival, plant yield, germination percentage, seedling height, and branches per plant (Adamu and Aliyu 2007). In different crops, effectiveness of different concentrations of sodium azide treatment on root length was observed. The barley group treated with 2.5 mM of sodium azide for 3 h time period showed the lowest length of root, that is, 9.1 cm on day 14 except for the group treated with NaN3 for 3 h of time period and observed on day 7 and this exposure had a strong effect on the length of the leaf (Jia and Li 2008). The decrease in seedling survival is due to physiological disturbance and cytogenetic damage. At higher mutagenic concentrations, many factors such as changes in cell activity showed high sensitivity (Maherchandani 1975).

Effect of NaN3 on Chromosomes

To estimate mutagen potency, analysis of cytoplasm during either mitosis or meiosis is known as one of the most reliable ways. It shows a clear image of plant sensitivity for different mutagens. The nature or mutation and action mechanism induced by NaN3 is now being understood and it was started by the discovery of metabolites produced by NaN3. During mitosis, the chromosomes are damaged by NaN3 as shown in bean (Kihlman 1959), barley (Nilan and Pearson 1975; Kleinhofs et al. 1974), and leukocytes of humans (Al-Qura:iny and Khan 2009). Hence, NaN3 induced abnormality in chromosomes which are either similar or a little superior to that of untreated controls. Sticky and bridge chromosomes, translocation, and lagging chromosomes are the most prominent abnormalities induced by NaN3. Inappropriate folding of chromosomes gives rise to chromosome stickiness making intermingling of chromatin fibers and chromosomes connected to each other through subchromatid bridges. With an increase in dose of NaN3, chromosome lagging also increases (Al-Qurainy and Khan 2009). The organization of spindle fibers and their movement during mitosis is dependent on ATP. Because of less availability and limited production of ATP molecules, the organization of spindle fibers in root tip cells treated with NaN3 may be disturbed, which eventually creates a disturbance in the chromosomal organization on the metaphase plate and chromosome migration toward their respective poles during anaphase (Al-Qurainy and Khan 2009). This leads to chromosomal aberrations such as sticky chromosomes, lagging chromosomes, and bridge formation as mentioned before. Hence mutagenic activities reduce the germination percentage and enhance the chromosomal abnormalities in mitotic cells of root tips (Siddiqui et al. 2007). Mutagens created changes in the structure of chromosomes and induced mutation that may be responsible for creating abnormalities in homologous chromosome pairing. Adegoke (1984) described the NaN3-induced damage in chromosomes, which results in the formation of chromosomal bridges during cell division and thus increased phenotypic changing. It also plays a major role in genetic sterility as described in rice (Mensah et al. 2005). Both colchicine and NaN3 are mutagenic agents and polyploidizing and used for a long time for creating polyploidy in plants. Ahoowalia (1967) reported the mutagenic effect of NaN3 on plant chlorophyll, yield, morphology, and sterility.

Sodium Azide Applications and Crop Improvement

For the improvement of crops, it is necessary to have genetic variability. These variations are created through natural or artificially induced mutation. This method has been used in the production of many improved cultivars and crops such as rice, soybean, vegetables, wheat, barley, ornamentals, and lupines, despite its limitation and advantages. The artificially induced mutation is a practical method to get improvement in crop genetics with the help of chemical or physical mutagens that enhance the mutation frequency as compared to natural occurrence. On the other hand, for broad use of these mutagens, high mutagenic activity is an important consideration which means that the use of a mutagen is not only dependent on its effectiveness but also on its efficiency as effectiveness of a mutagen has no implications inasmuch as chemical and physical mutagens are relatively inexpensive. However, reduced mutagen efficiency of mutagens can limit their usage (Al-Qurainy and Khan 2009). Mutagenic efficiency means the induction of a desirable trait without affecting other undesirable genetic characteristics of the plant. This is usually measured by proportion of the frequency of mutation and damage related to mutagen treatment such as chromosomal breakage, reduction in height, lethality, sterility, and so on. Mutagen usage for the improvement of crops helps in understanding the mutation induction mechanism and to quantify the frequency, also the changes of pattern in different plants by mutagens. The capability of mutagens to enter the cell of an organism for DNA interaction developed the toxic effect related to their mutagenic properties. Hence, their effects are generally because of direct interaction between the molecules of DNA and the mutagen (Al-Qurainy and Khan 2009). Some of the examples of plant crops successfully produced by the sodium azide treatment are given in Table 2.

Table 2 Plant crops successfully produced by the treatment of sodium azide

Common names of crops	Scientific names of crops	Mutated traits
Sunflower	*Helianthusannuus*	1. Reduced proanthocynidin and anthocyanin content 2. Resistant to mildew 3. Chlorophyll mutant line
Rice	*Oryza sativa* L.	1. Increased amylase content 2. Auxin resistant mutant
Groundnuts	*Arachis hypogaea* L.	Disease resistant
Oat	*Avena strigosa*	Disease resistant
Pea	*Pisum sativum*	Reduced pyridoxin
Maize	*Zea mays*	Resistant against striga (pathogen)
Sugarcane	*Saccharum officinarum*	Resistant to red rot

Mutagenic Effect of NaN3 on Root Growth and Regeneration of Somatic Embryo of Cotton

The tissue culture technique is considered an important method for plant improvement through in vitro mutagenesis, genetic engineering, and induction of somaclonal variations. Among many other techniques, plant somatic embryogenesis via callus induction is a widely used technique in various species of plants for the mutant regeneration, genetic transformation, and induction of somaclonal variations. Cotton, *Gossypium hirsutum L.*, is an essential fiber plant crop regarding the economy; in fact, 180 million humans are dependent on the production of cotton for seed oil and the textile industry (Benedict and Altman 2001). A cotton pigment produces a polyphenolic binaphthyl dialdehyde compound named gossypol and gives resistance to cotton. This compound has many characteristics such as antimicrobial, anticancer, male contraceptive, antioxidation, and anti-HIV (PICMA 1995). A proficient protocol has been developed for the increased regeneration of somatic embryo that includes oxygen supplements for the growing embryo (Shimazu and Kurata 1999), germination mediated by hemoglobin, and induced germination (Ganesan and Jayabalan 2004; Jayabalan et al. 2004).

In this analysis, in vitro mutagenesis mediated by mutagen sodium azide to develop improved frequency of cotton somatic embryogenesis was observed. In the improvement of the crop plant, mutation methods have confirmed their ability for developing useful variations. Because of in vitro difficulties in the regeneration of cotton, mutant lines of cotton regeneration were not reported (Rajasekaran et al. 1996).

To produce both genotypic and phenotypic variations, in vitro mutagenesis is an essential method. Natural variations found in regenerated plant lines are named somaclonal variations and in plantlets derived from callus, somaclonal variations are a very common mechanism. Both induce mutagenesis by mutagens and natural mutation, somaclonal variations, and result in the production of new traits without disturbing the rest of the genome. However, in contrast with natural variations, mutagenic compound induced mutations give efficient variation in plant crops. The impact and efficiency of mutagens for the improvement of crops has been reported by many scientists (Rutger 1992; Maluszynski 1990), as mentioned before. In vitro mutagenesis can help to tackle some limitations such as calculation of mutagenesis frequency of the mutated line having desired traits, the time required for regeneration of the mutated plant line, and techniques required for screening the effective mutated line (Maluszynski 1990). Chemical mutagen sodium azide is used widely due to its low cost, easy handling (Lundqvist 1992), and efficient mutagenic properties (Konzak et al. 1972).

3 Chemical Mutagenesis and TILLING

For the last decade, because of Targeting Induced Local Lesions in Genomes (TILLING) technology, the use of mutations induced by chemicals is more profound than any other method. In this technique, mutagenesis is balanced by the chromosomal DNA isolation of all mutated lines and by the screening of the mutated population at the DNA level with the help of molecular techniques. TILLING seeds are treated with a strong mutagen, as in basic mutagenesis, which randomly induces mutation in the genome, but to achieve mutation saturation in the genome, extra care is also required. Before development of the TILLING population, most scientists started their work by developing a kill curve by the use of selected mutagens, concentration of which were plotted against survivability of the seed and the general rule of thumb mainly aiming for a survival rate of 30–80 % (Wang et al. 2010; Chawade et al. 2010). Mutagenesis then followed by seed (M1) plantation which allowed self-fertilization and development of the next seed generation (M2). Usually, one seed for each line of M1 generation was propagated to develop the M2 generation and DNA isolation was done from every single plant of the M2 generation.

Given that the high mutation number per genome and large population size, it is considered that mutated alleles of all genes are present in the population. Target crop ploidy is a main thing to consider in the analysis of the optimal TILLING population size because it is assumed that then induced mutagenesis frequency and ploidy of the targeted crop are strongly interlinked. It is demonstrated that the frequency of mutation is high in hexaploid plants such as wheat and oat without making them fertile or killing them, as compared to diploid plants such as barley and rice. That's why the TILLING population rarely needs to go above 5000 individual lines. However, the range of 10,000 lines is frequently needed in the population of diploid plants (Chawade et al. 2010; Caldwell et al. 2004).

4 Sodium Azide and Gamma-Ray Radiation Mutagenic Efficiency in Rice

Many scientists have proposed the use of two different mutagen treatments to enhance mutation induction efficiency and effectiveness. Now the question is whether these combined mutagens have any extra effect on plant mutagenesis regarding mutation frequency. Lately, some mutagen combinations were tested on rice; that is, gamma rays were combined with different chemical mutagens such as MMU, HA, and NMU (Rao and Rao 1983), EMS (Rao 1977), DES and EMS (Kaul and Bhan 1977), and SA (Reddi and Rao 1988).

At the Centro de Energia Nuclear na Agricultura, in Piracicaba, São Paulo, 500 dormant and dried Brazilian rice variety IAC-1246 seeds were exposed to gamma rays of 10, 15, 20, and 30 Kr of Co60 source. In an experiment chlorophyll mutant lines of rice were created by the combination of sodium azide and gamma rays and with sole treatment of each mutagen as well. The azide treatment gave the highest percentage results of chlorophyll mutagenesis in rice, followed by combined treatment of sodium azide and gamma rays and the least percentage was given by gamma ray treatment. On the other hand, M2 plants mutant frequency was more efficient in combined treatment of 5 mM sodium azide and 15 Kr gamma rays than any of the solo mutagen treatments. In general, the mutagenesis frequency is more effective in sodium azide as compared to gamma rays (Ando and Montalván 2001).

5 Past Achievements in Induced Mutagenesis

The main strategy in mutation has been to improve the adapted varieties of plant by changing their one or two important characteristics. These characteristics include seed shattering, plant maturity, and height and disease resistance, which increased the quality and yields with traits such as malting quality, oil content and profile, quality, and size of starch granules. For example, short height mutation in wheat, maize, barley, and rice has significantly contributed to enhance grain yield. This allowed the use of nitrogen application in high doses. With the use of chemical and physical mutagens, various such types were being produced, for example, Calrose 76 (the semi-dwarf rice mutant) released in California has the property of stiff and short straw and has a main role in contributing to rice production in the United States, as did as the short height rice mutant named Basmati 370 in Pakistan. In India, many rice mutants via gamma radiation were released with maximum yielding cultivars under the series PNR; some are in early maturation and had small height (Chakrabarti 1995). Zhefu 802, considered an outstanding mutant of rice, was grown in China over more than 10.6 million ha for 10 years. In 1977, an aromatic indica variety of rice named RD6 was produced in Thailand through gamma radiation. This variety is still grown in Thailand even several years after its release. During the wet season of 1994–1995, this variety was planted on about 2.4 million ha (15.2 rai) which covered the 26.3 % area under rice during the season. In 1978, another mutant called RD15 was released which was planted over 0.2 million ha, equal to 3.2 % area under rice (Anonymous 1995). In *Japonica* rice, a thermosensitive genic male-sterile mutant, controlled by a recessive gene, has helped mainly to develop methods for production of hybrid rice varieties. In China, similar mutants were introduced by using gamma rays in indica rice named 26 Zhaizao (Ahloowalia and Maluszynski 2001).

Several mutants are released as cultivars; many others have been used as parents for the production of new cultivars. In Europe, the production of short height and high-yielding mutants of barley named Golden Promise and Diamant have had a major effect on the brewing industry. These mutants were then used as parents for many new barley cultivars in 1987, and had a main effect on supporting the development of the textile industry in Pakistan. This cultivar has the properties of determinate growth rate, heat tolerance, and bollworm attack resistance because of its early maturity, which made it a perfect cultivar for cotton and wheat rotation. In India, in the early years of the Green Revolution, the production of a mutant of Sonora named Sharbati Sonora showed great acceptance by customers because of its better grain color. Many high-yielding, early-maturing varieties of peanut called Yueyou series were produced in China, which were produced from crosses with mutants developed by radiation. A mutant variety of peanut TG-26 was recently developed at the Bhabha Atomic Research Center, Bombay, India.

At the farm level, India yielded 9.4 tons/h nuts. Based on induced mutation (Green 1986; Dribnenki et al. 1996), the production of a cultivar with good oil quality named linola, has the most recent and important role in changing oil quality as it had been done before in high oleic acid in sunflower and in canola from rapeseed. At present, some mutants that have reduced glycoalkaloid content in potato tuber (Love et al. 1996) have been reported. But the technology still needs more improvement for the propagation of crops such as yams, strawberry, plantain, date palm, and sweet potato.

Recently, mutants have been reported for reduced glycoalkaloid content in potato tubers. On the other hand, the technology has yet to be tested for the development of clonally propagated crops such as sweet potato, date palm, yams, plantain, and strawberry (Ahloowalia and Maluszynski 2001).

6 Use of Induced Mutations in Basic Research

6.1 Developmental Mutants

In *Arabidopsis*, various mutants have been used to observe genes that show response to plant growth hormones, that is, auxins, cytokinins, gibberellin, abscisic acid, and ethylene in the development of floral, formation of fruits, plant growth, senescence, and fruit ripening. The mutants make identification, isolation, and cloning of the genes possible, which helps to produce crops with increased tolerance to stresses, reduced agronomic inputs, improved yield, and longer shelf life (Ahloowalia and Maluszynski 2001).

There are induced mutations in many crops such as maize, pea, tobacco, barley, and *Arabidopsis thaliana* for the isolation and identification of genes that control the development of plants, especially floral parts formation, fruit ripening, formation of fruit and seeds, and the onset of flowering. These mutants engage growth hormones, phytohormones, including auxins, cytokinins, gibberellin, abscisic acid, ethylene, and brassinosteroids. The study of regulation of phenotype at the molecular level and biosynthesis level in plants had been a slow procedure (Ahloowalia and Maluszynski 2001).

The dissection of loci is now possible due to the ease with which many mutants can be identified and isolated among the *Arabidopsis* mutagenized population. In various cases, to study plants with different traits at the morphological as well as biochemical level, these genes have been isolated and cloned. In addition to that, in *Arabidopsis*, mutagenesis based on T-DNA insertion increased our knowledge of plant biochemistry, physiology, and development. Without the process of induced mutation, mutant production, and mutagenesis basis, this progress would not have been possible. The study of a mutant, named super root (sur1) which produces extra free auxins showed the genetics basis of auxin synthesis regulation. Another mutant, fass, reduces elongation of cells in the basal and apical axis, and demonstrated the usage of locus in auxin homeostasis and auxin conjugation (Ahloowalia and Maluszynski 2001).

There are various mutants that are effective for auxin transduction (axr1, axr4), auxin uptake, auxin inhibition, and auxin transport (aux1, pid, mp, lop1), and many others that are being used to analyze auxin metabolism (Leyser 1997). In the same way, many mutants with changed response to cytokinins are now accessible that help to create a better understanding of the nature of cytokinin action. Such mutants include photomorphogenesis mutants (det1, cop), cell division mutants, increased cytokinin levels (amp1), and cytokinin resistant mutants. With the decrease/increase in the specific transcripts, gene expression of plants can be effectively changed in response to cytokinins. Such kinds of genes are usually regulated by extra change such as auxins and light. In *Arabidopsis thaliana*, many mutants of cytokinin and related to its metabolism such as zea, cry1, ckr1, stp1, and ein2 have been isolated. They are cytokinin resistance and have explained that genes for cytokinin regulation may be involved in many biological processes such as photosynthesis, disease resistance, chloroplast development, and nutrient metabolism (Schmülling et al. 1997). Understanding main processes is important to understand plant crops with enhanced growth rate, yield, resistance to disease, and better nutrient uptake. In Japan, *Gibberellafujikuroiis* used to infect elongated rice seedlings resulted in the isolation of gibberellic acids in the form of crystalline (Yabuta and Sumiki 1938). In comparison to other cytokinins and auxin, mutants with changed elongation of shoot in maize and pea were used to analyze gibberellins early in 1955 and 1956. The mutation restored the wild-type phenotypes of dwarf mutants of maize and pea by the application of GA3. From then on, many mutants involved in enzymes that catalyze GA biosynthesis pathways (ls-1 and lh-2 in pea, an1 and d3 in maize, dx in rice, and gal-3 in *Arabidopsis*) and directly in GA synthesis, were isolated in maize, wheat, *Arabidopsis*, rice, and pea. A dwarf mutant of barley deficient in GA showed reduced amylase activity. Some other mutants such as spy and gai in *Arabidopsis* are GA responsive. Some mutants short in height such as D8 in maize and Rht3 in wheat are deficient in GA and do not respond when GA3 is applied (Ross et al. 1997). Improvement of several cereals such as rice, barley, wheat, and sorghum, and dwarf mutant whether induced or natural, have played an important role in the development of high fertilizer responsive and lodging resistance varieties.

The genetic study of signal transduction of abscisic acid has been based on several mutants deficient in ABA such as aba2 in *Nicotiana plumbaginifolia* and aba1 in *Arabidopsis* that are orthologous as revealed by mapping and transposon tagging isolation. Other mutants that give altered response to application of ABA such as abi1, abi2, abi3, and abi4 showed a marked decrease in the germination of seed (Merlot and Giraudat 1997). Such types of genes are highly useful for cereal varieties that sprout in situ in the period during seed maturation. A mutant etr1 of *Arabidopsis* that gives synthesis of ethylene has a main role in enhancing the shelf life of fruits, delayed senescence, and extended flower life demonstrated by its transfer to petunia and tomato (Wilkinson et al. 1997). Many such types of mutant such as the Nr mutant of tomato and ain, einif *Arabidopsis* have very limited response to ethylene. These mutants also have an important role in the trade of fruits such as mango, banana, pineapple, cut flowers, and papaya which spoil after ripening. Mutants that develop defective flowers known as homeotic mutants have been isolated in petunia, *Arabidopsis*, *Lycopersicon*, and*Antirrhinum*. Three groups of gene A, B, and C, single or in combination, control the development of organs in the four whorls of dicot flowers. These are the mutations in homeotic gene, GREENPETALS in petunia, FLORICULA, PISTILLATA, AGAMOUS, and SQUAMOSA in tomato (designated TAG1 that alter structures of flowers such as sepals, petals, anthers), GLOBOSA, DEFICIENS A, APETLA3, PLENA, and AGAMOUS in *Antirrhinum* lechomeotic mutant of leafy cotyledons, developed via insertion mutagenesis in *Arabidopsis*, are defective for embryo maturation that remain green (Meinke 1992).

The fis mutants that controlled the development of seed without fertilization, have an important role in understanding apomixes (Chaudhury et al. 1997). The mutant isolation that determines development of fruits, seeds, and flowers, has an important role in our understanding of the general patterns of plant development. The quality and yield of crop plants are determined by the development patterns in plant crops. The options of changing them will open new ways in plant genetics. The recent study on the maize mutant INDETERMINATE (ID1) verifies the signal translocation from the shoot apical meristem, where it develops flowering, to the leaves. This might be considered as a first step to the subtle florigen, concerned in the photoperiodic response of plant flowering (Ahloowalia and Maluszynski 2001).

6.2 Mutants for Changing Starch Quality

Starch is an important carbohydrate that is stored in tubers and seed amyloplasts. Most starch is produced in a few crops such as maize, oats, barley, potato, banana, rice, sorghum, cassava, sweet potato, plantain, and wheat. It can be divided into two macromolecules, amylopectin and amylose. Amylose is an important starch in linear shape formed of anhydroglucose units linked glycosidic linkage. On the other hand, amylopectin has many millions molecular weight and is in branched polymer developed by anhydroglucose units yet with 2–4 % branched form (Ahloowalia and Maluszynski 2001).

In most plants, starches are formed of about 70 % amylopectin and 30 % amylase. Mutation in biosynthesis of starch can change the concentration of both components that eventually will change the physical as well as chemical characteristics of starch granules and has been demonstrated in wheat, pea, rice, and maize. In maize, a large number of mutants are identified (Nelson and Pan 1995; Creech 1965). Among these mutants are the sugary (susu) in maize (Hannah et al. 1993) that has waxy (wx loci) and debranching characteristics.

In pea, several mutants have been induced by chemical mutagens (Blixt 1972). Six loci have been identified in pea that change the composition and use of starch. In one of them, the regosus loci (r), the dry seeds are wrinkled as explained by Gregor Mendel (Mendel 1865). Mendel analyzed the mutations derived because of a transposonlike addition in the gene (Bhattacharyya et al. 1990). Chemical mutagenesis produces single base pair changes in all alleles (MacLeod 1994). A main gene named Hardness (ha), located on the short arm of chromosome D of wheat controlled the texture gene (soft or hard). On the 5A and 5B chromosomes of hexaploid wheat, alleles for the hardness gene are present but not expressed. A 15 kDa marker protein for the softness of grain named Friabilin is constituted of two proteins, puroindoline a and b (pinA and pinB). This protein (soft starch) is present on the water-washed starch surface in higher concentration whereas hard wheat starch is in a small concentration. It is missing in the starch of durum wheat. Recent studies showed that the softness and hardness of wheat grain (*Triticum aestivum* L. em Thell) is connected to point mutation of glycine to serine in pinB or null mutation in pinA that follows the absence of pinA protein. These mutations demonstrate the hardness of grain. The complete connection between the hard texture of grain and mutation in pinB among 5D chromosomal substitution lines showed that pinB is involved in control of the texture of grain. It appears that mutation in either component of pinA, pinB, or friabilin can alter the hardness of grain (Giroux and Morris 1998).

7 Conclusion and Future Prospective

The currently available varieties of most staple crops do not fit into the vision of a highly effective but low-input system of crop production. This means a novel portfolio of cultivars of plant crops will need to be developed. By inducing mutation in crops, the potential of scientists of understanding and developing fundamental genic control that changes the expression of agronomic and crop characteristics to greatly improved. Consequently, induced mutagenesis is now an approach widely used in functional genomics as it greatly helps in gene identification and the explanation of their functions. Interestingly, functional genomics output named elucidated genes when used as molecular genetic markers, increasing the plant efficiency. Scientists are now applying other methods in addition to chemical and physical mutagenesis, such as combination of both chemical and physical mutagens and combination TILLING with mutagenesis.

This chapter demonstrates that techniques such as physical and chemical mutagenesis can be used to produce plant genotypes with the desired properties. Researchers have the goal to generate the tools that are the most suitable and effective for producing the desired genotypes (Bregitzer et al. 2002). On the other hand, it is still hard to guess if transgenic food could become the “norm” for ordinary consumers in the next few years. Somaclonal variations may be the more reliable mechanism for the early detection of desirable traits. Thus, induced mutagenesis techniques that gained great interest about the middle of the twentieth century are now worthy of further analysis and improvement by the use of different methods for the improvement of plants in the twenty-first century (Smith 2008).

Plant selection with the required properties is more significant compared to the methods used for mutation or production of variation. Consequently, the use of molecular probes gives a great chance in this regard. Molecular techniques with probes will become more significant in mutagenesis techniques, especially for changing superiority traits such as protein, starch, oil, and others in crop plants for industrial processing.

In vitro culture techniques decreased the quantity of cultural material up to a milligram; only small quantities of tissues and calli are used for mutation, and may be decreased to micrograms in the coming era when daily techniques are generated for these methods. Nowadays, the number of vegetatively propagated plants including sugarcane and banana, produced via in vitro mutagenesis is very low. However, many seeds propagated like maize, barley, soybean, rice, wheat, and rapeseed, among others are generated through cell-suspension culture. Although there are some problems, such as cells in suspension culture turn into clumps, it is expected that the irradiation dose needed for cell suspension culture for induced mutation would be lower than for callus culture. Hence, we should look forward to the advancement of daily techniques for seed and also for vegetatively propagated crops. Moreover, generation of methods of in vitro cell-selection for disease and toxin resistance can be used in culture media.

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Effect of Climate Change on Horticultural Crops

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Abstract The effect of global warming is now visible in many parts of the world. Abnormality in climate patterns, induced by accelerated warming, has started to affect a catchment-specific hydrologic cycle. Higher temperatures lead to a high rate of evaporation and dry conditions in some areas of the world. Severe weather events are now more common. Scientists believe that rapid warming in the last several decades is mostly due to human-induced changes in the atmosphere, on top of some natural variations. Impacts of climate change are complex as they can be both direct and indirect, the biggest casualty being natural resources such as agriculture. Agriculture is a carefully manipulated ecological system, the productivity of which could increase because higher levels of carbon dioxide in the atmosphere could allow a higher rate of photosynthesis. However, many interacting factors are at work. At higher levels of warming, estimated monetary impacts generally become negative, and studies, allowing for disastrous possibilities, can reach high negative outcomes. Moreover, the perennial plants (mostly fruit plants) are at more risk than annuals or seasonals.

Keywords Climate change • Impact • Plant responses • Quality • Yield

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1 Introduction

The phrases climate change and global warming and more recently global cooling are now part of our life. Climate change has come upon us in a relatively short space of time and is accelerating with alarming speed. It is perhaps the most serious problem that the civilized world has had to face. It is the subject of major international cooperation through the Intergovernmental Panel on Climate Change (IPCC) which was set up in 1988 by the World Meteorological Organization and the United Nations Environment Programme.

The Earth's climate has always changed in response to changes in the cryosphere, hydrosphere, biosphere, and other atmospheric and interacting factors. It is widely accepted that human activities are now increasingly influencing changes in the global climate (Pachauri and Reisinger 2007). Since 1750, global emissions of radiatively active gases, including CO_2, have increased rapidly, a trend that is likely to accelerate if increase in global emissions cannot be curbed effectively. Man-made increase in CO_2 emissions has come from industry, particularly as a result of the use of carbon-based fuels. Over the last 100 years, the global mean temperature has increased by 0.74 °C and atmospheric CO_2 concentration has increased from 280 ppm in 1750 to 368 ppm in 2000 (Watson 2001). Temperature is projected to increase by 3.4 °C and CO_2 concentration to increase to 1250 ppm by ~2095 under the A2 scenario, accompanied by much greater variability in climate and more extreme weather-related events (Pachauri and Reisinger 2007). Underlying these trends is much spatial and temporal heterogeneity, with projections of climate change impacts differing among various regions on the globe. Some of this is clear in the outputs from models that take into account geographic criteria such as land mass distribution, topography, ocean currents and water masses, and known meteorological features such as air streams. Nevertheless, historic data show seasonal and regional variation not accounted for in model processes (Barnett et al. 2006) that have major implications for practical processes such as crop sowing, harvest, or pest and pathogen infection and therefore all the activities derived from these effects.

Defining uncertainty is important in all areas of climate change research, not only in assumptions for stochastic or deterministic models, but in biological processes where knowledge or understanding is lacking. However, uncertainties are arguably greater when the implications of climate change on food security are considered.

2 Drivers of Climate Change

The Earth's climate is in a continuous state of change; it is inherent in the dynamic nature of our planet. Changes in the basic components that influence the state of the Earth's climatic system can occur externally (from extraterrestrial systems) or internally (from oceans, atmosphere, and land systems) through any one of the described components. For example, an external change may involve a variation in the sun's output which would externally vary the amount of solar radiation received by the

Earth's atmosphere and surface. Internal variations in the Earth's climatic system may be caused by changes in the concentrations of atmospheric gases, mountain building, volcanic activity, and changes in surface or atmospheric albedo. These forces will continue to have a major influence on our future climate.

2.1 Variations in the Earth's Orbit (Milankovitch Cycle)

The emerging consensus is that the threshold for dangerous climate change is on the order of 2 °C above preindustrial levels. The fact that the Earth's mean surface temperature has risen over the past century is not disputed. However, there are some (climate change skeptics) who dispute that anthropogenic emissions have been the main cause of the observed warming. It is indeed true that the Earth's mean surface temperature can vary considerably over time due to natural cycles, both long term (over millennia) and short term (over several years or decades). Nonetheless, the scientific consensus concludes with very high confidence that these factors alone could not account for the rapid increase in temperatures observed over the past 50 years. A key issue is the global warming debate is determining the anthropogenic contribution to warming, given that natural factors are known to cause significant variations in global mean temperatures.

Milankovitch cycles can cause global mean temperatures to vary as much as 5 °C between glacial and interglacial periods. However, these cycles take many centuries to cause perceptible changes to global temperatures. The Earth's orbit around the sun is subject to long-term variations. There are three principal effects on incoming solar radiation: the eccentricity (or stretch) of the orbit, with periods of approximately 95,000 years and 410,000 years; the tilt of the Earth's axis (approximately 41,000 years); and a wobble in the Earth's axis of rotation, which causes changes in the timing of perihelion (Fig. 1). Mean global temperatures can also vary up and down over periods ranging from several years to several decades as a result of regular climatic cycles and variations in the amount of solar radiation reaching the Earth's surface. The resulting changes to global mean temperatures are generally small and do not have a lasting impact on longer term global average temperatures. For example, variations in the amount of solar energy reaching the Earth over the past century have added an estimated 0.12 Wm^{-2} to atmospheric radiative forcing compared with the estimated 2.64 Wm^{-2} increase attributable to human activities. Although subject to long-term changes, it is their susceptibility to short-term anthropogenic influences that makes them of particular climatic interest.

2.2 Role of Greenhouse Gases

According to the computer models of climate, the effects of the orbital eccentricity cycle must be amplified or enhanced by some other factor. That additional factor has been identified as variations in the greenhouse gas concentrations present in the atmosphere. Most notable are the concentrations of carbon dioxide and methane, both of which are stored in large quantities in peat, tundra, and ocean sediments in colder climates, and are released into the atmosphere in warmer climates. Any warming due to orbital changes results in more carbon dioxide and methane being released into the atmosphere, leading to greater warming. Carbon dioxide (CO_2) and certain other trace gases, including methane (CH_4), nitrous oxide (N_2O), chlorofluorocarbons (CFCs), and tropospheric ozone (O_3), are accumulating in the atmosphere as a result of human activities too. All of these are greenhouse gases, or gases that absorb radiated heat from the sun, thereby increasing the temperature of the atmosphere. Additional, but minor greenhouse gases include carbon tetrachloride, methyl chloroform, chlorodifluoromethane (HCFC-22), sulfur hexafluoride, trifluoromethyl sulfur pentafluoride, fluoroform (HCF-23), and perfluoroethane. Because these gases absorb infrared radiation—that is, radiated heat from the sun—higher greenhouse gas concentrations lead to warming and global climate change. This occurs because the absorption of heat slows its eventual reradiation into space thereby warming the lower atmosphere. However, as human activities increase the atmospheric concentration of greenhouse gases, the atmosphere and ocean will continue to warm, and the overall global temperature will rise. Carbon dioxide accounts for 60 % of the increased radiative forcing and heat retention caused by greenhouse gases. A climate sensitivity (global warming for a stabilized doubling of carbon dioxide concentrations) in the upper part of the range adopted by the Intergovernmental Panel on Climate Change (IPCC) in its 2007 report, remains 1.5 to 4.5 °C (with some qualifications).

2.3 *Volcanism*

Volcanic activity is an important natural cause of climate variations because tracer constituents of volcanic origin affect the atmospheric chemical composition and optical properties. A weak volcanic activity results in gas and particle effusions in the troposphere (lower part of atmosphere), which constitute, on an average, the larger portion of volcanic mass flux into the atmosphere. However, the products of tropospheric volcanic emissions are short-lived and contribute only moderately to the emissions from large anthropogenic and natural tropospheric sources. Strong volcanic eruptions with a volcanic explosivity index (VEI; Simkin 1993) equal to or greater than 4 could inject ash and sulfur-rich gases into the clean lower stratosphere at an altitude about 25–30 km, increasing their concentration thereby two to three orders of magnitude in comparison with the background level. Chemical transformation and gas-to-particle conversion of volcanic tracers from a volcanic aerosol layer that remains in the stratosphere for two to three years after an eruption, thereby affects the Earth’s climate because volcanic aerosols cool the surface and the absorbing thermal IR and solar near-IR radiation (Stenchikov et al. 1998).

Volcanic eruptions such as the Mt. Pinatubo eruption in 1991, with global visible optical depth maximizing at about 0.15, cause perturbation of the globally averaged radiative balance at the top of the atmosphere reaching −3 Wm^{-2} and cause a decrease of global surface air temperature by 0.5 K. The radiative impact of volcanic aerosols also produces changes in atmospheric circulation, forcing a positive phase of the Arctic oscillation (AO) and counterintuitive boreal winter warming in middle and high latitudes over North America (Collins 2003; Stenchikov et al. 2004; Shindell et al. 2001). In addition, stratospheric aerosols affect stratospheric chemistry serving as surfaces for heterogeneous reactions liberating anthropogenic chlorine and causing ozone depletion.

3 Climate Change and Its Impact

Global warming is expected to have profound effects on India, although there are large uncertainties about the relative effects on the summer monsoon rains of global warming with or without taking account of aerosol (atmospheric particle) effects. Key potential impacts include:

- Higher temperatures increasing potential evaporation and duration of heat waves.
- Significant decline in winter rainfall leading to severe water scarcity during early summer months.
- More intense droughts over large areas adversely affecting crop production.
- The per capita availability of freshwater in India is expected to drop from around 1900 cubic meters currently to 1000 cubic meters by 2025 due to a combination of population growth and climate change.
- More intense floods, especially in the flood plains of the eastern Himalayan rivers, their major tributaries, and the delta regions.
- Coastal flooding and salinity intrusion from sea level rise in combination with the amplification of storm surges from more intense tropical cyclones in the Bay of Bengal.
- Rapid melting of Himalayan glaciers, leading initially to greater river flows and hence sedimentation and subsequent reduced flow, especially in the drier months.
- Serious health impacts due to heat-related stress and vectorborne diseases.
- Climate change will intensify other environmental pressures and impinge on sustainable development.

Overall, climate change would likely lead to more food shortages, and increased loss of life and infrastructure from coastal inundation and riverine flooding. Crop production is primarily determined by soil moisture, temperature, sunlight, and soil fertility. Over the course of this century, climate change is expected to lead to higher average global temperatures, changes in annual and seasonal precipitation patterns, and increases in the frequency and intensity of extreme weather events. Elevated concentrations of atmospheric carbon dioxide could also influence crop yields through the CO_2 fertilization effect. These factors will fundamentally alter crop yields and the distribution of agricultural/horticultural production. In some regions, changes in climatic conditions might improve crop yields, as is expected in the higher latitudes of Europe and North America. However, in most other regions, changes in temperature and water availability are expected to result in reduced yields, particularly in tropical regions, where temperatures are already at, or exceeding, optimal conditions for plant growth.

The IPCC's 2001 report projects global average surface temperature increases ranging from 1.4 to 5.8 °C by 2100 for non-climate–policy SRES scenarios, compared to the earlier IPCC IS92 range of 1.5 to 3.5 °C. The corresponding range from the 2007 IPCC report is 1.1 to 6.4 °C. The latest projected rate of warming is roughly two to ten times that observed during the twentieth century, which was about 0.6 °C. The rate is much faster than the average warming at the end of the last glaciation. The greater warming at the high end of the range, compared to that in the IS92 range is due to both greater carbon dioxide emissions in the high emissions scenarios and less sulfur emissions.

Although average global warming is of importance, most interest is in regional effects, for which more detailed estimates of regional warming are required. Warming in continental interiors and in the latitudes of the northern hemisphere is expected to be greatest with less expected over the oceans and windward coastlines. Indeed high northern latitudes may warm at several times the rate of the global average, and continental interiors up to twice as fast as the surrounding oceans. The least warming is expected over the southern ocean due to its capacity to transport surface heat into the deep ocean and possibly in the North Atlantic region, depending on the behavior of the ocean circulation. Warming may be greater in the eastern tropical Pacific than in the west, which may lead to a more El-Niño-like average condition (although year-to-year variability around that average may increase).

3.1 Variating Temperature

The interactions between short-term external solar radiative forcing and these internal radiative forcing agents are central to understanding and predicting near-term global climate trends. They operate through a complex feedback mechanism that can be either positive (i.e., self-enhancing) or negative (i.e., self-regulating or damping).

Positive feedback mechanisms affecting global climate appear to be widespread and particularly effective in response to temperature changes, which is a matter of special current concern. Increases in global temperature lead to increases in atmospheric water vapor, increases in plant respiration, decrease in CO_2 dissolved in the oceans, and an increase in methane emissions from wetlands. All of these act to increase the global concentration of greenhouse gases and, hence, to increase global temperatures further. Ice and snow cover is involved in important positive feedback effects because a more extensive cover creates higher albedo and lower temperatures that further expand the ice and snow, and decrease the surface albedo, allowing more absorption of incoming solar radiation and leading to increased surface heating and further warming.

Negative feedback mechanisms appear to be very important in the face of short-term radiative forcing and it appears that they can only reduce the rate of warming but cannot, of themselves, cause global cooling. Natural and anthropogenic aerosols are thought to have a net cooling effect but the magnitude is highly variable in time and space. Cloud cover effects are particularly complex, producing both positive and negative feedback. Negative feedback may operate when increased global heating leads to greater evaporation and greater amounts of high-altitude cloud cover, which reflect more incoming solar radiation and thus lessen the rise in global temperature.

The current rate of global temperature change is important, as it is most likely beyond the ability of ecosystems to adapt, and will also test the ability of humans to adapt. Stabilizing concentrations at the lowest possible level is the single most important means of limiting future temperature increase. Concentrations will only stabilize when emissions fall to a level equivalent to the natural rate at which the Earth can remove them from the atmosphere. To equal the natural removal rate and stabilize concentrations, anthropogenic emissions need to fall 80–90 % below current levels. If current emission trends persist, atmospheric greenhouse gas concentrations (CO_2) are expected to exceed double preindustrial levels before mid-century and possibly before 2040. To limit global warming to 2 °C would require concentrations to stabilize below 500 ppm CO_2.

Temperature obviously limits the geographical areas in which various crops can be grown. However, temperature is often not the only determinant: the effects of temperature extremes are usually associated with other factors such as availability of water, prevalence of high winds, and the duration and intensity of sunlight (insolation). An important aspect is that limitations imposed by extremes of temperature differ sharply from annual versus perennial crops.

3.1.1 High Temperature Limitations

The limiting effect of high temperatures on crop production takes two principal forms: limitation of vegetative growth and adverse effects on fruit settings. Vegetable crops subject to very high transpiration losses are obviously limited by the excessive transpiration concurrent with exposure to extremely high temperatures.

Plant breeders are having limited success in developing more heat-tolerant varieties because heat tolerance and cold tolerance in fruit setting have only moderate heritability and such inheritance is complex. A further complication is that the upper limit for fruit set can be correlated with humidity levels. Very high temperatures can also limit fruit setting of citrus fruits. In this case, intensity of insolation appears to be another limiting factor, because flowers within the leafy canopy, protected from direct exposure to sunlight, will usually set some fruit (Samedi and Cochran 1976). A less subtle effect of extremely high temperatures on fruit set of citrus is the “burning” or “scorching” of blossoms, particularly on young trees, that is occasionally reported from desert areas. Even without such drastic effects, fruit set of navel oranges is reported to be sharply affected by temperatures during the bloom period

(Davies 1986). A high-temperature effect causing no visible symptoms is a cessation of growth even though nutrients and soil moisture are adequate, as reported for citrus trees during very hot weather (Cooper et al. 1964).

3.1.2 Low-Temperature Limitations

The obvious limitation imposed by low temperature is killing of plant tissues by freezing. Most plant tissues can be destroyed by freezing temperatures suddenly imposed during a period of rapid growth. Some plants, given sufficient time under suitable conditions, can adapt themselves to freezing temperatures, and some cannot. The classical example, feared by fruit growers almost everywhere except in the tropics, is a freeze while the trees are in full bloom. This is much more drastic for deciduous fruit trees than for evergreen trees such as citrus. If the blossom-bearing wood is not damaged, such tropical or subtropical trees have a chance to replace fruit buds within the same bearing season, although yield and quality may be impaired. This cannot happen with deciduous fruit trees.

In freeze-susceptible tissues, free water freezes, forming crystals that disrupt cell membranes, whereas in freeze-resistant tissues the water is bound in the form of hydrophilic colloids. Freeze-hardy plants have hormonally controlled mechanisms enabling them to respond to gradual changes in temperature and day length in preparation for winter. Such changes are obvious with deciduous trees, vines, and shrubs, which shed their leaves, often after having displayed dramatic changes in leaf color. But for plants that survive a freeze without a prior hardening period, the water supercools to a surprising extent, although this protective mechanism is often negated by the presence of ice-nucleating bacteria (Ashworth 1986). Such bacteria are by no means ubiquitous, but they are very common and a real factor in freeze injury. Exposure to freezing but nonlethal temperatures can cause various chemical changes in plant tissue. For instance, it is very common for oranges that survive a freeze to develop white crystals clearly visible between the segment membranes. These are hesperidin, the principal flavone in citrus fruits, and although their presence sometimes causes alarm, they are completely nontoxic (Grierson and Hayward 1959).

3.2 Increasing Carbon Dioxide

Carbon is constantly moving between the three active reservoirs (the atmosphere, the terrestrial (land) system, and the oceans), and these exchanges are called carbon fluxes. In total around 41,000 billion tons of carbon (C) are available for exchange between the three principal reservoirs. The major reservoir of carbon is the ocean, which is estimated to contain around 38,000 GtC, or 93 % of all exchangeable carbon. The ocean can be further subdivided into the surface ocean (down to 100 m), which contains around 1000 GtC, and the deep ocean, which contains the remaining

37,000 GtC. The land carbon reservoir is estimated to contain just over 2000 GtC, about 5 % of exchangeable carbon. Of this, approximately 30 % is stored in vegetation and other living organisms and the remainder in the soil and detritus. The atmosphere is the smallest of the three active reservoirs and is estimated, at present, to contain around 800 GtC, roughly 2 % of exchangeable carbon.

There is also a vast reservoir of geological carbon (20,000,000 Gt) stored in the Earth's crust, mainly as carbonate rocks. Of this, a small fraction (about 5000 Gt) is stored as fossil fuels (coal, oil, and natural gas) and methane hydrates (5000–10,000 Gt). Natural annual carbon fluxes into and out of the geological reservoir are tiny (less than 0.1 % of the cycled carbon), so geological carbon is not generally considered part of the active carbon cycle. The ocean and land reservoirs both emit and absorb large quantities of CO_2. The difference between these opposing fluxes, plus emissions from human activities, determines the net annual addition of carbon (in the form of CO_2) to the atmosphere.

As CO_2 is responsible for 61 % of global warming, a doubling of the atmospheric CO_2 and a rise in other so-called greenhouse gases (methane, nitrous oxide, chlorofluorocarbons) would increase the mean global temperature, possibly as much as 4.5 to 6 °C. In addition, shifts in regional precipitation patterns as a result of rising atmosphere (CO_2) will probably result in decreased soil water availability in many areas of the world (Keeling et al. 1995; Wigley and Raper 1992; Allen 1994). Atmospheric CO_2 is an essential compound for life on Earth. Through photosynthesis plants obtain carbon for their growth and provide sustenance for other living things, ourselves included. In photosynthesis, solar energy is absorbed by a system of pigments, and inorganic atmospheric CO_2 is fixed and reduced into organic compounds. Reduction of carbon is a major function of photosynthesis and is quantified by realizing that plant organic matter is about 45 % carbon on a dry weight basis.

3.2.1 Plant Responses to Rising CO_2

Rising atmospheric CO_2 could benefit many economically important crops, especially the C_3; however, gains may or may not be realized in long-term growth because of the interaction of various environmental factors that complicate the issue. The photosynthetic mechanism of a plant species is the major determinant of how it will respond to rising atmospheric CO_2; understanding the mechanisms of photosynthesis accumulation of rising CO_2, and other environmental stresses, could potentially be translated into a basic framework for improving the efficiency of crop production in a future climate-changed world. Present understanding of photosynthetic carbon metabolism classifies terrestrial plants into three major photosynthetic categories: C_3, C_4, and Crassulacean acid metabolism (CAM). Each category possesses a unique set of anatomical, physiological, and biochemical features that allows them to adapt to a specific ecological niche (Ku et al. 1996). It is estimated that approximately 95 % of terrestrial plant species fix atmospheric CO_2 by the C_3 (i.e., photosynthetic carbon reduction or PCR) pathway, 1 % fix by the C_4 pathway, and 4 % by the CAM (Bowes 1993).

The present atmospheric CO_2 limits photosynthetic capability, growth, and yield of many crop plants, among which the C_3 species show the greatest potential for response to rising CO_2 (Allen 1994; Bowes 1993). Current atmospheric CO_2 and O_2 levels and C_3 Rubisco specificity factors translate into photorespiratory losses of 25 % or more for C_3 species. The projection that a rise in atmospheric CO_2 will resolve the deleterious effect of O_2 on C_3 photosynthesis but that it has a negligible effect on C_4 photosynthesis is indeed supported by experimental growth data. Exposure of C_3 plants to elevated C_4 generally results in stimulated photosynthesis and enhanced growth and yield (Drake et al. 1997; Allen et al. 1996). A compilation of the existing data available from the literature for C_3 agricultural crops, including agronomic, horticultural, and forest tree species, shows an average enhancement in net CO_2 exchange rates up to 63 % and growth up to 58 % with a doubling of the present atmospheric CO_2 (Kimball et al. 1993; Poorter et al. 1996). Long-term exposure to elevated CO_2 leads to a variety of accumulation effects, which include changes in the photosynthetic biochemistry and stomatal physiology and alterations in the morphology, anatomy, branching, tillering, biomass, and timing of developmental events as well as life cycle completion. A greater number of mesophyll cells and chloroplasts have been reported for plants grown under elevated CO_2. With respect to leaf photosynthetic physiology and biochemistry, accumulation occurs ranging from species-specific changes in the A/Ci (accumulation rate vs. intercellular CO_2) curves to alterations in dark respiration and biochemical components with Rubisco playing the leading role (Bowes 1996). In terms of dark respiration, exposure of plants to elevated CO_2 usually results in lowering the dark respiration rate, which can be explained by both indirect and direct effects. Whereas the mechanism for the indirect accumulation effect of elevated CO_2 on dark respiration may be related to changes in tissue composition, the direct effect appears to be an inhibition of the enzymes in the mitochondrial electron transport system (Gonzalez-Meler et al. 1997; Drake et al. 1999). Many C_3 species grown for long periods at elevated CO_2 show a downregulation of leaf photosynthesis, and carbohydrate source–sink balance is believed to have a major role in the regulation of photosynthesis through feedback inhibition (Arp 1991; Stitt 1991). Source–sink imbalance may occur during exposure to elevated CO_2 when photosynthetic rate exceeds the export capacity or the capacity of sinks to use photosynthates for growth, resulting in an accumulation of carbohydrates in photosynthetically active source leaves. Under elevated growth CO_2, although the extent to which starch and soluble sugars accumulate largely depends on the species, the increase of starch seems to be greater than that of soluble sugars in many plants and a correlation between starch accumulation and inhibition of leaf photosynthesis has been more frequently observed (Makino and Mae 1999). Also, for many plant species, longer exposure to elevated CO_2 results in a downregulation of Rubisco. Both "coarse" control, through lowering of the enzyme protein content, and "fine" control, through decreasing the enzyme activation state, play a role in the downregulation of Rubisco mediated by elevated CO_2. Coarse control suggests a reallocation of nitrogen resources away from Rubisco as well as an optimization of CO_2 acquisition with utilization of the fixed carbon (Woodrow 1994). Downregulation of Rubisco at elevated CO_2, however, is not a universal phenomenon, and claims of altering the enzyme activity need careful evaluation, as the basis on which Rubisco activity is expressed may vary or nullify the observation (Bowes 1993). In addition to Rubisco, there are reports that elevated CO_2 affects the regulation of sucrose phosphate synthase (SPS) and acid invertase. Levels of soluble sugars in plant cells have been shown to influence the regulation of expression of several genes coding for key photosynthetic enzymes (Sheen 1994; Jang and Sheen 1994; Smeekens 1998). The buildup in carbohydrates may signal the repression, but does not directly inhibit the expression, of Rubisco and other proteins that are required for photosynthesis. Although the signal transduction pathway for regulation of the sugar-sensing genes may involve phosphorylation of hexoses, derived from sucrose hydrolysis by acid invertase, via hexokinase, unknown gaps still exist between hexose metabolism and repression of gene expression at elevated growth (CO_2). Transcription of the Rubisco small subunit (rbcS), and to a lesser extent the large subunit (rbcL), appears to be strongly repressed by sucrose and glucose. Reduced expression of Rubisco genes and differential response of other photosynthetic genes have been reported for a variety of crops grown at elevated CO_2 (Moore et al. 1998). For many species, the expression level of rbcS transcripts, however, does not always correlate with the Rubisco protein content at elevated growth (CO_2). Furthermore, although photorespiration decreases under elevated CO_2, responses of the enzymes and/ or transcripts associated with the photorespiratory pathway have not been well investigated. Elevated CO_2 has little effect on the transcript level of glycolate oxidase in tomato but inhibits the accumulation of hydroxypyruvate reductase messenger RNA (mRNA) in cucumber (Bertoni and Becker 1996).

Photosynthesis of C_3 plants, in addition to CO_2, is influenced by high growth temperature regimes and Rubisco plays a central role in these responses. Temperature and CO_2 have interactive effects because a rise in temperature reduces the activation state of Rubisco and decreases both the specificity for CO_2 and the solubility of CO_2 relative to O_2, resulting in increased photorespiratory CO_2 losses as the temperature rises. Consequently, a doubling of atmospheric CO_2 and the concomitant inhibition of the Rubisco oxygenase reaction could partially offset the adverse effects of increased global temperature on C_3 photosynthesis (Long 1991). In addition, elevated CO_2 can compensate for the adverse effects of high temperature relative to the net photosynthetic rate.

3.2.2 Rising CO_2 and Limited Soil Water Availability

As atmospheric CO_2 rises, potential shifts in regional scale precipitation patterns could result in increased drought conditions in many areas of the world. Responses of plants to rising CO_2 in water deficit situations have been reviewed. Despite our understanding of the responses of leaf photosynthesis to elevated CO_2 as well as to soil water deficit, the interactions of CO_2 enrichment and drought stress are still uncertain. A reduction in stomatal conductance is a common response of plants to elevated growth (CO_2). Observations of a variety of C_3 and C_4 species indicate that a doubling of atmospheric CO_2 can also double the instantaneous WUE (Allen 1994; Morison 1993; Allen et al. 1985). As the CO_2 is increased, the improvements in WUE are the results of increased assimilation rate and decreased water loss, with the latter being more important under water deficit situations. As soil water becomes less available, the relative enhancement of photosynthesis and growth by elevated CO_2 tends to be greater, which can alleviate drought stress and delay its onset (Allen 1990; Bazzaz 1990; Morison 1993; Arp et al. 1993). A delay in the adverse effects of water deficit on leaf and canopy photosynthesis by elevated CO_2 has been reported for a number of plants. Studies conducted on a variety of plant species indicate that elevated CO_2 may actually prevent plants from succumbing to the rigors of environmental stresses and enable them to maintain essential growth processes (Idso 1998). Carbon dioxide enrichment also enhances water conservation and midday xylem water potentials in drought stresses plants and leaf water potentials.

3.2.3 Rising CO_2 and Light Intensity

Measurements of CO_2 enrichment effects on photosynthesis have usually been carried out with relatively high irradiance. In nature, photosynthesis occurs in both high and low light environments, and light-limited photosynthesis can account for half of the total carbon gain. Several studies show that C_3 photosynthesis is enhanced by elevated CO_2 even under light-limited conditions, and the enhancement rises with temperature (Drake et al. 1997).

3.2.4 Rising CO_2 and Nitrogen Nutrition

As CO_2 is just one of many organic substrates required by plants, long-term response of plant photosynthesis and growth to elevated CO_2 also depends on the availability of mineral nutrients and the way in which plants utilize them. Most studies of elevated CO_2 and nutrient interactive affects have focused on nitrogen (N) because it is a common limitation in many natural and agroecosystems. In plants grown under elevated CO_2, the overall N concentration usually decreases. This overall N decreases under elevated growth of CO_2, and might reflect either a higher N use efficiency due to reallocation of proteins, an ontogenetic drift leading to accelerated senescence as a result of faster growth, or inadequate N fertilization uptake and/or assimilation.

3.3 Precipitation and Evaporation

The water-retention capacity of air increases with temperature and is a key determinant of precipitation. The relationship is described by the Clausius–Clapeyron equation. Cold air is drier than warm air and this is the reason why the poles experience such levels of precipitation (they are essentially cold deserts) and why the equatorial regions have so much rain. As the planet warms, the atmosphere will tend to hold more water and the water cycle will intensify. For every 1 °C rise in Earth's mean surface temperatures, global precipitation is expected to increase by approximately 1 %. Increasing global temperatures will also result in more precipitation falling as rain, rather than snow, and more intense precipitation events. Warming will also change the seasonal melt rates of glaciers and mountain snow packs, which will, in turn, change the timing and magnitude of seasonal water flows. Higher temperatures will also increase evaporation rates, which can have significant impacts on the availability of soil moisture at different times of the year. All these changes are expected to result in increased frequency and intensity of both droughts and floods.

Global average precipitation (rain or snowfall) and evaporation are projected by climate models to increase by about 1–9 % by 2100, depending on which scenario and climate model is used. However, projected precipitation changes vary more from region to region, with increases over mid to high latitudes in both hemispheres. Decreases are projected in subtropical and lower mid-latitudes. This is generally associated with the polewards migration of the mid-latitude westerlys associated with a strengthening of the northern and southern "annular modes" of circulation and the related changes in surface pressure patterns. Surface pressure tends to increase at mid-latitudes and decrease at high latitudes.

Climate change will have significant effects on the global water cycle and could have far-reaching impacts on humans and natural ecosystems. Expected changes include variations in the distribution, timing, and intensity of precipitation events (rainfall, snow, hail, and cloud mist) and changes in the timing of seasonal water flows. Although some modifications to the global water cycle have already been observed, the changes over this coming century are expected to be much more pronounced. The impact on humans and natural ecosystems are expected to be significant. Access to water, both in terms of quality and quantity, has a major influence on the structure and location of economic activities, particularly agriculture and industry.

3.3.1 Rainfall Distribution

Although the impact of climate change on particular stages of the water cycle remains uncertain, aggregate global precipitation is expected to increase as the atmosphere warms, but it will not be evenly distributed across the planet. Some regions will become drier and others wetter. In some areas, average annual rainfall may remain unchanged, but rain may fall at different times of the year or in fewer, more intense, events. There is general agreement between most climate models concerning the broad regional trends in precipitation that are likely to occur with global warming, however, there remains considerable uncertainty about the precise magnitude and distribution of the changes.

Models suggest that the subtropics and mid-latitudes will generally become drier. In the southern hemisphere, the southern regions of Australia and Africa are likely to experience lower precipitation. In the northern hemisphere, the most pronounced drying will be in the Mediterranean region, southwest United States and Mexico, and probably West and Central Asia and Western China. In some areas, there could be reductions in available runoff of up to 30 % by 2050 if temperatures rise by 2 °C, and possibly up to 50 % if global mean temperature exceeds 4 °C. Some areas of the tropics may also become drier. For example, the East Amazon region of Brazil is expected to experience a reduction in rainfall that could accelerate the level of forest dieback already being experienced in the region, ultimately leading to significant ecosystem deterioration. Some regions are already experiencing drying trends. The southern regions of Western Australia have, since the mid-1970s, experienced a 15 % decline in average annual rainfall, and winter rainfall is 25 % below the long-term average. This has already adversely affected natural ecosystems and agricultural production.

The higher latitudes are expected to experience increased precipitation as atmospheric temperatures increase. Rainfall, runoff, and river discharge have already increased significantly in the higher northern latitudes, particularly in eastern Russia. Precipitation (falling mainly as snow) has also risen in the past two decades in Antarctica and Greenland. Some areas of the tropics are expected to receive more rain. Even the Sahara desert might receive elevated winter rainfall. For all regions that experience increased precipitation and rainfall intensity, there will be associated increased risks of flooding. Overall, since the mid-1990s, there has been a general drying in the mid-latitudes in both the northern and southern hemispheres and a noticeably wetter trend in the high latitudes of the northern hemisphere and Antarctica. Although this seems to be consistent with what the models suggest will happen under climate change, it is too early to judge whether these are permanent shifts in the underlying average precipitation patterns or part of regular cycles. However, there are some regions where it is uncertain whether wetting or drying trends will prevail as the models yield inconsistent or conflicting results.

3.3.2 Seasonal Water Availability

Although changes in the amount of annual rainfall are important in determining aggregate water availability for a given region, the timing and intensity of rainfall events is also critical. It is the changes in extreme dry and extreme wet periods, rather than changes in long-term averages, that can have the greatest impact. Aggregate rainfall may increase, but if it is compressed into a narrow time period much of the additional water may simply end up as increased runoff to the oceans, with little change in terrestrial water availability. If dry periods become even drier, this will tend to aggravate existing seasonal water shortages. In many regions seasonal water flows are influenced by the melt rates of mountain glaciers and snow packs. Over a billion people currently depend on dry season flows from glaciers and snow pack melt, including parts of the southwestern United States and the Andean region, but especially South Asia and Western China. A full 70 % of the summer flow of the Ganges is fed by Himalayan melt waters. The initial impact of global warming on glaciers is to increase the rate of summer melting and to increase water flows. In some areas, increased melt rates can cause rapid buildup of water in glacial lakes to the point where they burst and result in flash floods. This is already a serious risk in the Himalayan region. In Nepal, for example, several recent glacial lake bursts have resulted in major damage to infrastructure and loss of life.

Over time, as the glaciers and snow packs disappear, dry season water flows will diminish. This could result in water shortages and adverse impacts on agricultural production and people's livelihoods. By 2020, the Chacaltaya Glacier in Bolivia, which is an important source of water for La Paz, is expected to have melted completely, as will four of Ecuador's eight major feed water glaciers. Changes in water availability in South Asia are likely to become particularly severe in the next few decades as most of the major feed glaciers are disappearing rapidly, and this will have widespread repercussions for more than 1 billion people that depend on Himalayan melt water flows.

3.3.3 Thunder and Hail Storms

Thunder storms and their destructive winds are expected to become more frequent and severe as our climate changes. Longer hotter summers will generate warmer surface temperatures, causing the air to become more buoyant. Air, laden with moisture from increased evaporation, will rise into the atmosphere more rapidly and more often. Hail consists of small balls or larger pieces of ice (hailstones) with a diameter ranging from 5 to 50 mm; they can grow greater than 40 cm in diameter. When driven by high winds, hailstones can hit the ground at a deadly 130 km an hour. Of all the extreme weather events, hail causes the most economic losses in property and crop damage.

3.3.4 Sea Level Rise

The rate of sea level rise is actually likely to be quite slow. Sea level change over the next 100 years or so will be relatively modest, most probably up to 1.0 m and possibly only 0.5 m (although some estimates range as high as 1.5 m). Rises of this magnitude would have coastal and ecosystem impacts. However, the response of the oceans and ice caps is so slow to changes in atmospheric temperature that the full impact of current warming on sea levels will not be realized for centuries, and possibly a thousand years or more. It is this long-term impact that is sometimes described as the *commitment to sea level rise*.

There are two ways in which global warming can cause the sea levels to rise. First, the sea level can rise due to the thermal expansion of the oceans. As water warms, it expands and occupies a greater volume; when it cools, it shrinks and occupies a smaller volume. The same principle applies to the oceans but on a much larger scale. The second, the more visible, contribution to sea level rise is through the addition of more water from melting land-based ice. The principal source of this water will, at least initially, come from receding glaciers and mountain snow packs. However, in the long term (beyond 2050), it is the Greenland and Antarctic ice caps that will be the dominant forces determining sea level rise. If these ice caps were to melt completely, the sea level would be 65 m above current levels. The large expansions of sea ice that cover the North Pole and some areas of the sea off the coast of Antarctica will not, in fact, contribute much to the sea level rise. The reason for this is that they are already floating and have, therefore, displaced their own volume in the water.

Although the actual physical rise in sea levels and inundation of low-lying areas is relatively easy to visualize, there is a range of less obvious biophysical and socioeconomic impacts that will also affect coastal regions. These include loss of wetlands and wildlife breeding grounds; changes in storm surges, wave action, and coastal erosion/deposition patterns; increased agriculture/aquaculture loss and damage; saltwater intrusion to freshwater aquifers; and damage to coastal infrastructure.

3.4 Annual Versus Perennial Crops

Temperature limitations differ sharply for perennial and annual crops. For perennials (largely tree, vine, and bush crops, various grasses, and other pasture crops), ecological limits are usually set by winter temperatures. Few species are hardy enough to survive subarctic extremes of winter cold. In the tropics, the need for a cool winter rest period limits the cultivation of pome (e.g., apple and pear) and most drupe (e.g., peach, plum, cherry, apricot, almond, walnut, pecan, olive) fruits. Conversely, the lack of winter freeze hardiness limits the potential growing areas for purely tropical fruits (banana, mango, avocado, durian, mangosteen, etc.).

This set of limits is in sharp contrast to those applicable to purely annual crops such as almost all vegetables and grains, and annual flowers, for which summer temperatures are critical. All these annual crops require is about 3–5 months of suitable growing weather. Vegetables grow luxuriantly in the warm, long summer days.

3.5 Seed Dormancy and Germination

An important temperature-related difference should be noted between seed-bearing plants of the temperate zone and those originating in the tropics or subtropics. In areas that experience killing winter freezes, seeds must not germinate until the following spring. Exceptions to this principle are seeds of plants that bloom early enough in the spring to be able to establish mature plants before the onset of winter. Seeds of plants that evolved in tropical areas need no such protective device and so usually (but not always) can be germinated immediately on separation from the plant (Ellis 1991). “Stratification” is used for chilling treatments to break dormancy. For some seeds it has been demonstrated that dormancy is purely mechanical, being enforced as long as the tough impermeable testa is intact. Prolonged cold temperatures (most effectively between 2 and 6 °C) are definitely essential in such stratification.

Various treatments (such as presoaking) to encourage emergence of seeds used to be called “vernalization”, presumably because it hastened the effects of spring. But if seeds have been primed, subsequent permissible holding temperatures may be affected. Imbibitional chilling injury is of particular concern for seeds of plants of tropical origin, which are susceptible to chilling injury. For their seeds, the onset of chilling injury is related to rate of water uptake. Treatment with materials (such as PEG) that delay imbibition can be helpful but is not temperature specific. Too hot temperatures can also impede germination. Recalcitrant seeds occur in all climates, and temperature can be a factor in achieving successful germination (Taylor et al. 1992).

3.6 Dormancy, Bud Initiation, and Fruit Setting

The dormancy of winter-hardened plants is deceptive. Essential physiological and morphological changes are progressing and will do so only at the low temperature to which evolution has adapted such plants. Spring bulbs brought indoors and kept in warm temperatures after flowering will not bloom again. Such bulbs left in the winter ground (or held in correctly regulated cold storage) undergo histological changes. Such imposed temperature regimes are very precise: there are sharp differences in temperature requirements, not only among genera, but even between individual cultivars (Van Tuyl 1983). The same thing happens within the fruit buds of deciduous fruit trees and shrubs. Even normally hardy plants, such as oak trees, need time to adapt to winter temperatures. In addition to cold hardiness, cold hardening can induce disease resistance in addition to the customary physiological effects.

Even when fruit trees have bloomed satisfactorily, temperature can be a determinant of whether a good crop will be harvested. Most deciduous fruits need pollination, which is normally done by honey bees. If the temperature is not right, the bees just quit flying, and that can mean a very poor crop indeed. Even if the bees fly and pollen is spread, the pollen must germinate and the pollen tube grow down to the ovule, a process that can be severely restricted by unseasonably low temperatures (Vasilakakis and Porlingis 1985). And even when pollination has been successful, growth of individual fruits can be restricted by both too high and too low temperatures. Too high temperatures are more likely to affect fruit set of citrus than of deciduous fruits. Trouble is more apt to come from a combination of high temperature and high humidity, resulting in fungal invasion of the fruitlets (Frost and Soost 1968).

3.7 Chilling Requirement

One of the major determinants of good yields in many fruit trees is the availability of winter chill. Trees and shrubs that require winter chill rely on the occurrence of cold conditions during the winter in order to break their dormancy and initiate fructification. In spite of the importance of this phenomenon for horticultural production, the physiological details of this process are still relatively unknown, and the existence of several competing models to quantify winter chill suggests that the climatic conditions required to break a tree's dormancy are as yet relatively poorly understood and possibly vary between species (Kozlowski and Pallardy 2002; Rea and Eccel 2006). This is also reflected by the fairly elaborate structure of some existing models and by their specificity to a certain species or even variety (Richardson et al. 1974; Shaltout and Unrath 1983). Several authors suggest that a specie's chilling requirement is not necessarily fulfilled by a certain number of hours below a given temperature threshold. Warm temperatures might instead compensate for earlier chilling hours, or the breaking of dormancy might happen in two phases. The easiest and most common approach to approximating winter chill conditions, however, is to sum up the seasonal hours between 0 °C and 7.2 °C (Bennett 1994; Weinberger 1950). Because this approach is widely used in practical horticultural production, and for most fruit species, chilling requirements are typically given as hours within this range, it seems to be the most appropriate approximation of chilling conditions, allowing the widest possible conclusions (Table 1).

Table 1 Some fruit species with their chilling requirements

Low/No Chilling	Intermediate Chilling	High Chilling
Date (*Phoenix dactylifera* L.) **(0)**	Pomegranate (*Punicagranatum* L.) **(100)**	Walnut (*Juglansregia* L.) **(400)**
Lime (*Citrus aurantifolia* L.) **(0)**	Peach (*Prunuspersica* L.) **(200)**	Apple (*Malus x domestica*Borkh) **(400)**
Sweet Lime (*Citrus limettioides* L.) **(0)**	Apricot (*Prunusarmeniaca* L.) **(350)**	Pear (*Pyruscommunis* L.) **(600)**
Bitter Orange (*Citrus aurantium* L.) **(0)**	Almond (*Prunusamigdalus*) **(400)**	Plum (*Prunusdomestica*) **(700)**
Orange (*Citrus sinensis* L.) **(0)**	Grape (*Vitisvinifera* L.) **(100)**	
Banana (*Musa x paradisiaca* L.) **(0)**	Fig (*Ficuscarica* L.) **(100)**	
Papaya (*Carica papaya* L.) **(0)**		
Guava (*Psidiumguajava* L.) **(0)**		
Mango (*Mangiferaindica* L.) **(0)**		
Sapota (*Manilkarazapota* L.) **(0)**		

Minimum chilling requirement for the species according to Noel (2007) and Baldocchi and Wong (2008)

In subtropical fruit-growing regions, where chilling-sensitive crops are cultivated, chilling conditions occur during the coldest hours of the day during the winter. Such regions can thus be expected to react strongly to increases in daily minimum temperatures during the cold season. Several recent modeling efforts and long-term temperature observations have indicated that much of the recently observed global warming trend can be attributed to rising minimum temperatures, which have increased at a faster rate than mean or maximum temperatures (Easterling et al. 1997; Lobell et al. 2007: Vincent et al. 2005; Vose et al. 2005; Zhang et al. 2005). Perennial fruit production systems, which are long-term operations that depend on seasonally low temperatures, may thus be among the agricultural or horticultural systems most vulnerable to climate change.

3.8 Effect on Yield and Quality

Different crops require different temperature and soil moisture regimes for optimum yields. Water is generally the major limiting factor with regard to crop production. If there is insufficient soil moisture, as occurs during droughts, or there is too much, as occurs during floods or periods of excessive precipitation, yields decline and can even result in total crop loss. Most crops are very sensitive to temperatures above 35–40 °C as photosynthetic functioning can be impaired. Elevated temperatures tend also to reduce the growing period between sowing and harvest, thereby reducing the amount of light captured and the resulting biomass production.

The prevailing rainfall and temperature regime is a key determinant of the type of crop farmers choose to grow. As climate regimes evolve and migrate, so too will the crops that can be grown. Within any specific climate regime, the impacts of short-duration changes, such as heat waves, cold snaps, and flooding, can be very significant. Higher temperatures cause heat stress in plants. This means they grow less and produce less. At critical stages of the growing stage, such as flowering time, high and low temperature extremes can significantly reduce the formation of fruits. In some cases, the plants do not reproduce at all inasmuch as excessive heat causes sterility of the pollen. As extreme weather events are expected to become more frequent and intense as the planet warms, their impact on yields will also become more pronounced.

Yields are also expected to be affected by levels of surface ozone, which can be detrimental to plant growth even at very low concentrations. Ozone creates reactive molecules that destroy Rubisco, an enzyme crucial for photosynthesis. As fossil fuel use increases, so will surface ozone concentrations, and in major crop-growing regions of China and the United States, surface ozone levels are expected to rise by 25 % by 2050. A 2006 study on impacts of CO_2 and ozone concentrations showed that yields (simulating expected 2050 CO_2 and ozone levels) could fall by 10 % rather than increase as would be expected to occur with no ozone concentration change. The study also indicated delayed crop maturity, which could increase crop susceptibility to early frosts. Most crop models do not take into account the potential impact of surface ozone changes and, as a result, may tend to overestimate future crop production for some regions.

A temperature increase may be beneficial in areas that are very cold at present. Plants will have to adapt to new climate conditions more rapidly than they have ever had to do so before. Excessive rainfall results in floods. Waterlogged soil causes plant roots to rot and heavy rainfall damages tender young plants.

3.9 Temperature-Induced Ethylene Effects

Ethylene is the universal growth regulator. Among the more striking temperature-induced effects of endogenous ethylene are the "fall color" in deciduous woodlands, which results from the reaction of ethylene with plant pigments. The considerable stress of cool nights on a tropical fruit forces production of minute amounts of ethylene, with consequent loss of chlorophyll and development of carotenoids.

3.10 Effect on Crop Pathogens and Insects

3.10.1 Pathogens

The study of plant disease often begins with a discussion of the "plant disease triangle." The three legs of the triangle—host, pathogen, and environment—must be present and interact appropriately for plant disease to result. If any of the three factors is altered, changes in the progression of a disease epidemic can occur. The major predicted results of climate change—increases in temperature, moisture, and CO_2—can affect all three legs of the plant disease triangle in various ways.

Temperature has potential impacts on plant disease through both the host crop plant and the pathogen. Many mathematical models that have been useful for forecasting plant disease epidemics are based on increases in pathogen growth and infection within specified temperature ranges. Generally, fungi that cause plant disease grow best in moderate temperature ranges. Temperate climate zones that include seasons with cold average temperatures are likely to experience longer periods of temperatures suitable for pathogen growth and reproduction if climates warm (Wallin and Waggoner 1950). Earlier onset of warm temperatures could result in an earlier threat from late blight with the potential for more severe epidemics and increases in the number of fungicide applications needed for control. The host plants such as wheat and oats become more susceptible to rust diseases with increased temperature; but some forage species become more resistant to fungi with increased temperature (Coakley et al. 1999).

Moisture can affect both host plants and pathogen organisms in various ways. Some pathogens such as apple scab, late blight, and several root pathogens are likely to infect plants with increased moisture; forecast models for these diseases are based on leaf wetness, relative humidity, and precipitation measurements. Other pathogens such as the powdery mildew species tend to thrive in conditions with lower (but not low) moisture.

More frequent and extreme precipitation events that are predicted by some climate change models could result in more and longer periods with favorable pathogen environments. Host crops with canopy size limited by lack of moisture might no longer be so limited and may produce canopies that hold moisture in the form of leaf wetness or high canopy relative humidity for longer periods, thus increasing the risk from pathogen infection (Coakley et al. 1999). Some climate change models predict higher atmospheric water vapor concentrations with increased temperature; this also would favor pathogen and disease development. Increased CO_2 levels can affect both the host and the pathogen in multiple ways. Some of the observed CO_2 effects on disease may counteract others. Researchers have shown that higher growth rate of leaves and stems observed for plants grown under high CO_2 concentrations may result in denser canopies with higher humidity that favor pathogens. Lower plant decomposition rates observed in high CO_2 situations could increase the crop residue on which disease organisms can overwinter, resulting in higher inoculum levels at the beginning of the growing season, and earlier and faster disease epidemics. Pathogen growth can be affected by higher CO_2 concentrations resulting in greater fungal spore production. However, increased CO_2 can result in physiological changes to the host plant that can increase host resistance to pathogens (Coakley et al. 1999).

3.10.2 Insects

Insects are cold-blooded organisms; the temperature of their bodies is approximately the same as that of the environment. Therefore, temperature is probably the single most important environmental factor influencing insect behavior, distribution, development, survival, and reproduction. Insect life stage predictions are most often calculated using accumulated degree days from a base temperature and biofix point. Some researchers believe that the effect of temperature on insects largely overwhelms the effects of other environmental factors (Bale et al. 2002). It has been estimated that with a 2 °C temperature increase insects might experience one to five additional life cycles per season (Yamamura and Kiritani 1998). Although some climate change temperature effects might tend to depress insect populations, most researchers seem to agree that warmer temperatures in temperate climates will result in more types and higher populations of insects.

Researchers have shown that increased temperatures can potentially affect insect survival, development, geographic range, and population size. Temperature can affect insect physiology and development directly or indirectly through the physiology or existence of the host. Depending on the development "strategy" of an insect species, temperature can exert different effects (Bale et al. 2002). Some insects take several years to complete one life cycle; these insects (cicadas, arctic moths) will tend to moderate temperature variability over the course of their life history. Some crop pests are “stop and go” developers in relation to temperature: they develop more rapidly during periods of time with suitable temperatures. Increased temperatures will accelerate the development of these types of insects, possibly resulting in more generations (and crop damage) per year.

Parasitism could be reduced if host populations emerge and pass through vulnerable life stages before parasitoids emerge. Hosts may pass through vulnerable life stages more quickly at higher temperatures, reducing the window of opportunity for parasitism. Temperature may change gender ratios of some pest species such as thrips (Lewis 1997), potentially affecting reproduction rates. Insects that spend important parts of their life histories in the soil may be more gradually affected by temperature changes than those which are aboveground simply because soil provides an insulating medium that will tend to buffer temperature changes more than the air (Bale et al. 2002).

Lower winter mortality of insects due to warmer winter temperatures could be important in increasing insect populations (Harrington et al. 2001). Higher average temperature might result in some crops being able to grow in regions farther north. It is likely that at least some of the insect pests of those crops will follow the expanded crop areas. Insect species diversity per area tends to decrease with higher latitude and altitude (Gaston and Williams 1996; Andrew and Hughes 2005), meaning that rising temperatures could result in more insect species attacking more hosts in temperate climates (Bale et al. 2002). Based on evidence developed by studying the fossil record, Bale et al. (2002), concluded that the diversity of insect species and the intensity of their feeding have increased historically with increasing temperature.

Some insects are closely tied to a specific set of host crops. Temperature increases that cause farmers not to grow the host crop any longer would decrease the populations of insect pests specific to those crops. The same environmental factors that affect pest insects can affect their insect predators and parasites as well as the disease organisms that infect the pests, resulting in increased attack on insect populations.

Some insects are sensitive to precipitation and are killed or removed from crops by heavy rains. For some insects that overwinter in soil, such as the cranberry fruit worm and other cranberry insect pests, flooding the soil has been used as a control measure (Vincent et al. 2003). One would expect the predicted more frequent and intense precipitation events forecast with climate change to affect the insects negatively. As with temperature, precipitation changes can have an impact on insect pest predators, parasites, and diseases resulting in a complex dynamic. Fungal pathogens of insects are favored by high humidity and their incidence would be increased by climate changes that lengthen periods of high humidity and reduced by those that result in drier conditions.

Generally CO_2 impacts on insects are thought to be indirect: impact on insect damage results from changes in the host crop. Some researchers have found that rising CO_2 can potentially have important effects on insect pest problems. Insects sometimes feed more on leaves that have a lowered nitrogen content in order to obtain sufficient nitrogen for their metabolism (Coviella and Trumble 1999; Hunter 2001).

Increased carbon-to-nitrogen ratios in plant tissue resulting from increased CO_2 levels may slow insect development and increase the length of life stages vulnerable to attack by parasitoids (Coviella and Trumble 1999).

Climate-induced changes in biodiversity and ecosystems, such as reductions in the abundance of essential crop pollinators (such as bees) or natural insect control species (such as insect-eating birds), could also affect yields, as could expansions in the geographical ranges of pests and diseases.

3.10.3 Pest Management Practices

Although physiological changes in host plants may result in higher disease resistance under climate change scenarios, host resistance to disease may be overcome more quickly by more rapid disease cycles, resulting in a greater chance of pathogens evolving to overcome host plant resistance. Fungicide and bactericide efficacy may change with increased CO_2, moisture, and temperature. The more frequent rainfall events predicted by climate change models could result in farmers finding it difficult to keep residues of contact fungicides on plants, triggering more frequent applications. Systemic fungicides could be affected negatively by physiological changes that slow uptake rates, such as smaller stomatal openings or thicker epicuticular waxes in crop plants grown under higher temperatures. These same pesticides could be affected positively by increased plant metabolic rates that could increase pesticide uptake. It is not well understood how naturally occurring biological control of pathogens by other microbial organisms could change as populations of microorganisms shift under changed temperature and moisture regimes; in some cases antagonistic organisms may out-compete pathogens whereas in others pathogens may be favored. Exclusion of pathogens and quarantines through regulatory means may become more difficult for authorities as unexpected pathogens might appear more frequently on imported crops.

3.11 Land Degradation and Desertification

Land degradation and desertification are induced by several factors, primarily anthropogenic causes, which began in the Holocene era and continue at the highest pace today. The primary reasons for desertification are overgrazing, overcultivation, increased fire frequency, water impoundment, deforestation, overdrafting of groundwater, increased soil salinity, and global climate change (Wilson 2001). Nevertheless, projected levels of climate change clearly would worsen the land degradation and desertification that has occurred over the last several centuries as the human population has expanded, water resources have been harnessed and diverted, monocultures established, and forests cleared.

Extreme climatic events historically are the main cause of land degradation, amplified by unwise land clearing in marginal areas where soil needs vegetation cover to remain fertile and to prevent erosion. Increased frequency and severity of droughts and floods, and increased fire frequency and intensity, will increase wind and water erosion of soil and loss of soil fertility in many regions. More marginal land is likely to be exploited, increasing the synergetic interplay between climate change and loss of land cover, erosion, and reduced soil fertility. Floods, landslides, and related natural disasters will cause increased damage, loss of life, and poverty. The pressing need to substitute biomass for fossil fuels will also place further pressure on land resources, with possible unfortunate consequences for sustainability, food production, and human equity, although reforestation and biomass plantations may in some cases help protect or restore degraded land and provide jobs and income.

3.12 Effects on Field

People mostly look at temperature changes, but under climate change there are also other components of the climate system that are equally important. Surface water runoff is one such. In this case, the physiological effect actually has more effect on the water cycle than the radiative effect. The effect of runoff varies from region to region, with some regions even showing a decrease in surface runoff due to CO_2 physiological forcing as a result of reduced precipitation. A study in 2007 using the UK model, HadSM3, had recognized that the effect of physiological forcing might be equivalent to that of radiative forcing in increasing continental runoff. In the humid tropics and monsoon climates, increased intensities of rainfall events and increased rainfall totals would increase leaching rates in well-drained soils with high infiltration rates, and would cause temporary flooding or water saturation, hence reduced organic matter decomposition, in many soils in level or depressional sites. Soils most resilient against such changes would have adequate cation exchange capacity and anion sorption to minimize nutrient loss during leaching flows, and have a high structural stability and a strongly heterogeneous system of continuous macropores to maximize infiltration and rapid bypass flow through the soil during high-intensity rainfall.

In temperate climates, minor increases in rainfall totals would be expected to be largely taken up by increased evapotranspiration of vegetation or crops at the expected higher temperatures, so that net hydrological or chemical effects on the soils might be small. The negative effect on soil organic matter content of a temperature rise might be more than compensated by the greater organic matter supply from vegetation or crops growing more vigorously because of the higher photosynthesis, the greater potential evapotranspiration, and the higher water-use efficiency in a high CO_2 atmosphere. The temperature zone would thus be likely to have the smallest changes in soils, even in poorly buffered ones, directly caused by the effects of global change. A minor and probably slow, but very visible, change could be a reddening of presently brown soils where increased periods with high summer temperatures would coincide with dry conditions, so that the iron oxide hematite would be stable over the presently dominant goethite. This mineralogical change might decrease the intensity and amount of phosphate fixation.

4 Adapting to Biotic and Abiotic Stresses

Climate change will have major consequences on horticulture according to the Fourth Assessment Report of the United Nation's Intergovernmental Panel on Climate Change (2007). Certain regions of the world are expected to be warmer, others colder, some drier, and some wetter. For the Midwest, the near-term forecast is not so dire, although most projections for climate change forecast weather extremes including more frequent episodes of drought, flooding, heat waves, and other environmental problems. Climate change will affect horticulture because our crops have been adapted for growth in specific climate and ecological zones. Climate change will have the effect of shifting zones.

There are two general issues to consider with respect to crop plants and climate: one is the effects of climate change on plants (adaptation) and another is the influence of plants on climate change (mitigation). Because forecasts are for more severe weather because of climate change, there is a need to protect plants from environmental extremes by developing plants that are stress tolerant. Stress tolerance, the ability to withstand environmental stress, is a valuable trait in plants. Over the years, plant breeding programs have directly or indirectly selected for stress tolerance. Yet average yields may fall far short of their genetic potential largely because various plant stresses limit yield.

Scientists have made much progress recently in understanding plant responses to environmental stresses. It has been found that the responses to several stresses, such as cold, drought, and saline stresses involve complex signaling networks made up of many shared components. Because these signaling networks are complex, there are many entry points by which scientists can influence and enhance plant stress responses (Yamaguchi-Shinozaki and Shinozaki 2006).

Plants themselves can also affect climate through gas exchange, water transpiration, and carbon sequestration. Scientists are working to develop crops and farming practices that sequester carbon. Plants "fix" CO_2 through photosynthesis and release some of the fixed carbon through photorespiration. Plants store carbon in shoots and roots. Soil carbon is released through the action of soil microbes. Scientists are attempting to improve carbon fixation and reduce plant photorespiration and microbial degradation of soil carbon.

Conclusion

Globally climate change is under way, with about 20 % more carbon dioxide, the most important greenhouse gas, having been added to the total amount in the Earth's atmosphere since 1950. As carbon dioxide increases, the climate warms, with potentially disastrous outcomes. To build and to maintain a sustainable society, it is necessary to preserve the productive natural systems that support us. Renewable resources such as forests, biodiversity, soils, and fresh water must be treated in ways that ensure their long-term productivity. Their capacity for renewal must be understood and respected.

Improving agriculture is one of the highest priorities involved in achieving future sustainability. Many improvements in agriculture will be needed to feed the world's people adequately in the future. The negative environmental effects on agriculture, including loss of soil fertility, soil erosion, aquifer depletion, soil and water pollution, and air pollution, must be brought under control by using an array of methods. Many strategies exist to retard the loss of topsoil and degradation of agricultural lands, conserve water, conserve energy, and reduce reliance on agricultural chemicals. Moreover, plantation of horticultural (perennials) plants that are at greater risk can also help in mitigating the climate change effects by absorbing more radiation than annual or seasonal crops.

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Effect of Elevated Levels of Carbon Dioxide on the Activity of RuBisCO and Crop Productivity

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Abstract Atmospheric CO_2 concentration is now higher than it was at any time in the past 26 million years and is expected to nearly double during this century. This trend is of concern to agriculture because elevated atmospheric carbon dioxide levels have been shown to decrease the rates of photorespiration. Rubisco, the key enzyme in photosynthesis and photorespiration, exhibits dual activity and is known to be regulated by relative CO_2/O_2 ratio of the atmosphere. Terrestrial plants with a C_3 photosynthetic pathway respond in the short term to increased CO_2 concentration via increased net photosynthesis and decreased transpiration. Recent empirical evidence suggests that the warming may only be about 0.25 °C, so the primary effects on agriculture are likely to be the beneficial increases in crop yields and water use efficiency. However, researchers have shown that elevated levels of carbon dioxide inhibit nitrate assimilation in wheat and *Arabidopsis* plants. Another important implication of this study is the effect of elevated levels of carbon dioxide on the nutritional quality of the crop. Under elevated CO_2 most plant species show higher rates of photosynthesis, increased growth, decreased water use, and lowered tissue concentrations of nitrogen and protein. Rising CO_2 over the next century is likely to affect both agricultural production and food quality.

Keywords CO_2 concentration • Rubisco • Carboxylation • Oxygenation • Photosynthesis • FACE • Plant nutrition • Hidden hunger • Meta-analysis approach

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1 Introduction

All over the globe there is a concurrent increase in population and it is expected to exceed nine billion (Godfray et al. 2010), hence the requirement for food is constantly increasing (FAOSTAT 2013). Consequently, hordes of human activities such as deforestation for arable land, fossil fuel burning, and attempts to increase crop productivity are occurring in order to feed the growing population. Due to these anthropogenic activities elevation of atmospheric CO_2 and consequently temperature increase has been recorded globally. According to the fifth report of the IPCC, global warming is unequivocal (DTE Annual 2014), its effects are quite visible, the atmosphere and oceans have warmed, the amount of snow and ice have diminished, sea levels are rising, there is loss of biodiversity, fluctuating crop yields, and increase in the concentration of the greenhouse gases are observable universally. The World Meteorological Organization in its (2013) report stated that there are increases of 39 %, 158 %, and 20 %, respectively, in global average concentration of CO_2, CH_4, and N_2O since the start of the industrial era in 1750. Atmospheric CO_2 concentration is now higher than it was at any time in the past 26 million years. The current annual rate of increase in CO_2 concentration is expected to bring the levels to far above 600 ppm by the end of the current century (Schimel et al. 1996). Since 1960 the amount of CO_2 in the atmosphere has risen from 315 to 378 ppm (approximately 20 %). An elevated level of CO_2 is directly related to global warming which means an increase in the global mean temperature. Among the environmental factors, temperature is a major factor that affects growth, development, and yield of crops (Luo 2011). A warmer global climate change will result in the change in agricultural patterns by shifting food growing areas, changes in crop yields, increase in irrigation demands, and an increase in pests, crop diseases, and weeds in warmer areas. The World Bank estimates that by the mid-twenty-first century, crop yield would decrease by up to 30 % in South Asia due to climate change. The region is already experiencing warming, increasing variability of the monsoon rainfall, heavier downpours, and an increase in the frequency of drought and floods. Recent devastating floods of Jammu and Kashmir (2014) and Uttarakhand (2013) regions of India and Pakistan along eastern Afghanistan (2013), and the recent Hudhud cyclone (2014) at the southern coast of India are remarkable examples of climate change.

This trend of accelerated carbon emissions is of concern to agricultural production and food quality because elevated atmospheric carbon dioxide levels have shown strong diversified effects on crops. The quality of crops is a multifaceted and complex subject and involves different stages of growth and development including pre- and post-harvest and environmental and technological aspects. It also involves nutritional, elemental (zinc, iodine, etc.), and macromolecular (protein) composition in plant tissues (DaMatta et al. 2010; Taub et al. 2008; Hay and Porter 2006). There is growing evidence suggesting that many crops, notably C3 crops, may respond positively to increased atmospheric CO_2 in the absence of other stressful conditions (Long et al. 2004). However, the beneficial direct impact of elevated CO_2 can be offset by the effects of climate change, such as elevated temperatures, higher ozone levels, and altered patterns of precipitation (Easterling et al. 2000; Trenberth 2011). During early evolution the atmosphere was of high CO_2 concentration (4–5 times the present value) and that is the time when plants originated. During the last 25–30 million years CO_2 concentration has stabilized at a relatively low value.

The effects of elevated CO_2 are not uniform; some species, particularly those that utilize the C_4 variant of photosynthesis, show less response to elevated CO_2 than do other types of plants. Rising CO_2 is therefore likely to have complex effects on the growth and composition of natural plant communities. The preliminary effects of elevated CO_2 levels in most crop plants, particularly C3 plants, include biomass accumulation, development, and reproduction (Kimball 1983; Kimball et al. 1993; Poorter and Navas 2003). However, it has been observed in various studies that initial stimulation of the net photosynthesis rate is temporal and plants are not able to sustain the maximal stimulation, a phenomenon known as photosynthesis acclimation. In other words, plants on prolonged exposure to high CO_2 concentration exhibit reduced photosynthetic rates. Sucrose is known to interfere in the transcription of genes encoding proteins involved in CO_2 fixation and electron transport activity (Moore et al. 1999) and therefore photosynthesis slows down. Plants respond to these projected future levels of CO_2 from various types of enclosure studies conducted over the past three decades. Among these studies the most notable are Open Top Chambers (OTC) and Free Air CO_2 Enrichment (FACE) studies (Lewin et al. 1994; Hendry and Miglietta 2006). These studies revealed that photosynthetic carbon uptake is enhanced by elevated CO_2 despite acclimation of photosynthetic capacity (Leakey et al. 2009).

In a group of plants with or without phylogenetic relatedness such as C_4 or legumes showing acclimation, there is larger potential for the stimulation of photosynthetic carbon uptake because elevated CO_2 increases the carboxylation rate of Rubisco and decreases the rate of photorespiration (Long et al. 2004; Ainsworth and Rogers 2007). Genetic factors are known to play an important role in photosynthetic response to elevated CO_2 as shown by the PopFACE experiment (Scarascia-Mugnozza et al. 2006). Poplars exported more than 90 % of their photosynthate during the day and stored the rest of the overflow photosynthate as starch (Davey et al. 2006) which enabled the trees to avoid acclimation of photosynthetic potential and maintain maximal stimulation of photosynthetic carbon uptake at elevated CO_2.

In the era of global warming, it is very important to understand the impact of CO_2 enrichment, temperature, and other climatic changes on food crops to estimate future food production. This chapter primarily focuses on the expected elevated levels of CO_2 in the future, its effect on the activity of Rubisco, and the quality of crops. The apprehensions regarding the negative impact of elevated levels of CO_2 in times to come also lead to a short discussion on the direction of research to combat the problem.

2 Rubisco and Its Role in Photosynthesis

Ribulose 1,5bisphosphate Carboxylase Oxygenase (Rubisco) is a major soluble protein present in the plant cell. It is responsible for photosynthesis and photorespiration. Rubisco is one of the key enzyme proteins in the biosphere and accounts for half of total leaf proteins. It is a multisubunit enzyme having molecular weight of about 560,000 Da. It comprises two subunits, large and small. Small subunits are coded by the nuclear genome whereas the large subunit by the chloroplast genome. These subunits are associated to form the complex functional holoenzyme. It is located in the chloroplast stroma and is activated by an increase in pH and Mg^{2+} ion (Taiz and Zeiger 2006). It is a unique enzyme catalyzing carboxylation of RuBP to form two molecules of PGA and oxygenation of RuBP to form PGA and phosphoglycolic acid. The PGA is further metabolized by the C_3 cycle whereas phosphoglycolic acid is metabolized via photorespiratory or C_2 cycle (Kajala et al. 2011). Thus this protein exhibits dual enzymatic activity, carboxylation, and oxygenation of RuBP. The property of carboxylase/oxygenase is regulated by the relative CO_2/O_2 ratio of the atmosphere. If this ratio is high carboxylase activity is favored whereas a low ratio favors the oxygenase property. It has also been noted that during high temperature RuBP carboxylase loses its affinity for CO_2 and acts as RuBP oxygenase. However, the global increase in CO_2 levels has been shown to be linked with global warming. Therefore it is very important to discover the effect of CO_2 enrichment on crop productivity when environmental temperature is also increasing.

2.1 *Effect of Elevated Levels of CO_2 on Photosynthesis*

The study pertaining to the effect of elevated CO_2 on crop productivity was developed in the late 1970s and 1980s. During the early days the data were mainly obtained from use of indoor growth chambers through outdoor growth chambers, greenhouses, and later on studies were undertaken in open top chambers (OTC) to Free Air CO_2 Enrichment (FACE) studies. Under certain circumstances (Arp 1991; Ronchi et al. 2006; Stafford 2008) the results of greenhouses and OTCs were debated in the scientific world because of their limitations. Plants grown in the above-mentioned systems were not exposed to changing environmental conditions such as temperature, humidity, and wind (Ross et al. 2004; Long et al. 2006). In OTCs the conditions are warmer than the adjacent unenclosed fields and plants in them showed edge effect. It also gave limited access to pests and diseases but if they gain contact, high humidity and warmer temperature may worsen epidemics (Long et al. 2006). FACE acts as an alternative to the OTC and can minimize as far as possible lacunas associated with small pots and confined systems. It apparently mimics realistic future agricultural conditions (Dodd 2013; Ainsworth et al. 2008a). FACE studies have been conducted worldwide on a large number of plant communities including crops such as wheat, rice, sorghum, potato, grapes, cotton (Kimball et al. 2002), natural grasslands of Tasmania (Hovenden et al. 2006), and plantation forests of *Pinus* and *Populus* spp. (Norby et al. 2005).

In spite of all the advantages the main limitation of FACE is the cost of the large amounts of CO_2 that must be released during the experiments (estimated costs around US$1 million over a year) excluding the additional cost of the investigation (DaMatta et al. 2010). In addition to cost, other key points such as CO_2 versus temperature interaction evaluations and testing CO_2 above 550 ppm are rarely performed using the current FACE technology (Tubiello et al. 2007; Ainsworth et al. 2008b).

Drake et al. (1997) reported limitations in photosynthesis, when plants were first grown at a given CO_2 concentration and then transferred to different CO_2 concentrations. The first limitation was referred to as the limitation due to supply and utilization of CO_2. The second limitation was the supply and utilization of light, and the third refers to the utilization of triose phosphate. Several theoretical models have predicted that the doubling of atmospheric CO_2 concentration will increase the Earth's temperature by 2.5 °C to 4.3 °C, which could seriously disrupt agricultural production (IPCC 2007). The temperature response of crop growth and yield, respectively, must be considered to predict the CO_2 effects on the crops (Ziska and Bunce 1997; Porter and Semenov 2005). High temperatures reduce the net carbon gain in C_3 species by increasing photorespiration at ambient CO_2 levels. At elevated levels of CO_2, photorespiration reduces, thereby increasing photosynthesis and hence carbon gain (Badger and Price 2003). More recent empirical evidence suggests that the warming may only be about 0.25 °C, so the primary effects on agriculture are likely to be beneficial increases in crop yields and water-use efficiency. However, grain yield is known to increase marginally under increased CO_2 concentration. Apart from the tropical grasses, which constitute only 3–4 % of all known plant species, the rest of the plant species termed C3 plants lack optimal CO_2 concentration. This recent increase in CO_2 concentration will significantly stimulate growth, development, and reproduction in a wide variety of C3 plants (Kimball 1983; Kimball et al. 1993; Poorter and Navas 2003). The impact of increasing CO_2 concentration on plants has been lauded by some as “a wonderful and unexpected benefit from the industrial revolution” (Robinson and Robinson 1997). With the increasing human population, the major challenge is the demand for food. Several studies have indicated that two of the major crops, wheat and rice, show a positive response to elevated levels of atmospheric CO_2 (Mandersheid and Weigel 1997; Horie et al. 2000). Such an effort holds significant promise that cereal yields can be potentially increased as per the demand of the growing population. In a FACE experiment Ainsworth et al. (2008c) reported that elevated CO_2 increases photosynthesis, resulting in increased dry matter accumulation, leaf area, and plant height in trees and shrubs and to some extent in C_3 plants. Jablonski et al. (2002) evaluated 79 crop and native species at CO_2 enriched conditions and reported a 31 % increase in overall biomass of the plants. Yang et al. (2009) in a FACE study at 570 ppm of CO_2 reported there is an 8 % increase in number of panicles per unit area, 10 % increase in number of spikelets per panicle, and 4 % increase in grain biomass, and all of them taken together led to a 30 % increase in grain yield. De Souza et al. (2008) in an OTC-based study with an elevated CO_2 (380–740 ppm) on sugarcane reported 50 % increase in biomass and 29 % increase in sucrose accumulation. Similarly there have been many studies that have quantified the effect of increased CO_2 concentration and N utilization (Lam et al. 2012a). They further reported that elevated CO_2 concentration increases crop production by supplying an adequate amount of N either from soil, fertilizer, or biological N-fixation.

2.2 *Effect of CO_2 Concentration on the Activity of Rubisco and Nitrogen Assimilation*

Rubisco is the rate limiting enzyme in photosynthesis and its activity is largely affected by atmospheric CO_2 and nitrogen availability. It is mandatory to emphasize that maintenance of the C/N ratio is pivotal for various growth and development processes in plants governing yield and seed quality. It is therefore of prime importance to maintain the optimum levels of C and N within plants as well as externally in soil for proper growth and development (Paul and Driscoll 1997; Martin et al. 2002; Malamy 2005). In C_3 plants, Rubisco is the key photosynthetic enzyme involved in carbon assimilation and it is the major storage protein and source of nitrogen, which is utilized by the plants' reproductive components when Rubisco undergoes degradation during leaf senescence. Thus the effect of elevated CO_2 on plants is twofold: because of the decline in levels of Rubisco the process of photosynthesis becomes rate limiting, and there is reduction in the available nitrogen pool. Bloom et al. (2012, 2014)have shown that elevated CO_2 directly inhibits plant nitrogen metabolism, especially the assimilation of nitrates into proteins in leaves of C_3 plants. An optimum C/N ratio suggests increased CO_2 levels with lower nitrogen levels resulting in lower protein content. In leaf tissue, the ratio of nitrate to total nitrogen concentration and the stable isotope ratios of organic nitrogen and free nitrate clearly exhibited that nitrate assimilation was slower under elevated than ambient CO_2. Under CO_2-enriched conditions plants grow larger and dilute the amount of protein within their tissues (Ellsworth et al. 2004; Reich et al. 2006); there is also accumulation of carbohydrates within leaves, downregulation of Rubisco (Long et al. 2004), and carbon-enriched rhizosphere limits available N to plants (Reich et al. 2006). Recently several meta-analysis data indicated enriched CO_2 inhibits the assimilation of nitrates (Cheng et al. 2012; Pleijel and Uddling 2012; Myers et al. 2014). It further leads to reduced sink protein concentration because N supply to sinks during filling occurs from catabolized protein from senescing photosynthetic tissues (Hay and Porter 2006). This adversely affects grain quality particularly in cereal crops. It has also been observed that plant growth is slower under elevated than ambient CO_2 when nitrate serves as the sole nitrogen source and faster when ammonia is the only source of nitrogen (Matt et al. 2001; Bloom et al. 2002; Lekshmy et al. 2013). The detailed study on nitrate assimilation confirmed that elevated CO_2 inhibited leaf nitrate assimilation in field-grown wheat. It was observed that the percentage of total nitrogen that remained as unassimilated nitrate was higher under elevated than ambient CO_2 over a period of time. There is ubiquitous evidence supporting the above concept (Jablonski et al. 2002; Ziska et al. 2004). Several research groups have demonstrated that under elevated CO_2 conditions the protein concentrations in wheat grain, rice grain, potato, and barley decline by 8 %, whereas these crops, respectively, are the source of 21, 13, 2, and 0.3 % of the protein in the human diet (Myers 2014; Kimball et al. 2001; Erbs et al. 2010). This may result in diminishing the amounts of protein available for human consumption by about 3 % as atmospheric CO_2 reaches the levels anticipated during the next few years. Apart from N, other elements in grains are also filled by mobilization from vegetative pools (Hay and Porter 2006). Loladze (2002) reported that increase in photosynthesis under elevated CO_2 may be associated with increased plant requirements for P but decreased for N. Fangmeier et al.(1999) reported that elevated CO_2 may change the concentrations of different elements that respond similarly to N, such as S, Mg, Ca, K, and Zn. In order to achieve food security in times to come sophisticated strategies with respect to nitrogen fertilization are required in order to increase not only the grain yield but also the protein yields under elevated CO_2 levels.

2.2.1 Effect of Nitrogen Fertilizers

The scientists suggest that, as global climate change intensifies, it will be critical for farmers to manage nitrogen fertilization carefully in order to prevent losses in crop productivity and quality. The reversed N management practices may include greater use of legume intercropping or legume cover crops apart from fertilizers (Lam et al. 2012b; WUWT 2010). The probable effect of the increasing global atmospheric CO_2 concentration on agricultural yields was evaluated in a large number of species grown with CO_2 enrichment. A lot has been learned about the response of plants to elevated CO_2 levels from various sorts of enclosure studies conducted during the last three decades (Leakey et al. 2006, 2009). Open fields might respond less than greenhouses or growth chambers to increased CO_2 because nutrient levels in general worldwide agriculture are lower than those in the indoor studies, or open fields might respond more because the light levels are generally higher. However, keeping these limitations of the data in mind, the analysis showed that yields probably will increase by 33 % with a doubling of atmospheric CO_2 concentrations.

Legumes are important components of cropping systems and are major sources of vegetable oil and protein for human and animal consumption. They provide about 20 % of the world's protein for the human diet, and one fourth of the world's fats and oils (Harlan 1992). Legumes also help to enrich soil through their unique capability to form symbiotic relationships with nitrogen-fixing bacteria that capture atmospheric nitrogen and make it available for crop growth. In addition, legumes are traditionally used as green manure and cover crops in crop rotation to improve physical conditions of the soil. Legumes, too, are capable of responding to elevated CO_2 with increased photosynthesis and growth (Rogers et al. 2009). For most plants, growth under elevated CO_2 can alter the internal balance between carbon (gained via enhanced photosynthesis) and nitrogen (either unaffected or taken up in decreased amounts due to decreased uptake of water). In contrast, most legume species participate in close mutualistic relationships with bacteria that live in nodules formed on the plant's roots. These bacteria are able to "fix" atmospheric nitrogen, chemically reducing it to a form that can be taken up and used by plants. Under elevated CO_2 conditions, legumes may be able to shunt excess carbon to root nodules where it can serve as a carbon and energy source for the bacterial symbionts. In effect, legumes may be able to exchange the excess carbon for nitrogen and thereby maximize the benefits of elevated atmospheric CO_2. Many studies in controlled environments have shown that, compared to other plant species, legumes show greater enhancement of photosynthesis and growth by elevated CO_2 (Rogers et al. 2009).

Decreases in tissue nitrogen concentrations under elevated CO_2 are also smaller for legumes than for other C_3 species (Cotrufo et al. 1998; Jablonski et al. 2002; Taub et al. 2008). In FACE experiments, soybeans (a legume) show a greater response to elevated CO_2 than wheat and rice in photosynthesis and overall growth, although not in harvestable yield (Long et al. 2006). C_4 plants use a biochemical pump to concentrate CO_2 at the locations within the leaf where the Rubisco enzyme mediates incorporation of CO_2 by the Calvin–Benson photosynthetic cycle. Because CO_2 concentrations are already high within the bundle sheath cells, increasing atmospheric CO_2 concentrations above current levels has little direct effect on photosynthetic rates for C_4 species. C_4 species respond to elevated CO_2 by decreasing stomatal conductance; this may lead to some indirect enhancement of photosynthesis by helping avoid water stress under drought conditions (Leakey et al. 2009). Thus, increased stomatal closure under conditions of high CO_2 will result in reduced loss of latent heat there by increasing leaf temperature (Kimball and Bernacchi 2006). However, a new dimension was added to this study by the work of Rogers et al. (1998) in swards of perennial rye grass grown under conditions of additional 240 ppm CO_2. The study did not exhibit any reduction in the amounts of Rubisco as long as they received high levels of nitrogen from the soil. Under conditions of low soil nitrogen these plants displayed a 25 % reduction in the levels of Rubisco. Researchers removed a large portion of leaf from these plants and continued growing them under conditions of low nitrogen. The results showed increased levels of Rubisco to facilitate greater carbon uptake to repair the damage caused by removal of the major portion of the leaf. These and several other observations led to the conclusion that plants grown under conditions of elevated CO_2 levels require less nitrogen . This gives them the opportunity to reallocate some of the extra nitrogen to other metabolic processes required for optimal growth and development together with the required carbon gains through photosynthesis.

Effect of Elevated Levels of CO_2 on Photorespiration

Rubisco is a bifunctional enzyme possessing carboxylase as well as oxygenase activity. We have thus far discussed the effect of elevated CO_2 on the carboxylase activity thereby affecting photosynthesis. The oxygenase activity is responsible for the process of photorespiration, a metabolic pathway leading to loss of carbon from the plant. The question therefore is the effect of increased levels of CO_2 on the oxygenase activity and the associated implications of any potential changes in the quality and content of nutrition in the crops with a suggested futuristic increase in the levels of atmospheric CO_2.

Voluminous experimental data demonstrate that atmospheric CO_2 enrichment favors carboxylation over oxygenation, thereby increasing photosynthetic rates with concomitant reductions in photorespiratory rates (Taiz and Zeiger 2002). The rising CO_2 content of the air thus invariably leads to greater rates of net photosynthesis and a more efficient process of carbon fixation. Hence, less Rubisco is needed to obtain the carbon required for plant growth and development under CO_2-enriched conditions. *Arabidopsis thaliana* was grown at atmospheric concentrations of 1000 ppm of CO_2 for 40 days (Cheng et al. 1998); in this study the foliar Rubisco was found to be 34 % lower in concentration compared with the controls. However, the contents of glucose and fructose were enhanced more than 2-fold by elevated CO_2, and starch concentrations were increased more than 3.5-fold. Thus, although elevated CO_2 reduced the amount of Rubisco in leaves, photosynthetically derived sugars and starch still accumulated to tremendous values. Studies on *Leucadendron* species revealed a 30 % reduction in the activity of Rubisco when grown under a twice-ambient concentration of CO_2 (Midgley et al. 1999).

Several studies reported 40 % greater rates of net photosynthesis in the plants grown in a CO_2-enriched environment when compared with the plants grown under ambient CO_2 conditions. Similar results were reported in chalk grassland species exposed to CO_2 concentration of 600 ppm for 14 months (Bryant et al. 1998). In this study elevated levels of CO_2 caused an average reduction in Rubisco activity of 32 % while still exhibiting 28 % higher rates of photosynthesis compared with the controls at ambient CO_2 concentration. Similarly, work on grassland species for a period of two years by Davey et al. (1999) under elevated CO_2 concentration of 700 ppm showed a decline in Rubisco activity by an average of 27 % with a simultaneous increase in photosynthetic rates from 12 to 74 %.

One of the most consistent effects of elevated atmospheric CO_2 on plants is an increase in the rate of photosynthetic carbon fixation by leaves. Across a range of FACE experiments, with a variety of plant species, growth of plants at elevated CO_2 concentrations of 475–600 ppm increases leaf photosynthetic rates by an average of 40 % (Ainsworth and Rogers 2007). In FACE experiments, stimulation of photosynthesis by elevated CO_2 in C4 plants is only about one third of that experienced by C3 species. C4 plants also show little or no enhancement of growth (dry matter production) in these studies (Ainsworth and Long 2005). The very limited data available also show no increase in C4 crop yield in FACE studies (Long et al. 2006). Although there is little FACE data available on the effects of elevated CO_2 on plant nitrogen and protein concentrations, data from chamber experiments show C4 plants to be much less responsive than C3 plants in this regard (Cotrufo et al. 1998). The picture that emerges is that C4 plants are in general relatively unresponsive to an elevation of atmospheric CO_2 above current ambient levels.

3 Elevated CO_2 and Effects on Food Quality

Another important implication of this study is the effect of elevated levels of carbon dioxide on the nutritional quality of the crop. A CO_2-enriched environment stimulates higher photosynthesis and an increased growth rate. However, enhanced growth rate does not exhibit any correlation with the nutrient availability and elemental nutrient (Kant et al. 2012). As compared to preindustrial times, today plants are experiencing a global elemental imbalance (Loladze 2002). Plants are the foundation of the major food supply to the human population. The low concentrations of several essential micronutrients, such as iron, iodine, and zinc in modern crops contribute to the problem of micronutrient malnutrition popularly known as hidden hunger and are affecting the economy and health of more than 50 % of the world population (Loladze 2002).

Photosynthesis and stomatal behavior are crucial to carbon and water metabolism, therefore growth of plants under elevated CO_2 leads to a large variety of secondary effects on plant physiology. The availability of additional photosynthate enables most plants to grow faster under elevated CO_2. The FACE experiments have shown increased dry matter production on an average by 17 % for the aboveground and more than 30 % for the belowground portions of plants (Ainsworth and Long 2005; de Graaff et al. 2006). This increased growth is also reflected in the harvestable yield of crops, with wheat, rice, and soybean all showing increases in yield of 12–14 % under elevated CO_2 in FACE experiments (Ainsworth 2008a; Long et al. 2006). Increased levels of CO_2 also lead to changes in the chemical composition of plant tissues. Due to increased photosynthetic activity, carbohydrates (sugars and starches) per unit leaf area increase on an average by 30–40 % under FACE-elevated CO_2 (Ainsworth 2008a; Ainsworth and Long 2005). Leaf nitrogen concentrations in plant tissues typically decrease in FACE under elevated CO_2 with nitrogen per unit leaf mass decreasing on average by 13 % (Ainsworth and Long 2005). This decrease in tissue nitrogen is likely due to several factors such as dilution of nitrogen from increased carbohydrate concentration, decreased uptake of minerals from the soil as stomatal conductance decreases (Taub and Wang 2008), and decrease in rate of assimilation of nitrate into organic compounds (Bloom et al. 2010). This in turn is likely to affect human nutrition as well. In FACE experiments, protein concentrations in grains of wheat, rice, and barley as well as potato tubers decrease by 5–14 % under increased CO_2 (Taub et al. 2008). The elevated CO_2 may also affect the concentrations of calcium, magnesium, and phosphorous in the crop plants (Loladze 2002; Taub and Wang 2008).

Recently Hamada et al. (2014) reported the effects of extreme climate on the chemical composition of temperate grassland species under ambient and elevated CO_2. In an enriched CO_2 environment different C_3 and C_4 plant species show reduced forage quality through a lower crude protein content (Wand et al. 1999), whereas in combination with high temperature, fiber content increased in *Medicago sativa* and as a result digestibility was reduced (Sanz-Sáez et al. 2012). In another report elevated CO_2 induced an increased C/N ratio in soybean (Ainsworth et al. 2002) and tannin accumulation in *Lotus corniculatus* (Carter et al. 1999). The changes in plant chemical composition in response to global climate change are very complicated because these effects are species dependent. It can be seen at the carbohydrate level (Fisher et al. 2002; Oliveira et al. 2013). In legumes under elevated CO_2, the C:N ratio is lower, C:P ratio is higher, and N:P ratio is higher than in nonleguminous plants (Lee et al. 2003)

4 Conclusion and Future Prospects

Under the conditions of continuous consumption of fossil fuels, CO_2 concentration will rise; simultaneously economic growth and development will result in increase in other greenhouse effect gases such as methane, nitrous oxides, chloro-fluorocarbons, and their substitutes. In this scenario, elevated CO_2 is increasing crop productivity in plants which is the demand of the time in order to feed the global population. However, plant responses to climate change are very complicated and species-group-specific. Interactions between elevated CO_2 and extremes of climatic conditions were observed in many cases. It has been found that elevated CO_2 amplified or reduced the impact of the extreme climatic condition. It has further been found that the nutritional quality of crops grown in elevated CO_2 will lead to hidden hunger and affect the economy as well as the health of the global population. The need of the hour is a multidimensional approach to the problem of crop productivity and its nutritional quality. The meta-analysis approach including FACE, proteomics, and genomics along with metabolomics will give us insight to overcome the problem of micronutrient malnutrition as a consequence of elevated levels of atmospheric CO_2. Adaptation to gradual changes in climate is possible, however, sudden changes would be more serious and therefore mitigation strategies need to be followed.

1. Selections of plants that exhibit higher reproduction capacity under elevated CO_2
2. Germplasm selection that can grow under conditions of elevated CO_2 and high temperature and incorporation of these traits into desirable crop production cultivars to improve flowering and seed set
3. Change in planting schedule and other crop management procedures to optimize yields under changed climatic conditions
4. Selection of species that grow under conditions of high temperature and require less water for growth
5. Altered irrigation strategies to overcome conditions of drought

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Insect Pest Resistance: An Alternative Approach for Crop Protection

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Abstract From experience with insect resistance caused by synthetic chemical insecticides, it is clear that no single management tactic can provide lasting solutions to the insect pest problem. Biological control is a component of integrated pest management strategies that minimize insecticide spray applications and move towards ecofriendly systems of pest management. Successful utilization of host plant resistance, phytochemical products, pheromones, biological control agents such as predators, parasitoids, entomopathogenic bacteria, virus, nematodes, and fungi can help to control many destructive pests to achieve sustainable crop protection.

Keywords Insecticide • Resistance • Biological control • Biopesticides

1 Introduction

Insects are responsible for major crop losses. Each year, billions of dollars are spent worldwide on insect control in agriculture (Jackie et al. 2012). Despite this expenditure, up to 40 % of a crop can be lost to insect damage, particularly in developing

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countries (Oerke 2006). According to an estimate, about one third of global agricultural production has been destroyed annually by over 20,000 species of insect pests in the field and storage (Tables 1 and 2) (Mariapackiam and Ignacimuthu 2008), and approximately US$10,000 million dollars of loss has been reported from India alone (Sandhu et al. 2012). In addition to direct impacts on yield, insects also reduce yields by making crops more susceptible to disease-causing pathogens (Haq et al. 2004). The threat of insects to agriculture is set to increase as the planet warms. In order to feed the projected nine billion people by 2050, farmers must increase their cereal yield by at least 40 % (Maxmen 2013). Therefore, the need to keep insects away from destroying food crops has become even more urgent.

Over the last five decades chemical insecticides have been the backbone of insect control and cultivators had to rely on the conventional groups of insecticides such as organochlorines (DDT, BHC), cyclodienes (aldrin, dieldrin, endosulfan), organophosphates (monocrotophos, quinalphos, chlorpyriphos, profenophos, dimethoate,

Table 1 Crop losses (%) due to insect and mite pests during pre- and post-green revolution, worldwide [adapted from Benedict (2003)]

Crop	Pre-green revolution (A) (1965)	Post-green revolution (B) (1988–1990)	Changes in loss (B–A)
Barley	3.9	8.8	+4.9
Cotton	16.0	15.4	–0.6
Maize	13.0	14.5	+1.5
Potatoes	5.9	16.1	+10.2
Rice	27.5	20.7	–6.8
Soybean	4.4	10.4	+6.0
Wheat	5.1	9.3	+4.2
Average	10.8	13.6	+2.8

Table 2 Crop losses (%) due to insect pests during pre- and post-green revolution in India [adapted from Dhaliwal et al. (2007)]

Crop	Pre-green revolution (A) (early 1965s)	Post-green revolution (B) (early 2000s)	Changes in loss (B–A)
Cotton	18.0	50.0	+32.0
Groundnut	5.0	15.0	+10.0
Other oilseeds	5.0	25.0	+20.0
Pulses	5.0	15.0	+10.0
Rice	10.0	25.0	+15.0
Maize	5.0	25.0	+20.0
Sorghum and Millets	3.5	30.0	+26.5
Wheat	3.0	5.0	+2.0
Sugarcane	10.0	20.0	+10.0
Average	7.2	23.3	+16.1

phosalone, metasystox, acephate, phorate, methyl parathion, etc.), carbamates (carbosulfan, carbaryl, thiodicarb, methomyl), pyrethroids (cypermethrin, deltamethrin, fenvalerate, λ-cyhalothrin, etc.), and formamidines (chlordimeform and amitraz) (Kranthi 2007). One of the most spectacular episodes of insect control began in 1945–1946 with the commercial introduction of the synthetic insecticides such as dichloro-diphenyl-trichloroethane (DDT), followed by other organophosphate and carbamate pesticides introduced in the 1960s (Nicholson 2007). These synthetic insecticidal compounds became popular due to their long residual action and wide toxicity spectrum. A world without pesticides would lose 78 % of fruits, 54 % of vegetables, and 32 % of cereal crops (Cai et al. 2009).

Indiscriminate, inadequate, and improper use of these synthetic organic pesticides in crop pest management programs around the world caused tremendous damage to the environment, development of resistance in target pests, pest resurgence, detrimental effects on nontarget organisms, and impact on human health (Casida and Quistad 1998; Shen and Zhang 2000; Niyaki 2010; Al-Zaidi et al. 2011) along with new and potentially dangerous insecticides to which pests have already gained resistance (Pimentel and Burgess 1985). As a chemical insecticide is repeatedly used against a population, unaffected individuals survive to pass their genes on to following generations. Over time, a greater and greater proportion of the insect population is unaffected by that same insecticide. Impact of insect resistance to the environment has posed a burning and alarming situation. In addition to the damage done by the increasingly large number of surviving resistant insects, attempts to control insecticide resistance can indirectly cause secondary pest outbreaks that do yet more crop damage (Hoy 1998). In 1979, the United Nations Environmental Programme declared pesticide resistance "one of the world's most serious environmental problems." In 2009 the European Union brought in a new framework directive requiring that all member states should achieve a level of sustainable use of pesticides (European Union 2009). In view of all these problems, the availability of many broad-spectrum chemical pesticides is declining as a result of the evolution of resistance (Ishtiaq et al. 2012) and legislation (Chandler et al. 2011). This chapter outlines the current state of knowledge of insect pest resistance and alternative approaches to combat insect resistance.

2 Insecticide Resistance

Resistance to synthetic insecticides is a critical problem in several parts of the world. Melander (1914) first reported insecticide resistance. Since then the subject has received ever-greater attention due to the increasing inability to control agricultural pests through chemical means (Georghiou 1986; Brogdon and McAllister 1998). Insecticide resistance is a measurement of an insect's ability to tolerate the toxic effects of a particular insecticide, resulting in the repeated failure of the product to achieve an effective level of control when used according to the label recommendations (Luckmann and Metcalf 1982). Resistance has been reported for all insecticide classes for one or more key pest species (Georghiou 1986), including stored product insects. Shankarganesh et al. (2012) observed resistance against conventional as well as new chemistry insecticides for quinalphos, monocrotophos, lindane, endosulfon, benzene hexachloride, avermectins, spinosad, fipronil, indoxacarb, and chitin synthesis inhibitors. A comprehensive database (Arthropod Pesticide Resistance Database) by the Insecticide Resistance Action Committee, Michigan State University, provides thorough information for insect species resistant to different pesticides along with locations where resistance is reported (www.pesticideresistance.com). Development of pest resistance to pesticides has forced farmers to use extensive doses of insecticide, which is a worldwide concern in term of pesticide residue (Pimentel et al. 1992).

3 Resistance in Major Insect Pests

Broad-spectrum chemical insecticides have been the primary control agent for agricultural pests, with about 40 % targeted to the control of lepidopteran insects (Brooke and Hines 1999). *Helicoverpa* spp. (Lepidoptera: Noctuidae) are polyphagous pests of at least 181 plant species from 49 families, including cotton, corn, soybeans, tobacco, and chickpea (Trowell et al. 2000; Sivakumar et al. 2007). It has now been recognized as one of the most serious pests due to its mobility, high polyphagy, short generation duration, and high reproductive rate (Sharma 2005), causing enormous economic problems (Estebanez-Perpina et al. 2001; Downes et al. 2007) and is widely distributed in Asia, Africa, Australia, Europe, the Mediterranean, and the semi-arid tropical regions of the world. *Helicoverpa* causes an estimated loss of US$927 million in chickpea and pigeon pea, and more than US$5 billion on different crops worldwide (Sharma 2005). Almost 30 % of all pesticides used worldwide are directed against cotton bollworm, *Helicoverpa armigera* (Hubner; Ahmad 2007), which is known to develop resistance to almost all the insecticides used for its control (Kranthi et al. 2002; Lawo et al. 2008; Prasad et al. 2009). Most reported cases of insecticide resistance worldwide have evolved with resistance against pyrethroids, organophosphates, carbamates, organochlorines, and recently against the macrocyclic lactone spinosad (Aheer et al. 2009) and *Bacillus thuringiensis*-derived toxins (Zhang et al. 2011). Jackson (2014) describes newer molecules of insecticides for the control of *Helicoverpa* infesting cotton, soybeans, corn, sorghum, and peanuts.

Nair (1981) reported *H. armigera* “not a serious pest” of cotton in India. A few years later the pest was noticed to cause heavy economic losses to crops such as cotton, chickpea, and pigeonpea, and was found to withstand a sustained insecticide pressure. Subsequently high levels of resistance to synthetic pyrethroids in *H. armigera* were confirmed by Dhingra et al. (1988) and McCaffery et al. (1989). Phokela and Mehrotra (1989) studied pyrethroid resistance in different strains of *H. armigera* and stated that pyrethroid resistance appears to be mainly due to the high rate of metabolism in the resistant strains. By 1992, *H. armigera* resistance to insecticides had emerged as a great challenge to pest management in Asia and Australia. McCaffery (1998) declared that *H. armigera* has developed resistance to virtually all the insecticides that have been applied against it in any quantity in Asia and Australia. In Australia *H. armigera* is a major problem as it has developed resistance to many of the chemical insecticides that have been used for its control (Trowell et al. 2000; Estebanez-Perpina et al. 2001; Patankar et al. 2001; Downes et al. 2007; Sivakumar et al. 2007). Unlike other lepidopteran species, *H. armigera* larvae don't migrate far from their original host plant, consequently their populations in agricultural areas are exposed to consistent selection pressure, leading to greater resistance to insecticides (Fitt 1994). Cotton has historically been one of the largest users of insecticides worldwide (Anonymous 1995). A report on "insecticide resistance management in cotton" by Kranthi (2007) provides information on insecticide resistance in cotton pests.

Spodoptera spp. (Lepidoptera: Noctuidae) is a major pest of subtropical and tropical agricultural crops with an extensive host range of economically important crops. Tobacco cutworm, *Spodoptera litura* (Fabricius), is widely distributed throughout the world (Anand et al. 2009). It has been reported to feed on 112 cultivated food plants worldwide (Mousa et al. 1980), of which 40 are grown in India (Basu 1981; Muthukrishnan et al. 2005) including tobacco, cotton, groundnut, jute, maize, rice, soybeans, tea, cauliflower, cabbage, and castor (Matsuura and Naito 1997; Sahayaraj and Paulraj 1998; Sharma and Bisht 2008). Similarly, Egyptian cotton leafworm, *S. littoralis* (Boisduval), is also recognized as one of the most destructive agricultural lepidopteran pests within the subtropical and tropical regions, and *S. frugiperda* (Smith) occurs widely in various agricultural crops of the western hemisphere (Clark et al. 2007; Murua et al. 2009). During the late 1970s, *S. litura* was found to exhibit resistance to several conventional insecticides recommended for its control (Ramakrishnan et al. 1984). The synthetic pyrethroids were introduced into India and several other countries in 1980 to control major crop pests (Kranthi 2007). Excessive use of insecticides, especially synthetic pyrethroids, led to problems of insecticide resistance in *S. litura* and *H. armigera* (Prabhaker et al. 1985). Tong et al. (2013) reported field resistance of *S. litura* to carbamates (thiodicarb or methomyl) was significantly higher than that of organophosphates and pyrethroids.

Among sucking pests, aphids were reported to have developed resistance against organophosphates (Ahmad and Aslam 2005; Ahmad and Akhtar 2013), pyrethroids (Zhang et al. 1997; Ahmad et al. 1999; Herron et al. 2001), and carbamates (Bobert et al. 1994). Whitefly (*Bemisia tabaci*) was found resistant to BHC, Endosulfan, Diamethoate, Phosalone, Acephate, Monocrotophos, Quinalphos, and carbaryl (Prasad et al. 1993). However, leaf hopper (*Empoasca devastans*) was reported to be resistant to cyclodienes, organophosphates, and pyrethroids (Challam and Subbaratnam 1999; Jeyapradeepa 2000; Ahmad and Akhtar 2013).

The control of stored product insect pests relies mostly upon the use of synthetic residual insecticides and fumigants around the world (Athanassiou and Palyvos 2006). Stored-grain pests have also developed resistance to chemicals that were considered to be more effective than DDT, including lindane and malathion

(Sayaboc and Acda 1990; White and Lambkin 1990). Long-term uses of a single fumigant increase the risk of resistance development among stored-grain pests. Phosphine has been a widely used fumigant for the control of stored grain insects for almost half a century (Chaudhry 2000) and stored-grain pests such as lesser grain borer, *Rhyzopertha dominica* (F.); red flour beetle, *Tribolium castaneum* (Herbst); and rice weevil, *Sitophilus oryzae* (L.) have been reported to develop resistance against phosphine (Sartori et al. 1990).

Biotechnology-derived crops (transgenic crops) reduced the use of pesticides by 21,000 tonnes (Sankula 2005). Commercial development of insecticidal genes has focused on the *Bacillus thuringiensis* (Bt) toxins (Bravo et al. 2007; Pigott and Ellar 2007). More recently there have been reports of field resistance to Bt crops in cotton bollworm, *Helicoverpa* spp. (Luttrell et al. 1999; Ali et al. 2006; Ali and Luttrell 2007; Carriere et al. 2010), armyworm *S. frugiperda* (Storer et al. 2010), pink bollworm *Pectinophore gosspiella* (Bagla 2010; Dhurua and Gujar 2011), and western corn rootworm *Diabrotica virgifera* (Gassmann et al. 2011). The most common mechanism for Bt resistance is the disruption of binding of Bt toxin to receptors in the midgut membrane. This disruption may be caused either by mutations in the receptor that blocks binding (Heckel et al. 2007) or changes in expression of the receptors (Jurat-Fuentes et al.2011; Tiewsiri and Wang 2011). Mutations in cadherin genes are responsible for Bt resistance in *H. armigera* (Yang et al.2007), *Heliothis virescens* (Gahan et al. 2001), and *Pectinophora gossypiella* (Morin et al. 2003). Resistance to Bt in *Ostrinia nubialis* is due to reduced midgut protease activity resulting in less activation of the protoxins (Huang et al. 1999; Li et al. 2004; Li et al. 2005). Pest resistance management prevents or delays the adaptation of pest species to any defense mechanisms. Transgenic cotton known as Ingard expressed the *Cry1Ac* gene. To preserve the susceptibility of lepidopterans to Bt toxins Ingard cotton was replaced by Bollgard II, which expressed both the *Cry1Ac* and *Cry2Ab* genes (Downes et al. 2007). However, the detailed information on the biotechnological approaches for the control of insect pests in crop plants has been reviewed by Jackie et al. (2012).

4 Integrated Pest Management to Combat Insect Resistance

The increasingly serious problems of pest resistance along with contamination of the biosphere associated with broad-spectrum synthetic pesticides have led to the need for effective biodegradable pesticides with greater selectivity. From the experience with DDT and synthetic pyrethroids, the global community needs to be made aware that no single management tactic is likely to give satisfactory control of chronic pest species. Integrated pest management (IPM) applies multiple methods to suppress pest populations, thereby reducing dependence on conventional insecticides in sustainable crop protection (Norhisham et al. 2013). After the introduction of biological pesticides, the strategies are to minimize insecticide spray applications and to move towards ecofriendly systems of pest management.

4.1 Host Plant Resistance

An alternative to chemical insecticides is host plant resistance, which can result in population reduction of insect pests and fewer insecticide treatments and offer farmers an economical and ecologically reasonable means of suppressing insect pests (Smith 1989; Jyoti and Brewer 1999). The use of insect-resistant cultivars may cause a slowdown in the rate of development of resistance to insecticides in insect populations. Plant resistance to insects is the genetically inherited qualities that result in a plant of one variety or species being less damaged than a susceptible plant lacking these qualities (Smith 1989). According to Painter (1951) maize, resistance to *H. zea* and *S. frugiperda* may be defined as "The relative amount of heritable qualities possessed by the plant which influence the ultimate degree of damage done by the insect." Variation in host-plant quality can result from intrinsic factors, such as genetic or ontogeny, or from extrinsic factors such as soil conditions or environmental variation (Bergvinson 1994). Pseudo or false resistance may, however, occur in susceptible plants due to an earlier than normal planting, low levels of insect infestation, or variations in temperature, day length, soil chemistry, and plant or soil water content.

Cultivars with a low to moderate level of resistance to insect pests have been identified in pigeonpea, chickpea, cowpea, blackgram, greengram, and fieldpea (Sharma et al. 2008). Scott and Davis (1981) released the first germplasm with resistance to *S. frugiperda* and stated that the germplasm resistance to pests plays a critical role in the success of any plant resistance research program. However, considerable progress has been made in the identification and development of crop cultivars with resistance to the major pests in different crops; there is still a need to transfer resistance genes into high-yielding cultivars with adaptation to different agro-ecosystems (Sharma and Ortiz 2002). Three types of resistance are recognized: nonpreference (for shelter, food, and oviposition), antibiosis (adverse effects of the plants on the biology of insects), and tolerance (ability of the plant to withstand damage or recover from damage caused by populations of insects that would decimate a susceptible plant). As host plant resistance is a biologically, ecologically, economically, and socially feasible method of crop protection, it must be the hub of integrated approaches to pest management. It can also be used safely and compatibly in combination with any of one or more of the conventional integrated components (Wiseman 1994).

4.2 Biopesticides

Biopesticides are an important group of pesticides that can reduce pesticide risks. They are derived from animals, plants, and microorganisms. Plant-derived materials are naturally occurring chemicals extracted from plants and are more readily biodegradable, less likely to contaminate the environment, and less toxic to nontarget organisms. Often their effects are not as long lasting as those of synthetic pesticides (Ebenezer 2010). Successful utilization of phytochemical products can help to control many destructive pests. In many parts of the world, locally available plants are currently in wide use to protect crops and stored products against damage caused by insect infestation (Khater 2012). Based on the physiological activities of insects, Jacobson (1982) conventionally classified the plant components into six groups, namely, repellents, feeding deterrents/antifeedants, toxicants, growth retardants, chemosterilants, and attractants. Talukder (2006) has listed 43 plant species as insect repellents, 21 plants as insect feeding deterrents, 47 plants as insect toxicants, 37 plants as grain protectants, 27 plants as insect reproduction inhibitors, and 7 plants as insect growth and development inhibitors. The botanical insecticides that have primarily been used and are commercially available include ryania, rotenone, pyrethrin, nicotine, azadirachtin, and sabadilla, among others (Yallappa et al. 2012).

4.3 Pheromones

Many insects find each other over long distances by emitting chemical signals or pheromones. Entomologists have determined the chemical structure of pheromones for many pest species and duplicated them synthetically. They are used to monitor pests, disrupt mating, and cause the mass trapping of adults. Field trials on the population dynamics of *S. litura* using light and pheromone traps indicated its activity throughout the year (Nandihalli et al.1989). Adoption of sex pheromone trapping can effectively suppress adults, largely decrease larvae or egg mass density, and the damage rate of *S. litura* (Yang et al. 2009).

4.4 Biological Control

To counteract the environmental contamination caused by chemical insecticides, attention and efforts were directed to the use of biological control agents. Biological control is defined as the action of natural enemies (predators, parasitoids, and pathogens) that maintains a host population at levels lower than would occur in the absence of those enemies (Ehler 1990). Biological control represents the introduction of entomophagous organisms with classic innoculative techniques or the increase of natural populations of predators, parasitoids, and pathogens (van Lenteren 2000; Bale et al. 2008). A large range of microorganisms such as bacteria, viruses, fungi, and protozoans have since been identified as potential candidates for use in biocontrol strategies against insect pests (Table 3). In certain developed and developing countries a number of microbial biopesticides have been registered for field application on various vegetables, fruits, and other agricultural crops, horticulture, and forestry. A review by Linker et al. (2009) provides detailed information on insect management by nonchemical means.

Table 3 Biopesticides registered under Insecticides Act, 1968 [adapted from Gupta and Dikshit (2010)]

S. No.	Biopesticide
1	*Bacillus thuringiensis* var. *israelensis*
2	*Bacillus thuringiensis* var. *kurstaki*
3	*Bacillus thuringiensis* var. *galleriae*
4	*Bacillus sphaericus*
5	*Trichoderma viride*
6	*Trichoderma harzianum*
7	*Pseudomonas fluoresens*
8	*Beauveria bassiana*
9	NPV of *Helicoverpa armigera*
10	NPV of *Spodoptera litura*
11	*Neem based pesticides*
12	Cymbopogan

4.5 Predators and Parasitoids

A number of predators such as *Andrallus spindens* and *Harpactos costalis* (Hemiptera: Pentatomidae), *Agrypnus fusci*pes and *Broscus punctatus* (Coleoptera: Elateridae;Chari and Patel 1983), and *Podisus nigrispinus* (Heteroptera: Pentatomidae;Thomas 1992), have been reported feeding on *Spodopteran* larvae (Batalha et al. 1997; Zanuncio et al. 1998; Zanuncio et al. 2008). In India, 33 predators are reported to occur on *H. armigera* (Romeis and Shanower 1996). The most common predator species belong to Pentatomidae, Reduviidae, Coccinellidae, Carabidae, Formicidae, and Araneidae (Zalucki et al. 1986; Romeis and Shanower 1996; Sharma 2001). Likewise, parasitoids such as *Apanteles flavipes, A. ruficrus, A. vitripennis, Chelonus heliope, C. formosanus, Microphilis* sp. (Hymenoptera: Braconidae), *Blepharella lateralis, Perebaea orbata,* and *Strobliomyia egyptia* (Diptera: Techinidae) may also limit the population of the *Spodopteran* pest (Chari and Patel 1983). In most areas, species of *Telenomus*, *Trichogramma*, and *Trichogrammatoidea* are important egg parasitoids, whereas *Campoletis flavicincta* and *C. Chloride* (Hymenoptera: Ichneumonidae) is a larval parasitoid on *S. frugiperda* and *Mythimna separata*, respectively. Tachinid fly, *Carcelia illota* (Diptera: Tachinidae), is a larval pupal parasitoid of *H. armigera* (Chaudhari 2013).

4.6 **Bacillus thuringiensis** *(Bt)*

Insects have many types of natural enemies and can easily be infected with pathogens. Soil serves as a natural home and reservoir for many kinds of insect pathogens, including bacteria, viruses, protozoa, fungi, and nematodes. *Bacillus thuringiensis* Berliner was first formally described from Thuringia, Germany, in 1911 and has been available in commercial formulations for control of insect pests since the 1930s (Beegle and Yamamoto 1992). This has led to a reduction in chemical pesticide use and an additional financial gain for farmers. After ingestion with food, Bt crystal (Cry) δ-endotoxin proteins insert into the membrane of insect midgut epithelial cells and bind to receptors, forming pores and causing cellular lysis and fatal damage to the midgut epithelium (Bravo et al. 2007). A number of other insecticidal proteins have been identified that also target the insect midgut (Harrison and Bonning 2010). Bt stands out representing approximately 95 % of microorganisms used in biological control of agricultural pests in different cultures (Lambert et al. 1992). Hansen and Salamitou (2000) reported that the application of Bt is estimated at 13,000 tons commercially formulated in the world. At present several Bt-based commercial formulations, mostly based on naturally occurring isolates, are available and a few are shown in Table 4.

Genetic modification of Bt can potentially provide a much larger array of novel insecticidal genes that are otherwise beyond the scope of conventional breeding. In 1987, genes encoding the Bt endotoxins were transformed into tobacco and tomato plants (Fischhoff et al. 1987; Vaeck et al. 1987). Transgenic plants armed with Bt toxins are defended against some of the most notorious pests, reducing the need for insecticidal sprays (Tabashnik 1997). Genetic engineering has created transgenic varieties of many crops that express Bt toxins. In the United States, registered Bt crops use different combinations of 11 Bt endotoxin (Tabashnik et al. 2009). Application of Bt toxins towards insect pest management has involved both spray formulations of Bt crystals/spores and crops genetically engineered to express Bt toxin genes. However, entomologists have documented three cases of field-evolved resistance to Bt crops (Frisvold and Reeves 2010).

4.7 Baculoviruses

Insect viruses can provide safe, effective, and sustainable control of a variety of insect pests. They are highly specific in their host range, usually limited to a single type of insect. Baculoviruses are the most intensely studied insect pathogenic viruses belonging to the family *Baculoviridae*. They are among the most important potential microbial control agents and are used as biopesticides. There are two genera of baculoviruses: nucleopolyhedroviruses (NPV) and granuloviruses (GV). Infection by entomopathogenic viruses occurs by ingestion. Then virions bind to receptors in the gut and penetrate epithelial cells. Infection spreads to the hemocoel and then to essential organs and tissues, particularly fat bodies. *H. armigera* possess by far the most reported resistance cases to a wide range of chemical pesticides worldwide (Mironidis et al.2013). NPVs are effective against several species of *Helicoverpa* on cotton, corn, sorghum, soybeans, tobacco, and tomato.

The *H. armigera* nucleopolyhedrovirus (HaNPV) (Cherry et al. 2000) and the *Cydia pomonella* granulovirus (CpGV) (Huber 1974) were used worldwide for biological control. Locally isolates of HaNPV have been produced and applied to different crops in Australia, India, and China (Moscardi et al.2011). The baculovirus for *S. exigua*, SeMNPV, is specific and highly pathogenic in both the field and the laboratory.

Table 4 Commercial *B. thuringiensis*-based bioinsecticides [adapted from Ninfa and Garcia (2009)]

Company	Commercial name	Active ingredient	Target pest
Certis	Agree WG	*B. thuringiensis* v. *aizawai*	Lepidopterans
Certis	Condor	*B. thuringiensis* v. *kurstaki*	Lepidopterans
Certis	CoStar	*B. thuringiensis* v. *kurstaki*	Lepidopterans
Certis	Crymax	Genetically engineered *Bt* v. *kurstaki* and *Bt* v. *aizawai*	Lepidopterans
Certis	Deliver	*B. thuringiensis* v. *kurstaki*	Lepidopterans
Certis	Jackpot WP	*B. thuringiensis* v. *kurstaki*	Lepidopterans
Certis	Javelin/Delfin	*B. thuringiensis* v. *kurstaki*	Lepidopterans
Certis	Lepinox WDG	*B. thuringiensis* v. *kurstaki*	Lepidopterans
Certis	Turix WP/Agree WP	*B. thuringiensis* v. *kurstaki*	Lepidopterans
AFA Environment Inc.	Agribac	*B. thuringiensis* v. *kurstaki*	More than 30 insect species
Valent Biosciences Corp.	Dipel	*B. thuringiensis* v. *kurstaki*	Lepidopterans
Valent Biosciences Corp.	XenTari	*B. thuringiensis* v. *kurstaki*	*Spodoptera* ssp. and *P. xilostella*
Valent Biosciences Corp.	Biobit	*B. thuringiensis* v. *kurstaki*	Lepidopterans
Valent Biosciences Corp.	Novodor	*B. thuringiensis* v. *tenebrionis*	Coleopterans
Valent Biosciences Corp.	VectoBac	*B. thuringiensis* v. *israelensis*	Mosquito and fly larvae
Valent Biosciences Corp.	Teknar	*B. thuringiensis* v. *israelensis*	Mosquito and black fly larvae
Valent Biosciences Corp.	GnatrolDG	*B. thuringiensis* v. *israelensis*	Larval stage of Sciarid mushroom flies
Valent Biosciences Corp.	Foray	*B. thuringiensis* v. *kurstaki*	Lepidopterans
Som Phytopharma	Lipel	*B. thuringiensis* v. *kurstaki*	Lepidopterans
Biotech International	Biolep	*B. thuringiensis* v. *kurstaki*	Lepidopterans
Valent Biosciences Corp.[a]	Thuricide	*B. thuringiensis* v. *kurstaki*	Lepidopterans and certain leaf-eating worms

[a] Valent BioSciences has also acquired exclusive marketing rights to Thuricide biological insecticide. Thuricide is a registered trademark of Certis, USA

However, the use of SliNPV has been very successful to control *S. littoralis* (Adel-Sattar et al. 2012). Baculovirus LdMNPV is a potential biocontrol agent for defoliator, *Lymantria dispar* (Solter and Hajek 2009). Beas-Catena et al. (2014) overviewed currently available baculovirus biopesticide technology, and mentioned that the slow speed of killing target pests is a serious disadvantage of wild-type baculoviruses which promotes the development of recombinant baculoviruses to kill insect pests faster than the parent wild-type virus. However, to date no recombinant baculovirus-based biopesticides are commercially available.

4.8 Entomopathogenic Nematodes

Entomopathogenic nematodes (EPNs) have a worldwide distribution and have been described from 23 nematode families (Koppenhofer 2007). Of all the nematodes studied for biological control of insects, families Heterorhabditidae and Steinernematidae (order: Rhabditida) have received the most attention because they possess many of the attributes of effective biological control agents (Grewal et al. 2005; Koppenhofer 2007) and have been utilized as classical, conservational, and augmentative biological control agents. Considerable attention has been directed over the past few decades to genus *Heterorhabditis* and *Steinernema* and their mutualistic associate bacterial partners, *Photorhabdus* and *Xenorhabdus* (Boemare 2002; Forst and Clarke 2002). In both *Steinernema* and *Heterorhabditis* there is a single free-living stage, the infective juvenile (IJ), which carries in its gut bacteria of the genus *Xenorhabdus* and *Photorhabdus*, respectively (Boemare et al. 1993). On encountering a suitable insect, the IJ enters through the mouth, anus, or spiracles and makes its way to the haemocoel (Kaya and Gaugler 1993). In the hemocoel, the IJ releases cells of its bacterial symbiont from its intestine. Bacteria multiply rapidly in hemolymph and produce toxins and other secondary metabolites, which contribute to the weakening of the host's defense mechanism; finally the host dies because of poisoning or failure of certain organs. Total hemocyte counts were also noticed to be reduced significantly in Colorado potato beetle, *Leptinotarsa decemlineata*, after injection of the entomopathogenic nematode, *S. carpocapsae* (Ebrahimi et al. 2014).

Lepidopteran species during feeding or resting on the soil surface are good targets for ambusher EPNs when soil moisture is sufficient for IJ survival and infectivity (Lacey and Georgis 2012). Laboratory experiments and field releases of EPN show their successful use to control insect pests (Shapiro-Ilan et al. 2002; Laznik et al. 2010). Divya et al. (2010) tested nematode suspension at 25 ml per plant (at 1000 IJs/ml) on potted cotton leaf and reported all the stages of larvae of *H. armigera*, *S. litura*, and *Galleria mellonella* were highly susceptible to EPN, *H. indica*. Agnello et al. (2014) stated that a persistent entomopathogenic nematode population could help to reduce the number of apple pest, *Conotrachelus nenuphar*, larvae residing in the orchard floor. Foliar applications of nematodes have also been successfully used to control the quarantine leaf-eating caterpillars on various crops

(Choo et al. 1989; Cuthbertson et al. 2003). EPNs can also be applied, at the infective juvenile stage, in conjunction with other biological and chemical pesticides, fertilizers, and soil amendments (Krishnayya and Grewal 2002). The efficacy of nematodes in the field can be variable and is affected by environmental conditions. Commercially available nematodes are *S. carpocapsae, S. feltiae*, *S. riobrave*, *H. bacteriophora*, and *H. megidis* (Linker et al. 2009). The review on EPN implementation into crop production systems by Laznik and Trdan (2012) provides important information. Current uses of *Steinernema* and *Heterorhabditis* nematodes as biological control agents are shown in Table 5.

4.9 Entomopathogenic Fungi

Entomopathogenic fungi are key regulatory factors of insect populations in nature. Most fungi can cause natural outbreaks when environmental conditions are favorable. More than 700 species of fungi from around 90 genera are pathogenic to insects (Wraight et al. 2007; Leger et al. 2011; Hemasree 2013). However, few have been thoroughly investigated for their use against insect pests in agriculture. The earliest studies with entomopathogenic fungi occurred in the early 1800s and concentrated on developing ways of managing diseases that were devastating the silkworm industry. However, the action of entomopathogenic fungi is slow and adequate conditions are needed to maintain their viability and pathogenicity (Lord 2005); they are considered an important component in the integrated control of different chewing and sucking insect pests. Entomopathogenic fungi grow well under 20–25 °C and high relative humidities (Ferron 1977). Insects killed by fungi often have a “fuzzy” appearance caused by the growth of the fungus out of the exoskeleton. During the colonization phase, the pathogen produces a wide range of secondary metabolites that may suppress the host’s immune system (Vilcinskas et al. 1997; Vey et al. 2002). Entomopathogenic fungi produce extracellular proteases, chitinases, and lipases that degrade the insect cuticle, allowing hyphal penetration to the nutrient-rich insect hemolymph (Charnley and St. Leger 1991).

Fungal infection starts from the adhesion of conidia to the host cuticle, by nonspecific hydrophobic mechanisms Boucias et al. (1988), followed by germination and cuticle penetration into the hemocoel, where fungal cells are propagated by budding until the mycosis-affected host dies from nutrition depletion (Feng et al. 1994).

Entomopathogenic fungi are being developed worldwide for the control of many pests of agricultural importance (Ferron 1985; Thungrabeab and Tongma 2007). They are often not species specific and often have a broad host range. The review by Ambethgar (2009) outlines the potential of entomopathogenic fungi in insecticide resistance management for sustainable pest management. Hussain et al. (2012) also reviewed the current status of entomopathogenic fungi as mycoinsecticides. *Beauveria bassiana* (Balsamo) Vuillemin and *Metarhizium anisopliae* Sorokin are the two most recognized species and grow naturally throughout the world. Out of

Table 5 Current use of *Steinernema* and *Heterorhabditis* nematodes as biological control organisms [adapted from Shapiro-Ilan and Gaugler (2010)]

Crop(s) targeted	Pest common name	Pest scientific name	Efficacious Nematodes[a,b]
Artichokes	Artichoke plume moth	*Platyptilia carduidactyla*	Sc
Vegetables	Armyworm	Lepidoptera: Noctuidae	Sc, Sf, Sr
Ornamentals	Banana moth	*Opogona sachari*	Hb, Sc
Bananas	Banana root borer	*Cosmopolites sordidus*	Sc, Sf, Sg
Turf	Billbug	*Sphenophorus* spp. (Coleoptera: Curculionidae)	Hb, Sc
Turf, vegetables	Black cutworm	*Agrotis ipsilon*	Sc
Berries, ornamentals	Black vine weevil	*Otiorhynchus sulcatus*	Hb, Hd, Hm, Hmeg, Sc, Sg
Fruit trees, ornamentals	Borer	*Synanthedon* spp. and other sesiids	Hb, Sc, Sf
Home yard, turf	Cat flea	*Ctenocephalides felis*	Sc
Citrus, ornamentals	Citrus root weevil	*Pachnaeus* spp. (Coleoptera: Curculionidae)	Sr, Hb
Pome fruit	Codling moth	*Cydia pomonella*	Sc, Sf
Vegetables	Corn earworm	*Helicoverpa zea*	Sc, Sf, Sr
Vegetables	Corn rootworm	*Diabrotica* spp.	Hb, Sc
Cranberries	Cranberry girdler	*Chrysoteuchia topiaria*	Sc
Turf	Crane fly	Diptera: Tipulidae	Sc
Citrus, ornamentals	Diaprepes root weevil	*Diaprepes abbreviatus*	Hb, Sr
Mushrooms	Fungus gnat	Diptera: Sciaridae	Sf, Hb
Grapes	Grape root borer	*Vitacea polistiformis*	Hz, Hb
Iris	Iris borer	*Macronoctua onusta*	Hb, Sc
Forest plantings	Large pine weevil	*Hylobius albietis*	Hd, Sc
Vegetables, ornamentals	Leafminer	*Liriomyza* spp. (Diptera: Agromyzidae)	Sc, Sf
Turf	Mole cricket	*Scapteriscus* spp.	Sc, Sr, Sscap
Nut and fruit trees	Navel orangeworm	*Amyelois transitella*	Sc
Fruit trees	Plum curculio	*Conotrachelus nenuphar*	Sr
Turf, ornamentals	Scarab grub[c]	Coleoptera: Scarabaeidae	Hb, Sc, Sg, Ss, Hz
Ornamentals	Shore fly	*Scatella* spp.	Sc, Sf
Berries	Strawberry root weevil	*Otiorhynchus ovatus*	Hm
Beehives	Small hive beetle	*Aethina tumida*	Hi, Sr
Sweet potato	Sweetpotato weevil	*Cylas formicarius*	Hb, Sc, Sf

[a] Nematodes listed provided at least 75 % suppression of these pests in field or greenhouse experiments

[b] Nematode species are abbreviated as follows: Hb = *Heterorhabditis bacteriophora*, Hd = *H. downesi*, Hi = *H. indica,* Hm = *H. marelata*, Hmeg = *H. megidis*, Hz = *H. zealandica*, Sc = *Steinernema carpocapsae* Sf = *S. feltiae*, Sg = *S. glaseri*, Sk = *S. kushidai*, Sr = *S. riobrave*, Sscap = *S. scapterisci*, Ss = *S. scarabaei*

171 products, about 68 % were based on *B. bassiana* and *M. anisopliae*, reviewed by Faria and Wraight (2007). Commercial formulations of entomopathogenic fungal pesticides are given in Table 6.

Beauveria bassiana is able to cause high levels of mortality in Coleoptera, Lepidoptera, Hemiptera, Diptera, Hymenoptera, and Orthoptera (Haas-Costa et al. 2010). Karthikeyan and Selvanarayanan (2011) reported 86.67, 86.67, and 73.33 % larval mortality of *S. litura*, *H. armigera*, and *Earias vittella*, respectively, caused by *B. bassiana*. Ujjan and Shahzad (2014) noticed that the *B. bassiana* strain PDRL1187 caused 50 % mortality of adult mustard aphid population after 6.4 days, at conc. 6.3×10^{12} spores per acre. Wang and Zheng (2012) identified a new virulent of *B. bassiana* isolate (*B. bassiana*-CYT5) against western flower thrip, *Franklimiella occidentalis* Perganda. They reported 93.08 % mortality of *F. occidentalis* six days post inoculation in the concentration of 1×10^8 conidia/mL. Qin et al. (2010) revealed that integration of insecticidal protein Vip3Aa1 into *B. bassiana* enhances fungal virulence to *S. litura* larvae by cuticle and *Per Os* infection. Pinnamaneni et al. (2010) stated that overproduction of chitinase of the *Bbchit1* gene can promote the infection efficiency of *B. bassiana* in aphids. Fungal infection of aphids was also accelerated by overexpressing a silkworm chitinase or a hybrid chitinase in *B. bassiana* (Fang et al. 2005; Fan et al. 2007). Contreras et al. (2014) evaluated liquid

Table 6 Commercial formulations of entomopathogenic fungal pesticides [Adapted Bhattacharyya et al. (2004)]

Fungus	Product and Company	Formulation
Aeschersorzia aleyrodis	Koppert, Holland	Wettable powder
Beauveria bassiana	Naturalis™, Troy Bio-Science, USA	Liquid formulation
B. bassiana	Conidia, AgrEvo, Germany, Columbia	Suspendable granules
B. bassiana	Brocani™, Laverlam, Columbia	Wettable powder
B. bassiana	Boverol, Czeck Republic	Wettable powder and dry pellets
B. bassiana	Mycontrol-WP/Mycotech. Corp. USA	Wettable powder
B. bassiana	Ostrinil/Natural Plant Protection/France	Microgranules of mycelium
B. brongniarti	Betel/Natural Plant Protection/France	Microgranules of mycelium
B. brongniarti	Engerlingspilz, Andermatt, Biocontrol, Switerzarland	Barley kernels colonized with the fungus
M. anisopliae	Bio-path™, Eco Science, USA	Conidia on a medium placed in trap/chamber
M. anisopliae	Biogreen, Biocare Technology Pvt. Ltd, Australia	Conidia produced on grains
M. anisopliae	Biologic Bio1020, Bayer AG Germany	Granules of mycelium
Paecilomyces fumosoroseus	Pfr 21/WR Grace USA	Wettable powder
Verticillium lecanii	Mycotal/Koppert/Netherlands	Wettable powder
V. lecanii	Vertalec/Koppart/Netherlands	Wettable powder

formulation of *M. anisopliae* on different populations of tomato borer *Tuta absoluta* and reported the potential of *M. anisopliae* to control pupae of the lepidopteran borer at the recommended rate. Strains of *M. anisopliae* are more virulent towards *S. litura* larvae (Venkata et al. 2013). Rijal et al. (2008) reported that a number of *H. armigera* larvae in treated plots with *M. anisopliae* and *B. bassiana* were significantly lesser than the control plots during the vegetative, flowering, and pod-setting stages of chickpea. Bentonite-based liquid formulation of *M. anisopliae* was observed to be most effective against *H. armigera* larvae in soyabean (Agarwal et al. 2012).

Severe infections of *Nomuraea rileyi* were observed in *S. litura* and *H. armigera*, attacking green gram (Ingle et al. 2004). Domenico et al. (2009), in laboratory bioassays, observed *N. rileyi* kill 80 % of *S. frugiperda* larvae. *Isaria* sp. was found causing natural epizootics in the sweet potato whitefly, *Bemisia tabaci*, in the Lower Rio Grande Valley of Texas. Its low lethal concentrations and high virulence against *B. tabaci* make this fungus a promising biocontrol agent (Cabanillas and Jones 2009). Hussein et al. (2013) reported that *I. fumosorosea* strain CCM 8367 has strong insecticidal effects against *S. littoralis*. However, Mustu et al. (2011) noticed that *B. bassiana* isolate was more effective than *I. farinosa* isolate against wheat stink bug, *Aelia rostrata*. In the cotton pest *B. tabaci* and *Aphis gossypii*, 100 % mortality caused by *Lecanicillium* (*Verticillium*) *lecanii* was reported by Karthikeyan and Selvanarayanan (2011). *Fusarium* species are pathogenic to insects belonging to Lepidoptera, Coleoptera, Hemiptera, and Diptera (Teetor-Barsch and Roberts 1983; Humber 1992). Rajesh et al. (2009) noticed larval susceptibility and 100 % eggs mortality of *S. litura* infected by *F. lateritium* and *M. anisopliae* at 10^6 conidia/ml. Meyer et al. (2007) characterized *Hirsutella citriformis* Speare infecting the Asian citrus psyllid, *Diaphorina citri* Kuwayama in Florida. Hall et al. (2012) noticed that 23 % of *D. citri* adults, observed on mature leaves, were killed by *H. citriformis.* They further mentioned that mummified cadavers were most abundant on citrus leaves during the fall and winter months. Beneficial effects were observed in using the two fungi together compared to separate applications. Combined utilization of selective insecticides in association with fungal pathogens can also increase the efficiency of control by reducing the amount of insecticides, minimizing environmental contamination, and pest resistance.

5 Conclusion

Over the last five decades cultivators have had to rely on conventional synthetic chemical insecticides for insect pest control. Resistance has been reported for all insecticide classes for one or more key pest species. The availability of many broad-spectrum chemical pesticides is declining as a result of the evolution of resistance and legislation. The increasingly serious problems associated with broad-spectrum synthetic pesticides have led to the need for effective biodegradable pesticides with greater selectivity.

The use of insect-resistant cultivars may cause a slowdown in the rate of development of resistance to insecticides in insect pest populations. Plant-derived materials may result as repellents, feeding deterrents/antifeedants, toxicants, growth retardants, chemosterilants, and attractants. Pheromones, however, may be used to monitor pest populations, disrupt mating, and achieve mass trapping of adults. A number of predators have been reported feeding on insect pests. In certain countries entomopathogenic bacteria, virus, nematodes, and fungi have been registered for field application on various vegetables, fruits, and other agricultural crops, horticulture, and forestry.

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Biofertilizer for Sustainable Rice Production and Reduction of Environmental Pollution

Umme Aminun Naher, Radziah Othman, Qurban Ali Panhwar, and Mohd Razi Ismail

Abstract Rice is the staple food for more than half of the world's population. Rice production needs a huge amount of chemical fertilizer application, especially urea, which is one of the causes of global warming and groundwater pollution. Nitrous oxide emission and nitrate leaching can be reduced only via the reduction of chemical nitrogen fertilizer use or by developing a mechanism whereby the plant can get atmospheric nitrogen directly without any loss in the soil system. After nitrogen the second most important nutrient is phosphorus. Phosphorus availability is very much pH dependent. It may prevail in the soil but may not be bioavailable to the plant. In this case a group of microorganisms can help to make bioavailable phosphorus and simultaneously reduce use of chemical phosphorus fertilizer. Biological nitrogen fixation by the free-living bacteria and solubilization of insoluble organic and inorganic phosphorus by microorganisms are well documented. Free-living diazotroph, phosphate solubilizing bacteria, and plant growth-promoting bacterial strains containing biofertilizer are commonly used for the production of field crops. Biofertilizer containing these microbes will supplement the need for chemical fertilizer and will ensure a healthy environment. The objective of the chapter is to discuss briefly the scope and potential of biofertilizer containing free-living diazotrophs, phosphate-solubilizing bacteria, and plant growth-promoting rhizobacteria for sustainable rice production in an ecofriendly environment.

Keywords Biological nitrogen fixation • Diazotrophs • Global warming • Fertilizer • PGPR • Phosphate-solubilizing bacteria

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1 Introduction

Because of increasing global population, the high demand for food leads agriculture to rely on inorganic fertilizer. Fertilizers play a central role between food security and environmental degradation, which can be minimized but not eliminated. Agriculture currently contributes to about 30 % of total global emissions (up to 80 % in some countries) of the greenhouse gases that are the driving force for climatic change. The world population is increasing about 2 % per year and the nitrogen fertilizer demand in agriculture is increasing approximately equivalent to the rate of increase in the population (FAO 1992). The manufacture of N fertilizers, the burning of fossil fuels, and the cultivation of leguminous crops resulted in N fixation which increasingly exceeds the natural fixation of N_2. Over the next few decades, this alteration of the N fixation cycle will become more severe (Walker and Steffen 1999). Annual production of 77×10^6 tons ammoniacal-N requires 0.1×10^9 tons of oil equivalent per year (Bockman et al. 1997). An average of 1.3 tons of oil or the equivalent of that much energy is needed to fix 1 ton of ammonia (Ladha and Reddy 1995).

2 Fertilizer Consumption

Global rice production is fully dependent on chemical fertilizers, although every year some scarcities of chemical fertilizer (Table 1) remain. In the year 2020 the global targeted food production is 321 million tons which will require 28.8 million tons of chemical fertilizer. But the availability projected only 21.6 million tons with a deficit of about 7.2 million tons of chemical fertilizer (Sheraz Mahdi et al. 2010). In this situation biofertilizer can be a complementary source to chemical fertilizer.

2.1 Nitrogenous Fertilizer

Nitrogen is the most used fertilizer in rice production (Hakeem et al. 2011, 2012a, b, c). It is proved that to produce 1 ton of rough grain, 15 kg of nitrogen is needed. Asia is the highest consumer of nitrogen fertilizer (64 %) followed by America (FAO 2008; Fig. 1).

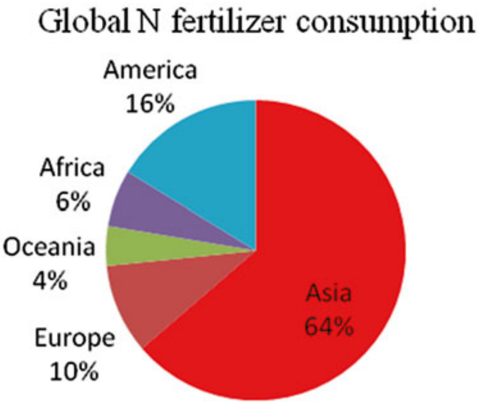
Free-living nitrogen-fixing bacteria containing biofertilizer are able to supply 25–40 % of the nitrogen requirement by a biological process in rice plants

Table 1 World fertilizer supply and demand in the year 2012

Fertilizer (1000 tons)			
	N	P	K
Total supply	154,199	43,299	43,213
Total demand	139,140	40,426	36,453
Deficit/Surplus	15,059	2873	6760

Note: *N* nitrogenous fertilizer, *P* phosphatic fertilizer, *K* potash fertilizer
Source: Adapted from FAO (2008)

Fig. 1 Global nitrogen consumption in the year 2007/2008 to 2011/2012. *Source*: Adapted from FAO (2008)



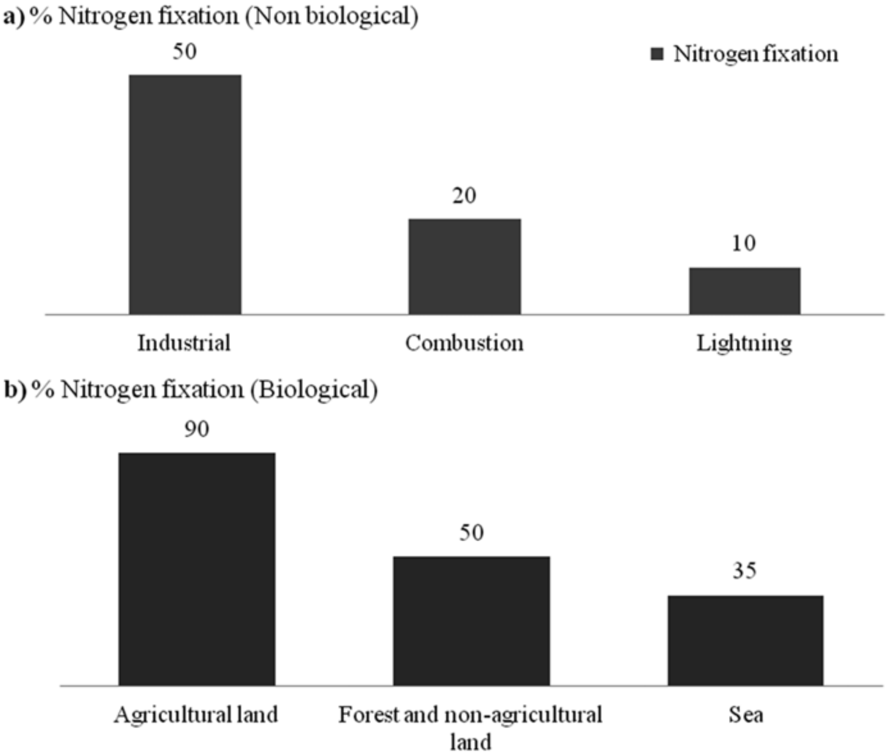


Fig. 2 Global nitrogen fixation nonbiological and biological process. (**a**) Nitrogen fixation (Non-biological), (**b**) Nitrogen fixation (Biological). *Source*: Adapted from Bezdicek and Kennedy (1998)

(Naher et al. 2011). About 90 % of soil nitrogen in agricultural land is derived from biological nitrogen fixation, whereas industrial fixation is only 50 % (Fig. 2). The contribution of nitrogen-fixing bacteria in the nitrogen cycle proves its important role in the soil nitrogen-fixation process.

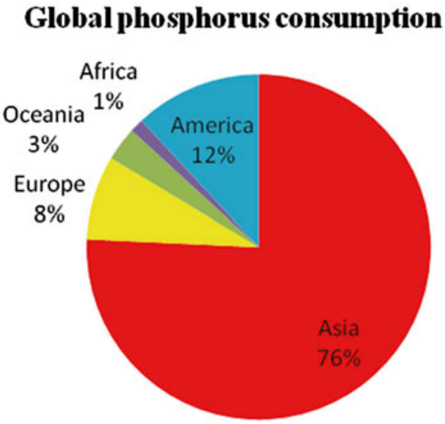


Fig. 3 Global phosphorus consumption in the year 2007/2008 to 2011/2012. *Source*: Adapted from FAO (2008)

Application of nitrogenous fertilizer increases NO_2 emission. In that consequence, biofertilizer has the potential to reduce global warming. Moreover, biofertilizer consists of organic carrier materials that improve soil carbon reserve.

2.2 Phosphate Fertilizer

Like nitrogen, Asia is the highest user of phosphatic fertilizer (Fig. 3). The higher consumption of phosphate fertilizer significantly shows the importance and huge demand of phosphate fertilizer. In soil around 95 % of P is in insoluble organic form, hence, it is very important to focus on the availability of P and its fixation problems. The plant availability and uptake of this nutrient element is largely governed by the soil pH. In low soil pH, P is fixed by Fe and Al, and at high pH, Ca. The plant-available form only remains at pH 5–7. There are some microorganisms that make organic and inorganic fixed soil P available by the production of organic acids or enzymes (Panhwar et al. 2012). Among the microbes *Pseudomonas*, *Bacillus*, and *Rhizobium* are important. There are some fungi that are also able to solubilize insoluble inorganic soil P. Mycorrhiza plays an important role to increase plant P uptake by the extended hyphal root in the upland crop.

3 Mechanism of Biofertilizer for Plant Growth Promotion

Biofertilizer contains a single or a combination of living microorganisms which is applied to the soil or plant directly to improve plant growth and yield. Free-living nitrogen-fixing microorganisms contained in the biofertilizer increase plant growth by supplying the nitrogen nutrient element and phosphate-solubilizing bacteria, increasing the availability of the phosphorus nutrient element to the plant roots.

In addition to nutrients microbes play an important role in plant growth promotion by the production of phytohormones (Panhwar et al. 2014a). The common phytohormone produced by the bacteria is indoleacetic acid, which promotes plant root growth. The vast root architecture help plants to absorb nutrients and water from the surroundings. The common bacteria genera used in biofertilizer preparation are *Rhizobium*, *Burkholderia*, *Bacillus*, *Aspergillus*, *Pseudomonas*, and *Azotobactor*, among others. These are also known as plant growth-promoting rhizobacteria (PGPR). Mycorrhiza biofertilizer is popular for management of the phosphorus nutrient in many vegetables, fruits, upland rice, and plantation crops (Naher et al. 2013a).

Plant growth promotion by microorganisms is achieved in several ways, such as associative N_2 fixation and its transfer to plants (Urquiaga et al. 1992), alteration of plant hormonal balance (Glick 1995), and solubilization of minerals, thus facilitating uptake. Secretion of succinic and lactic acid by certain PGPRs stimulate root growth and relieve environmental stress (Yoshikawa et al. 1993). The colonizing by *Azospirilla* that changes root morphology is suggested to be the production of auxin, which leads to an increase of root hairs and lateral roots (Hadas and Okon 1987). Rethati et al. (2000) reported that N_2-fixing associations of various Hungarian rice cultivars with diazotrophic bacteria, *Azospirillum brasilense*, and endophytic diazotroph, *Herbaspirillum seropedicae*, among them the growth-promoting effect of *A. brasilense* was explicit whereas *H. seropediceae* was elicit in consequential plant reactions. Rediers et al. (2003) found rice plant colonization by *Pseudomonas stutzeri* A15, to be able to express the *miaA* gene. The gene involved in the production of cytokinin was *trans*-zeatin. Expression of an auxin-responsive promoter in *Arabidopsis* indicated that the plants were able to detect bacterially synthesized IAA (O'Callaghan et al. 2001). In addition to growth improvement, PGPR can solubilize phosphorus through production of organic acids (Nautiyal et al. 2000). Several species of *Burkholderia* such as *B. vietnamiensis*, *B. unamae*, *Azoarcus*, *Azorhizobium caulinodans*, *Azosprillum* sp., and *Herbaspirillum* sp. show Aminocyclopropane-1-carboxylate (ACC) deaminase activity in the rhizosphere. ACC could be degraded by plant-associated bacteria and result in a growth-promoting effect (Dobbelaere et al. 2003).

4 Role of Biofertilizer for Sustainable Rice Production

In addition to chemical fertilizer, alternative crop and resource management strategies to sustain crop productivity and profitability are needed. Sustainable agriculture and food security imply a high output from agricultural systems. These systems must be economically viable, environmentally sound, socially acceptable, and politically supportable (Reeves 1999). In this case biofertilizer can be a new approach for sustainable rice production (Panhwar et al. 2014b). Biofertilizers containing free-living nitrogen-fixing bacteria and phosphate-solubilizing bacteria have the potential to supply the nitrogen element and to make insoluble organic and

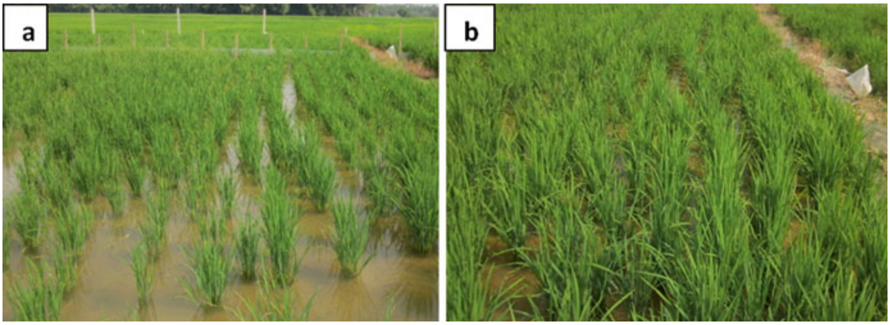


Fig. 4 Comparison of (**a**) farmer's plot versus (**b**) biofertilizer with ground magnesium limestone (GML) applied acid sulfate soil

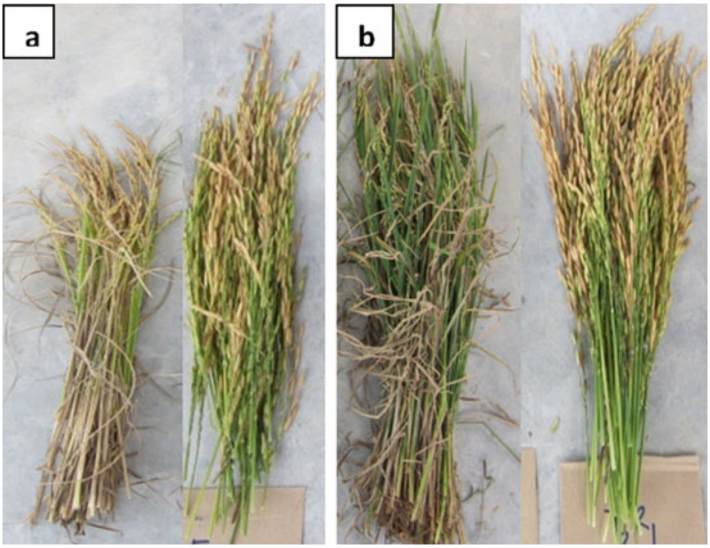


Fig. 5 Effect of biofertilizer on grain yield of rice (**a**) farmer's plot versus (**b**) biofertilizer with ground magnesium limestone (GML) applied plot

inorganic P nutrient available for rice production. A large number of biofertilizers are being used in many countries such as China, India, Pakistan, Egypt, Vietnam, and Indonesia (Kennedy and Cocking 1997). Recently, Malaysia has also been using several products. Valid field data showed a significant increase in grain yield in the farmer's field (Figs. 4 and 5). Application of biofertilizer with 30 % reduced chemical nitrogen fertilizer increased the rice grain yield by 69 % and straw yield 35 %, compared to the farmer's usual practice (Table 2). To prove the efficacy of biofertilizer, Nguyen et al. (2001) trialed 60 farmers with reduced nitrogen fertilizer and found a significant increase in grain yield. This result proves substantial benefits to farmers with reduced input costs, and more income from enhanced grain yield.

Table 2 Effect of biofertilizer on rice production in farmer's field Melor, Kelantan

Treatment	Grain yield (tons ha^{-1})	Grain yield (%) increase	Straw yield (tons ha^{-1})	Straw yield (%) increase
Farmer's practice	4.2	–	7.9	–
Full chemical fertilizer	5.1	21	9.2	16
Biofertilizer[a]	7.1	69	10.7	35

[a] Biofertilizer with 30 % reduced chemical fertilizer

5 Efficacy of Biofertilizer

The efficacy of biofertilizer depends on many factors, one of which is the plant–microorganism association. Beneficial microbes get carbon from root exudates or soil organic matter. The preferences of sugar uptake are mediated in plant growth-promoting bacteria according to their structure, availability of carbon substrates, and mode of living. Rhizosphere carbon sources determine the plant–microbe association. Three groups of diazotrophic bacteria were categorized based on physiological and biochemical characteristics: In group 1, the ability to use glucose as the carbon source and no requirement of biotin; group 2, glucose and biotin required; and group 3, similar to group 1, but able to reduce NO_2^- to N_2. Several diazotrophs were reported to have depended on different carbon sources and chemotaxis characteristics found among them. However, the nitrogen fixation by free-living diazotroph or plant association is fully dependent on carbohydrate substrates (Naher et al. 2013b).

Earlier, biofertilizers were mostly prepared with single strains. A new concept, multistrain biofertilizer, has recently been created. A multistrain biofertilizer with different functions has more efficacy than single-strain biofertilizer. For example, a biofertilizer containing nitrogen-fixing and phosphate-solubilizing microorganisms poses a dual function. It can fix atmospheric nitrogen and simultaneously make phosphorus bioavailable. Moreover, biofertilizer containing many strains can supply more growth phytohormone, another potential increment for plant growth promotion. However, to get the benefit from any biofertilizer the following points need to be considered:

1. The carrier material in biofertilizer should be rich in nutrient and carbon sources otherwise the strain will not survive in the biofertilizer.
2. The strains should be suitable for that particular environment. Strain survival and desired number are essential for colonization with the host plant.
3. The biofertilizer should be suitable for that particular crop to which it is applied. Plant–microbe association is very important. If the microorganism does not form an association with that particular crop, the plant will not benefit.
4. The fast-growing strain should be used in nonsterile carrier material.
5. Before application of biofertilizer, the desired population should be confirmed.

6 Summary and Future Prospective

Biofertilizer can mitigate partial requirement of chemical fertilizer. Use of biofertilizer improves crop productivity, and reduces the use of chemical N and P fertilizer with promotion of a natural source of P instead of chemical phosphatic fertilizer. It promotes more plant growth (15–50 %) than chemical fertilizer. Application of biofertilizer improves the beneficial microbial community throughout the crop growing season. In an environmental context, biological nitrogen-fixing bacteria that fixes atmospheric nitrogen reduces use of chemical N fertilizer by one fourth. Reduction of chemical nitrogen fertilizer reduces nitrous oxide emission and nitrate leaching. The natural source of phosphate rock can be used instead of chemical phosphate fertilizer as phosphate-solubilizing bacteria can solubilize rock phosphate and make it available to the plant. In addition to reducing the cost of chemical fertilizer, biofertilizer ensures a higher yield benefit to the farmers and a safe environment.

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Bread Wheat (*Triticum aestivum* L.) Under Biotic and Abiotic Stresses: An Overview

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Abstract Wheat, a major cereal crop, is subject to several biotic and abiotic stresses. These stresses affect the crop's yield globally. Different mechanisms have been adopted by plants to counter the wide range of biotic and abiotic stresses faced. The scarcity of irrigation water leads to moisture stress in the wheat crop. The quantitative trait loci tool is used to map the moisture-tolerant inherited genes. Genes that are drought tolerant have been identified in other crops and scientists are planning to introduce them into the wheat genomes. Similarly, understanding the heat stress tolerance pathway is underway. Moreover, cryoprotectant genes that code for proteins which help the plants gain tolerance to severe cold can be transformed into commercial wheat varieties to tackle cold stress. Several genetic engineering techniques are being developed to minimize micronutrient and waterlogging stress. Biotic stresses include parasitic and nonparasitic diseases. In order to ward these off, plants use systemic acquired resistance and induced systemic resistance, but these are not sufficient when stress reaches its extreme. Seedborne diseases result in lightweight shriveled kernels resulting in an overall reduction in the crop yield. There is also a range of pathogenic fungi and viruses that cause various leaf and root diseases in wheat. Disease control strategies are underway to limit the damage to the wheat crop. Furthermore, soil moisture level, the depth of seed plantation, PH control for fungal growth reduction, and use of certain antibiotics in the soil can greatly reduce the risk of biotic stress-related wheat diseases. In addition to all of these aspects, pivotal to maximize wheat productivity is genetic improvement where harnessing and exploiting smartly via state-of-the-art technologies pointing towards genetic resource diversity is paramount as a means for providing high levels of allelic variation around all major stress constraints.

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1 Introduction

Wheat, the third largest cereal crop, is grown globally under spring, winter, and facultative environmental habitats. Modern wheat cultivation started in the Middle East about 9000–11,000 years ago and as a consequence of increased geographical farming, bread wheat became a common staple food from China to England (Heun et al. 1997; Nesbitt 1998; Dubcovsky and Dvorak 2007). Wheat is the sole source of energy for nearly 35 % of the world population (Dreisigacker 2004). Its success depends partly on its wide adaptability plus high yield potential and also on the gluten protein fraction that confers the viscoelastic properties which allow dough to be processed into bread, pasta, noodles, and other food products. Wheat also contributes essential amino acids, minerals, vitamins, beneficial phytochemicals, and dietary fiber components to the human diet. Two important characteristics of wheat are its gluten content and low amylase activity; properties that allow wheat to be blended with other flours such as rye and oats for specific purposes (Tatham and Shewry 2008). Wheat varieties are characterized by hardness, kernel colors, and their planting time. Each wheat class has its own relatively uniform characteristics related to milling, baking, or other food use (Taylor et al. 2005). Wheat is classified into six groups such as

(a) Hard red winter wheat
(b) Durum wheat
(c) Hard red spring wheat
(d) Hard white wheat
(e) Soft red winter wheat
(f) Soft white wheat

Wheat is one of Pakistan's major cereal crops and essential for ensuring food security projections for the nation. According to the Food and Agriculture Organization (FAO), Pakistan is the ninth largest wheat-producing country, accounting for 3.04 % of the world's wheat production from an area of 3.57 % of the world. Wheat is the leading food grain of Pakistan and a diet staple of the people. It occupies a central position in the formulation of agricultural policies. It contributes 14.4 % to the value added in agriculture and 3.1 % to the gross domestic product (GDP). The national productivity level of wheat in the year 2012–2013 was 24,231,000 tons showing 3.2 % increase as compared to year 2011–2012 which gave 23,473,000 tons (Source: Pakistan Bureau of Statistics). Factors that influence yield outputs are various biotic and abiotic stress constraints augmented by environmental factors which adversely affect growth, metabolism, and yield. Drought, salinity, low and high temperatures, floods, pollutants, and radiation are the important stress factors limiting the productivity of crops (Lawlor and Cornic 2005). There is sufficient

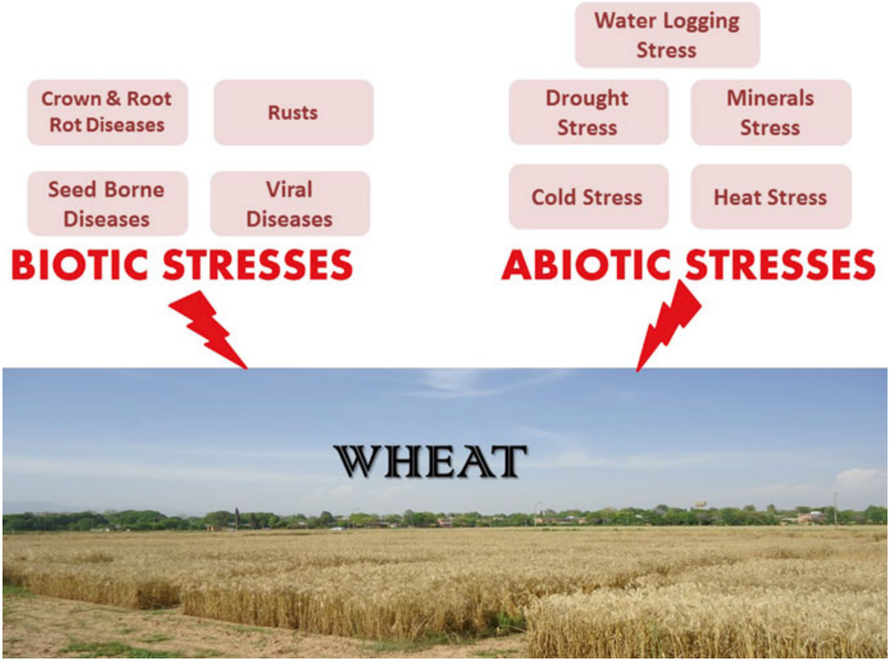

Fig. 1 Major biotic and abiotic stresses to wheat

genetic variation in the wheat gene pool that can be ensured for continued improvement of wheat adaptation to abiotic stress (Trethowan and Mujeeb-Kazi 2008). The diverse biotic (insects, bacteria, fungi, and viruses) and abiotic stress constraints (light, temperature, water availability, nutrients, and soil structure; Lichtenthaler 1996) interact to affect wheat yield and production across the world. Several biotic and abiotic stresses that influence wheat productivity are represented in Fig. 1. Biotic stress refers to plant and pathogen interaction. Plants and pathogens, throughout their life cycle, interact with a wide variety of organisms that significantly affect plant health in various ways. Organisms always require some form of indirect or direct contact in order to infect (Peterson 1974). To understand the main mechanisms of biological control that could be mutualism, neutralism, protocooperation, predation, commensalism, competition, amensalism, and parasitism, there are a number of environmental stimuli, comprising light, gravity, physical stress, temperature, nutrient availability, and water to which plants respond actively (Pal and Gardener 2006). Along with these, a wide range of chemical stimuli generated by the type of soil and plant-associated microbes also serve as vital stimuli. Such stimuli are responsible for either conditioning or inducing plant host defenses that ultimately increase resistance against infections by the wide range of pathogens through biochemical changes. Host defense induction can be local and/or systemic in nature, depending on the type, source, and amount of stimuli (Vallad and Goodman 2004; Lichtenthaler 1996).

Systemic acquired resistance (SAR) occurs where the pathogenic infection is initiated by salicylic acid production, a compound that usually gives rise to the expression of pathogenesis-related proteins which may include a diversity of catalysts and enzymes regulating different defense mechanisms (Thakur and Sohal 2013). Induced systemic resistance (ISR) of plants against pathogens is a widespread phenomenon that has been intensively investigated with respect to the underlying signaling pathways as well as to its potential use in plant protection. Elicited by a local infection, plants respond with a salicylic-dependent signaling cascade that leads to the systemic expression of a broad spectrum and long-lasting disease resistance which is efficient against fungi, bacteria, and viruses. Changes in cell wall composition, de novo production of pathogenesis-related proteins such as chitinases and glucanases, and synthesis of phytoalexins are associated with resistance, although further defensive compounds are likely to exist but remain to be identified (Clarke et al. 2000; Heil and Bostoc 2002).

2 Abiotic Stresses in Wheat

The land per capita and water resources are depleting rapidly and will diminish during the coming decade. To meet the increasing global demand for wheat, yield must be increased up to 1.6 % per annum. Some ways must be found to cope with this problem of keeping pace with the population increase and alleviating world hunger or by elevating crop production in an ecosystem that fosters sustainable intensification. Crop management research (CMR) can also contribute towards resolving this problem by generating high-yielding varieties that can support in enhancing production up to 50 % (Lynam 2004). One of the major limiting factors in wheat growth and production is abiotic stresses. The major objective of scientists in the twenty-first century is to increase and stabilize crop production more or less in those areas with a highly variable and fragile climate which poses one of the paramount challenges for agricultural exploration (Mahajan and Tuteja 2005). Eventually, crop management, a combination of tolerance/resistance to various abiotic and biotic stresses, adaptive traits, and production economics will determine the productivity in stressed environments (Brown and Rieseberg 2005). Therefore the focal points for research should be improving the understanding and characterization of the target climatic variables, identification of efficient selection and screening methodologies, selection of morphophysiological stress adaptive traits, and the practice of most sustainable crop management assays.

2.1 Heat Stress

Another global stress in wheat is heat stress. As global warming intensifies, heat stress may gain huge mass. Heat stress in wheat is known to cause an array of physiological, biochemical, and morphological changes that affect its growth and development. For a decade, heat stress has caused a significant decrease in wheat yield and has made the world struggle to match the record production figures, thus posing a critical challenge in maintaining food security. Usually types of spring wheat are more fragile than winter types. Heat stress above 30 °C may significantly reduce the percentage of germination which may double germination time. This also influences root production which drastically reduces the normal amount. High temperatures, typically above 34 °C, affect final grain weight by reducing the duration of grain filling due to suppression of current photosynthesis (Fokar et al. 1998; Brestic et al. 2014), and by directly inhibiting starch biosynthesis in the endosperm (Telfer et al. 2013).

2.1.1 Effect of High Temperature During Vegetative Phase

A rise in temperature during the vegetative growth phase may have no significant negative impact on plant growth. However, during anthesis and grain-filling stages huge alteration in metabolic and growth processes occurs.

2.1.2 Effect of High Temperature During Reproductive Phase

During the reproductive phase, high temperatures may result in decreased seedling leaf mass or pollen sterility. Irreversible damage originated by prolonged exposure to high temperatures as sudden heat shocks may damage the thylakoids resulting in leakage of cellular contents. This is why the reproductive phase is regarded as the most sensitive phase, because just a few degrees elevation in temperature is closely associated with reduction in biomass, rate of grain filling, and yield (Bita and Gerats 2013).

Higher plants exposed to excess heat, at least 5 °C above their optimal growing conditions exhibit a characteristic set of cellular and metabolic responses required for the plants to survive under the high-temperature conditions (Guy 1985). High stomatal conductance and maintenance of cell wall stability are the characteristics possessed by varieties that show the best tolerance under heat stress (Shah and Paulsen 2003). Biochemically, the gliadins tend to increase whereas the HMW (high molecular weight) glutenins in the grain reduce during the high temperature, accompanied by accelerated transcription and translation of heat shock proteins (Bray 1994), the production of phytohormones such as abscisic acid (ABA), antioxidants, and other protective molecules (Maestri et al. 2002).

2.1.3 Wheat Tolerance to Heat Stress

Within the gene pool of wheat, large genetic diversity is present for most traits. The following strategies can be employed to develop heat tolerance in wheat:

1. The T1BL.1RS translocation in wheat may also bestow heat tolerance (Zhao et al. 2012). In a recent study, screening of 102 Pakistani wheat cultivars and candidate lines was done in order to identify the rye T1BL.1RS translocation. This rye 1R chromosome short arm has contributed enormously to increase genetic diversity in wheat. Many varieties were found to have this translocation (Tahir et al. 2014).
2. Despite the importance of wheat as a significant cereal crop, current information of its genome sequence is inadequate for functional genomics. Sequencing of the wheat genome is quite a challenge because of its large genome size (16,000 Mb) but is already underway. However, mapping and characterizing ESTs (expressed sequence tags) offers a manageable approach to the complex architecture and functioning of the wheat transcriptome and helps in unraveling the genetics of the heat stress response. To understand the regulation of heat stress tolerance, detailed information about these ESTs and their functional annotation is necessary. Therefore expression profiles have been analyzed under different hormones/elicitors and various developmental and growth stages.
3. It is well worth considering exploring the underlying mechanism and practicing different breeding tools that may bear fruit in the near future.
4. Genetic engineering and producing transgenic wheat with a heat-tolerant gene is also under consideration.

2.2 *Drought Stress*

Drought is one of the major constraints to wheat production worldwide affecting its growth, development, and yield. About 45 % of wheat production is affected by drought. The scenario should be that the productivity per area of the crop is not just maintained but also increased substantially (Fedoroff et al. 2010). Drought stress retards plant growth, inhibits formation of primary and secondary roots, and encourages formation of stout roots thus affecting grain yield. In Pakistan, out of 22.45 million ha cultivated area, only 6.34 million ha land are irrigated by canal water, and about 12.52 million ha are cultivated through tube well and other sources, whereas no water is available for the remaining 3.59 million ha (Khalil et al. 2014). For this we should focus on the strategies regarding genetic solutions, that is, wheat germplasm with drought tolerance or enhanced water efficiency and development of water-use efficient varieties with refined agronomic practices.

2.2.1 Wheat Tolerance to Drought Stress

The wheat plant has naturally evolved diverse responses to drought stress that help the plant to minimize the damage caused by it and to maintain cellular homeostasis. Drought tolerance studies on the genetic level are not often conducted because a trait that offers drought tolerance in one location or year may not especially confer tolerance in other years or locations. This is because complex hypothetical combinations of various traits are responsible for the tolerance (Yang et al. 2007). The following strategies are under consideration to improve drought tolerance in wheat:

1. Quantitatively inherited genes are basically responsible for controlling drought tolerance in any environmental condition. In wheat the detection of such tolerance is explored by using the quantitative trait loci (QTL) tool. Understanding the genetic basis of complex traits affecting yield under drought is crucial for sustainable improvement of wheat in breeding programs. Enormous advancements in genomic resources and tools in recent years have greatly assisted mapping and cloning QTLs and the corresponding genes (Borevitz and Chory 2004; Bray 1994).
2. Molecular marker systems for crop plants were developed to create high-resolution genetic maps and exploit the genetic linkage between markers and important crop traits (Edwards et al. 1987). A large number of marker × trait associations have facilitated the use of molecular markers for marker-assisted selection (MAS) in bread wheat and are gaining momentum in several countries (Gupta et al. 2008).
3. Many specified proteins synthesized under water scarcity have been isolated and characterized. The water stress-specific proteins (stress induced) have been described by different groups such as

    (a) Dehydrins (polypeptide),
    (b) LEAs (late embryogenesis abundant),
    (c) RABs (responsive to ABA),
    (d) Storage proteins (in vegetative tissues).

    These protein formations are encoded by many genes. One of the stress-induced genes among several of the candidate genes frequently involved in tolerance is rd29DREB1A. Such an abscisic-acid–dependent pathway-induced gene is expressed under cold stress and dehydration conditions in rice. The introduction of this gene from rice to wheat may manipulate the biochemical pathways converting wheat into a drought-tolerant crop (Hu et al. 2007).
4. Normally a plant can withstand about 30 % of water loss. Scientists proposed that resurrection plants or desiccation-tolerant plants can be used as model plants for drought studies as they can withstand about 90 % of water loss (Bartels and Salamini 2001).
5. Genetic engineering of wheat can be done to help develop drought tolerance by altering gene expression or by accumulating those metabolites that help coping with drought such as ABA, largely hydrophilic proteins, largely hydrophilic proteins, and osmotically active compounds (Ramachandra-Reddy et al. 2004).

2.3 Cold Stress

Wheat, being the most adaptable crop, can withstand temperatures as low as 1–4 °C which is considered to be the minimum temperature for growth. Cold stress is commonly referred to as plant response to freezing temperatures (Gusta and Chen 1987).

Table 1 Effect of temperature on different biological processes and physiological phases in wheat

Processes	Temperature minimum (°C)	Temperature optimum (°C)	Temperature maximum (°C)
Lethal limits	−17.2	–	47.5
Leaf initiation	−1	22	24
Shoot growth	3.0	20.3	>20.9
Root growth	2.0	<16.3	>25.0
Grain filling	9.2	20.7	35.4

Approximately 80 million ha of the total wheat growing area are affected by cold stress globally. Areas near the equator and spring wheat face more damage and as night temperatures fall below 10 °C, shoot and root growth diminish completely. Before flowering, cold conditions can delay anthesis or cause severe sterility (Xin and Browse 2000; Sanghera et al. 2011). In the case of winter wheat, low temperature greatly reduces root growth with increased fructan and sugar levels along with a dramatic drop in osmotic potential. Winter wheat leaves are usually smaller and transpire less. To withstand much lower subzero temperatures, the expression of proteins, lipids, and sugars doubles in the cold-hardened wheat (Fowler 2001). Under very low temperature the critical adaptive mechanism improving survival is cold hardening or acclimatization. During cold hardening, the level of several proteins is considerably increased (i.e., proline, glutathione, TaADF and dehydrins), which play a significant role in decreasing the osmotic potential and serve as cryoprotectants (Abdin et al. 2002). The effect of temperature on different biological processes and physiological phases in wheat is summarized in Table 1.

2.3.1 Wheat Tolerance to Cold Stress

As many as 15 out of 21 chromosomes in wheat have been found to influence tolerance to low temperatures (Stushnoff et al. 1984). Polymorphism exists between different wheat varieties for cold stress tolerance. The *Fr1*-frost tolerance gene is located on the chromosome 5AL, close to vernalization factor Vrn1 and *Fr2* is linked to Vrn 3. Both of them are linked together but can be separated (Snape et al. 1997). The heritability of these genes is very high, approximately 60–90 %. For cold tolerance an absolute level can be improved by finding genetic diversity among the wild wheat relatives (Sãulescu and Braun 2001). The physiology of tolerant lines is highly understood, whereas the genetic variability is low especially in the present gene pool which also renders it difficult to move forward swiftly beyond the current level. However, the transformation of existing genes into commercially acceptable wheat varieties can fairly improve cold stress tolerance in them (Kobayashi et al. 2002). Frost tolerance of ten Bulgarian winter wheat and five foreign cultivars was studied by Ganeva et al. 2013 with different effects of chromosome 5A and their association with microsatellite alleles (Ganeva et al. 2013).

2.4 Waterlogging Stress

The common occurrence of waterlogging stress in both high rainfall and irrigated environments is more than 10 million ha globally. In sensitive varieties, up to 50 % massive decrease in root mass, three quarters in the shoot with a significant drop in stomatal conductance occurs. In roots, mineral concentration increases, especially sugars whereas in shoots mineral content decreases. Genotypes with well-developed parenchymatous tissues for transportation are considered to be tolerant in waterlogged conditions (Belford 1981; Drew 1983; Smirnoff and Crawford 1983; Justin and Armstrong 1987; Barrett-Lennard et al. 1988; Thomson et al. 1990; Huang et al. 1994). Genetic variability among varieties for tolerance involves large differences, although its occurrence is relatively lower. However, the inheritance is additive and relatively simple.

2.4.1 Wheat Tolerance to Waterlogging Stress

This stress can be highly minimized by utilizing breeding and engineering solutions. It is recommended that to achieve waterlogging tolerance, an incremental process be followed by first incorporating adaptive traits from local, national, or international germplasm with known tolerance, and then combining other adaptive traits relevant to the target environment. Screening of "primary synthetic hexaploid wheat" has been done to discover tolerance against waterlogging (Villareal et al. 2001).

2.5 Mineral Stress

Mineral stress is the suboptimal availability of essential nutrients or toxicity of nutrients or nonnutrient materials such as aluminum, cadmium, sodium, manganese, or some other heavy metals (Jonathan and Samuel 2004). About 40 million ha of wheat area experience mineral stresses globally, mainly due to soil alkalinity and acidity. Mineral stress is due to the amendment of chemical fertilizers, sludge and sewage irrigation, and atmospheric deposition (Ranieri et al. 2005).

2.5.1 Wheat Tolerance to Mineral Stress

The techniques of amendments that have been developed until now are often quite costly and impractical. The following approaches can be applied to confer tolerance against micronutrient stress:

1. Breeding of such plants that are mineral stress tolerant can be an alternative approach with the integration of farming strategies.

2. In spite of that, ecological, biological, and economic considerations have proven to be more efficient than the breeding solutions.
3. Single dominant genes are responsible for controlling tolerance and efficiency to various nutrient stresses. Thus easy genetic gains can be projected by conventional breeding.
4. Genomics can be used as a tool in understanding plant responses to mineral stresses in a changing environment.

For exhibiting good expression of variability of such tolerance at the genomic level, the location and alteration of specific mineral-tolerant plants are identified. Through one survey analysis in 1990, 190 soils from 15 countries were tested by Sillanpaa (1990).

3 Biotic Stresses to Wheat

Common wheat and durum are attacked by numerous diseases and pests but it is an amazing fact that only 5 % of pests and less than 20 % of diseases are of significant importance posing a real threat to wheat productivity (McIntosh 1998). Plant diseases are basically divided into two types, nonparasitic and parasitic. Nonparasitic diseases are mainly caused by mutagens and environmental factors whereas parasitic diseases are caused by living organisms such as bacteria, fungi, viruses, and the like. Wheat is largely affected by fungal species. Most commonly these diseases are wheat rusts which are stem, leaf, and stripe. Wheat diseases can be classified into three categories:

(a) Seedborne diseases
(b) Viral diseases
(c) Wheat rusts

3.1 Seedborne Diseases

Seedborne diseases infect seeds from infested grain or soil, resulting in a poor stand or seedling blight making them toxic for human use. Common seedborne diseases are *Stagonospora nodorum* leaf blotch, head blight or scab, loose smut, common bunt, karnal bunt, leaf spot diseases, and crown and root rot diseases (Kumar et al. 2008; Majumder et al. 2013).

3.1.1 *Stagonospora nodorum* Leaf Blotch

Leaf blotch is caused by *Stagonospora nodorum*. The fungus requires warm and humid weather to grow. It is both a seedborne and foliar pathogen. It infects many varieties of wheat but mainly white winter wheat. As a result of infection, lightweight, shriveled kernels with molds are produced hence affecting yield (Bai and Shaner 1994).

3.1.2 Head Blight or Scab

It is caused by *Fusarium* spp. that not only reduces yield but also produces the toxin deoxynivalenol which is lethal for consumption (Nedelnik et al. 2007). It is found that up to 17 *Fusarium* spp. can cause head blight but the most common are *F. graminearum*, *F. avenaceum*, and *F. poae* (Bai and Shaner 1994).

3.1.3 Loose Smut

Loose smut is caused by *Ustila gonuda* tritici. It is an asymptomatic disease that reduces yield and production of wheat by converting grain and parts of the head to smut spores. As a result, the infected plant has no grains left to harvest (Agarwal 1981). Recent research has been conducted using PCR and ELISA techniques in the assessment of loose smut incidence in seed lots (Wunderle et al. 2012).

3.1.4 Common Bunt

Likewise, common bunt can also be devastating. It is caused by *Tilletia foetida*, *T. contraversa*, and *T. caries*. It is also known as stinking smut. It gives a foul fishy odor to the grain, making it unfit for the milling process (Mathre 2000). Smut-infected heads have a bluish-green cast instead of whole green color (as in the case of normal heads). Producers are strictly condemned for selling smutty grain (Klem and Tvaruzek 2005).

3.1.5 Karnal Bunt

Karnal bunt is caused by *Tilletia indica*. Common wheat and durum are its major hosts. Seeds with reduced viability and quality are produced thus making them unfit for human consumption due to chemical changes in the seeds (Rai and Singh 1978). Pakistan, Nepal, Iraq, Iran, Afghanistan, and Mexico are the major countries facing this disease (Matsumoto and Bell 1989; Majumder et al. 2013; Kazi et al. 2013). International wheat trading has an infection permissible limit of less than 3 % (Mujeeb-Kazi et al. 2006).

3.1.6 Leaf Spot Diseases

Leaf spot diseases include powdery mildew, leaf rust, glume blotch, *Septoria tritici* leaf blotch, and spot blotch. All of these diseases are weather and humidity dependent. To develop a disease, they require the leaf surface to be wet or the humidity level to be near 100 % for a certain period of time (McMullen and Adhikari 2009; Bolton et al. 2009).

- Symptoms of powdery mildew include white or grey powdery growth on leaves. It doesn't kill the plant but weakens it (Stromburg 2010).
- Leaf rust occurs in mid to late May in many parts of the world as it requires warm and humid weather (Bolton et al. 2008; Zhang and Meakin 2003).
- Glume blotch occurs in the hot and humid weather of June (Leonard and Bushnell 2003)
- *Septoria tritici* leaf blotch and powdery mildew occur in the early spring and are favored by cool and humid weather (Goswami and Kistler 2004).
- Of global significance in warm tropical areas is *Cochliobolus sativus* (spot blotch) which is the major wheat production biotic stress constraint in Bangladesh. Of national importance, this disease emerged in 2009 and warrants attention as we move forward to maximize wheat yields. Its molecular elucidation has recently surfaced and mapping initiatives are being harnessed (Zhu et al. 2014).

3.2 Crown and Root Rot Diseases

Crown and root diseases include *Cephalo sporium* and take-all. Both are caused by soil-residing fungi. In take-all, the base and stem of the premature plant appear bland and scurfy. In *Cephalo sporium*, the entire length of the leaf blades is covered by alternating yellow and brown stripes. These diseases are caused by planting wheat year after year in the same field. The extent of the disease is increased if grass weed, such as quack grass, becomes established in the field. The root rots of wheat, oat, and barley are among the least conspicuous but are destructive diseases, and are caused by many species of fungi living in soil, seed, and dead plant refuse. Root rots refer to diseases that affect roots and basal portions of culms. It should also be noted that seasons and climate have a large impact on disease type. *Cercosporella* root rot is prevalent in winter wheat areas whereas *Helmintho sporium* and *Fusarium* root rots are prevalent in spring wheat regions. Several species of bacteria and fungi have been isolated from barley kernels and wheat. Most of them are saprophytic showing weak pathogenicity, however, some species of *Alternaria* are nonpathogenic and are commonly associated with kernels of grain (Jones and Sutton 1996).

3.3 Viral Diseases

This category includes wheat spindle streak mosaic and barley yellow dwarf disease.

3.3.1 Wheat Spindle Streak Mosaic (Wheat Yellow Mosaic)

Wheat spindle streak mosaic is a soilborne viral disease that usually appears in early May in most parts of the world. The upper leaves of the affected plant show short, spindle-shaped, yellow streaks. That is why it is also called yellow mosaic disease.

If the weather is persistent and cool, the disease symptoms may intensify over time, otherwise disappear (Hershman 2011; Jianping 1993).

3.3.2 Barley Yellow Dwarf Virus

Barley yellow dwarf is a vector-dependent disease, transmitted by aphids. Symptoms include a stunted shoot with reddish or yellowish leaf tips and no heads. Yield loss can be up to 50 % (Miller and Rasochova 1997). The virus can be characterized on the basis of serotype difference (Ali et al. 2013). Molecular markers are being identified and used for the detection of barley yellow dwarf virus in bread wheat (Ayala et al. 2001).

3.4 Rusts

Wheat and other *Triticum* species are attacked by eight different species and subspecies of rust fungi. Wheat can develop the following types of rusts:

1. Stem rust (*Puccinia graminis* f. sp. *tritici*)
2. Stripe rust (*Puccinia striiformis* f. sp. *tritici*)
3. Leaf rust (*Puccinia triticina* causes "black rust", *P. recondita* causes "brown rust", and *P. striiformis* causes "Yellow rust" (Cummins 1971; Horst 2013; Bennett and Scott 1971)

These rusts include many different races but are very host specific. They produce five kinds of spores, but only urediospores and aeciospores can infect grain and grass. In view of the fact that a single rust pustule produces 350,000 spores, rust spread is therefore quite rapid and deadly (Peterson 1974). Crop damage is caused by the growth of rust fungus and development of spores on wheat leaves and stems. As a result, essential nutrients and water needed for the development of wheat kernels are used by the pathogen (water requirements in rusted wheat are much higher than in healthy wheat). Consequently, kernels are shriveled to such a prodigious extent that many of them become so chaffy and light that they blow away with the chaff during the process of threshing. The rest of the kernels obtained are shrunken to half or one third of normal size (Schumann and D'Arcy 2010).

3.4.1 Stripe Rust

This type of rust lives all year round and is also known as yellow rust and glume rust of wheat. Its scientific name is *Puccinia striiformis*. This disease poses a serious threat to wheat production in cooler regions; warm spring temperatures reduce the development of this disease and the risk of yield losses. Stripe rust epidemics occurred in 1999 and 2005 in Kansas, United States (Basnet et al. 2014a, b) and the

Table 2 Taxonomy of *Puccinia striiformis*

Kingdom	Fungi
Phylum	Basidiomycota
Class	Pucciniomycotina
Order	Puccinales
Family	Pucciniaceae
Genus	Puccinia
Species	Striiformis

most recent in 2010 in Central Asia and the Caucasus (CAC; Ziyaev et al. 2010). Research indicates that a new population of the stripe rust is becoming adapted to the hot environment therefore it is likely to remain a potential threat. Scientific classification of *Puccinia striiformis* is summarized in Table 2.

Symptoms of Stripe Rust

Infection can occur at any stage of plant life. Symptoms include chlorotic patches on leaves, orange or yellow blister-like pustules called uredia. Basically it is a disease of leaves but it also affects awns and base. Large amounts of spores are produced in blister-like lesions (Williams PG, Ledingham GA 1964). They stick to the clothes of individuals as orange dust when someone walks through heavily diseased fields (Wellings et al. 2007). Modification of stripe rust symptoms occur due to genetic resistance. Its symptoms match bacterial black chaff and Septoria leaf blotch. It is also sometimes confused with leaf rust and stem rust but lesions of stem rust are a little bit darker as compared with stripe rust and its lesions are not well arranged but are distributed all over the leaf. Stripe rust uses water and nutrients at the expense of the host plant and dries out the plants (Line 2002; Ehrlich and Ehrlich 1963).

Control and Genetic Resistance to Stripe Rust

The most cost-effective way to control stripe rust is the planting of disease-resistant varieties. Pakistani wheat production is also threatened by stripe rusts and researchers are trying to develop a resistant variety of wheat by using molecular markers (Sobia et al. 2010). The fungus that causes stripe rust has the capability to mutate itself due to which it continuously changes. This can overcome the other resistant varieties. Foliar fungicides have the ability to control stripe rust. It is applied when the plant is at an active stage of development; it provides protection to the upper leaves which are involved in the production of grains and energy (Chen et al. 2009). The strobilurin class of fungicides is used which is most effective against stripe rust if applied before infection. A premix of two classes or the triazole class of fungicides is used if infection is already present. The triazole class of fungicide has more remedial activity (Horst 2013). Recently, DNA markers closely linked with the resistance locus of stripe rust were identified and validated by Indian scientists in collaboration with an Australian team working in Australian Winter Cereal Collection (Randhawa et al. 2014; Espino et al. 2011).

3.4.2 Stem Rust

Stem rust is basically caused by the fungus *Puccinia striiformis*. It is also known as black rust (Cook and Veseth 1991). Stem rust was known to be one of the most recently feared diseases (Boyd et al. 2013). Resistance has been developed against stem rust but new pathogens may arise, and therefore resistance to new pathogens has not been developed and is still a threat to the cereal crop worldwide. It is very important to maintain resistance against stem rust in wheat in order to have food security (Chaves et al. 2013a, b; Schumann and Leonard 2001). The taxonomy of *Puccinia striiformis* is summarized in Table 3. Basically stem rust is heteroecious in that it needs two hosts to complete its life cycle. An alternate host for this rust fungus is *Berberis vulgaris* which is found in the northern hemisphere (Barnes 1979). The plant itself has been very useful to humans because of its wood, bark, and fruit production. The alternate host became a major contributor of new combinations of genes in the pathogen which made it more virulent than the previous strain. The variation in the pathogen made the resistance mechanisms against it difficult, and thus new pathogen variations arose every year (Singh et al. 2008a, b).

Favorable conditions for stem rust are:

1. Hot days with temperatures ranging from 25 to 30 °C
2. Wet leaves either by dew drops or rain
3. Mild nights with temperature ranging from 15 to 20 °C (Schumann and Leonard 2001; Chen 2005; Roelfs 1989; Roelfs et al. 1992; Leonard and Szabo 2005)

Symptoms of Stem Rust

Infections that occur in cereals and grasses mainly occur on stem and leaf sheaths. Infections may also be located on leaf blades (Roelfs 1988). The initial symptom seen is the yellowing or whitening of the leaf a few days after infection. A pustule, a few millimeters long, is produced by damage of the host's epidermis because of

Table 3 Taxonomy of *Puccinia graminis*

Kingdom	Fungi
Phylum	Basidiomycota
Class	Urediniomycetes
Order	Uredinales
Family	Pucciniaceae
Genus	Puccinia
Species	Graminis

pressure of dark red urediniospores formed during infection (Leonard 2001). The pustules, usually diamond shaped, grow up to 10 mm long and as time progresses, infection persists and forms black teliospores, because of which stems appear black in later seasons (Farkas and Király 2006).

Genetic Resistance to Stem Rust

Genetic resistance is the common mechanism used to counteract stem rust. New races of the fungus arise from mutations due to which resistance genes become ineffective but a few genes have been identified that were effective in producing a resistance to stem rust. The *Sr31* gene became famous worldwide (Pretorius et al. 2000; Rohringer et al. 1979). The *Sr31* gene occurs on a segment of the chromosome in rye that was transferred to wheat by interspecific hybridization. This hybridization became really popular because the *Sr31* gene gave a good quality yield for wheat crop production and it also gave extra additional genes for resistance against rust diseases (Sharma et al. 2013). But unfortunately, in Uganda 1999, a new race rendered the *Sr31* gene susceptible (Pretorius et al. 2000). This new stem rust race was highly virulent. Uganda, Kenya, Ethiopia, Yemen, and some parts of Iran faced this epidemic (Singh et al. 2011a, b). Ug99 generation of the stem rust fungus has been through mutations and has increased its virulence allowing it to cross the resistance barrier and thus affect wheat crops worldwide posing a great threat to wheat production across the globe (Sharma et al. 2013; Kolmer 1996; Singh et al. 2011a, b).

3.4.3 Leaf Rust

The most common rust disease in wheat is leaf rust which is caused by a fungus, *Puccinia triticina* (Bolton et al. 2008). The specie is heteroecious, so it requires a uredinial/telial host and substitute aecial/pycnial host to complete its full life cycle. The uredinial host is most commonly wheat and the aecial host is *Isopyrum fumaroides* or *Thalictrum speciosissimum* (Singh et al. 2008a, b). Loss of wheat yield due to *P. triticina* infection usually results in low kernel weights and decreased kernel numbers per head (Samborski 1985; Goyeau et al. 2007). Currently the fungus is recognized as a very important pathogen globally, causing major yield losses over enormous geographical regions and areas (Basnet et al. 2014a, b). The taxonomy of *P. triticina* is summarized in Table 4. Globally, the main host of *P. triticina* is the common hexaploid *Triticum* spp. *P. triticina* also infects durum, *T. turgidum* ssp., *T. dicoccoides*, and *T. dicoccon* (Saari and Prescott 1985). A form of *P. triticina* has been found on diploid *A. speltoides* in Israel, which is not usually present on wheat. Infections of *P. triticina* have not been found in natural stands of wild races of wheat. However, these species can be infected when they are inoculated with *P. triticina*, which is pathogenic to normal wheat (Sears 1956).

Table 4 Taxonomy of *Puccinia triticina*

Kingdom	Fungi
Phylum	Basidiomycota
Class	Urediniomycetes
Order	Uredinales
Family	Pucciniaceae
Genus	Puccinia
Species	Triticina

Molecular Aspects of Pathogenicity of Leaf Rust

Research has still to be taken into consideration to find out more information about the molecular and biological studies of *P. triticina. P. triticina* cannot be cultured in vitro, and because of that there is a scarcity of molecular information (Mains and Jackson 1926). *P. triticina* has a large genome size, about 100–124 Mbp (Chen 2005). Transient expression and insertional mutagenesis were carried out on *Puccinia triticina* using biolistics (Webb et al. 2006) and transformed species were selected which change from avirulence to virulence (Kolmer and Liu 2000). Two mutants showed virulence in wheat carrying *Lr21* which encoded a calmodulin binding protein and a chitin synthase. The calmodulin-dependent signaling pathway shows important roles in virulence and the life cycle of the fungus. Disruption of the chitin synthase gene causes a decrease in fungus virulence (Kumar et al. 2014). Many research strategies have been used to study the transcriptome of *P. triticina*. An expressed sequence tag was developed that represented every stage of the life cycle of *P. triticina*. Thirteen cDNA libraries were made from urediniospores, germinating urediniospores, and the haustorial phase. More advances are being made to look more closely at the molecular pathogenecity of *P. triticina* (Hu et al. 2007).

4 Disease Control and Management

High-quality and disease-free seeds are planted to control a disease. To attain resistance, crops are grown in disease gardens where naive crops are exposed to different pathogens. The crops that grow normally in the disease location are picked and further tested. After approval and field testing, they are introduced in the market. More root-rot resistant spring wheat includes Apex, Thatcher, and Marquis whereas Kota, Kubanka, and McMurachy selections are moderately resistant (Pugsley 1971). Production fields should be inspected from head emergence level through harvest to check any possible contamination. Seed should be cleaned thoroughly to remove shriveled and lightweight kernels and should go through a germination test. Only seeds with 80 % or more germination capability should be introduced to fields (Chaves et al. 2013a, b). Pathogens with a higher evolutionary rate are prone to develop genetic resistance and are difficult to be fought by plants (McDonald and Linde 2002). It was studied by Bolley (1909) that fungal wheat diseases were caused if crop rotation is not practiced. Many pathogens survive in soil, on refuse of crops, and on wild grasses. So, crop rotation and summer fallow are necessary to avoid pathogenicity (Bolley 1909). Greenhouse and field tests show that deep digging and seeding increase pathogenicity and decrease the yield. Seeds should be adequately and properly planted in seed beds, ensuring soil moisture level and temperature. They should also be planted after Hessian fly safe date (time of pest arrival in area) to avoid possible seedling diseases. Certain fungicides are effective foliar diseases. Adding large amounts of specific antibiotic organisms or their extracts can greatly reduce/eliminate some soilborne diseases. Seedling bight of wheat and barley (*Helminthosporium*) can be decreased by applying antibiotic organism cultures at the time of plantation. S. D. Garrett recommended acid phosphates for *Pythium* infections as an unbalanced phosphorus nitrate relationship predisposes its attack to wheat. Most fungi live in an acidic habitat; pH can also be increased to avoid fungal development. Proper liming of soil can increase pH above 6.2, which prevents *Cephalosporium* stripe formation. Genetically modified wheat races can be introduced that are resistant to certain fungal and viral attacks (Bushnell 1972; Chen et al. 2013).

5 Conclusion and Future Prospects

Scientists have been trying for centuries to develop tolerance in wheat for all stresses. One method is to transfer genes for stress tolerance in plants that can convert a stress-susceptible plant into a tolerant one. Strategies of this system are explained in Fig. 2. No matter what strategy is adopted, the main and final goal is to get the highest yield as the world's population is increasing day by day and providence of food security is the primary issue of this era. In addition to a lot of research, there is still much to explore to get the best genotypes with more tolerable traits and higher yields. For biotic stresses, the current scenario is to obtain durable resistance that is based upon minor genes.

These wheat varieties have been a continuous feature in wheat improvement programs globally. Biotic stresses have kept researchers more concentrated in their efforts due to changing scenarios of pathogen virulence where fungal race shifts throw off variants that are a perpetual hazard and one can never become complacent with any promising variety under cultivation. Varietal resistance sooner or later gets overcome. Rusts are the most destructive with a dynamic nature. As said by Dr. N. E. Borlaug, "Rust never sleeps." Contrary to that, abiotic stresses are more under environmental control where long-lasting tolerant varieties can be obtained. Abiotic stresses therefore come under "static system." The progress made in yield enhancement, biotic and abiotic stress constraints control, and innovativeness will generate new efficient technologies that will allow optimism to reign and forecast a 2050 picture with high hopes to feed the global populace of 9.2 billion swiftly growing to 10 billion by 2055. As we are setting our sights towards the future 2050 vision, our optimism is high because new technologies have emerged on the working platforms

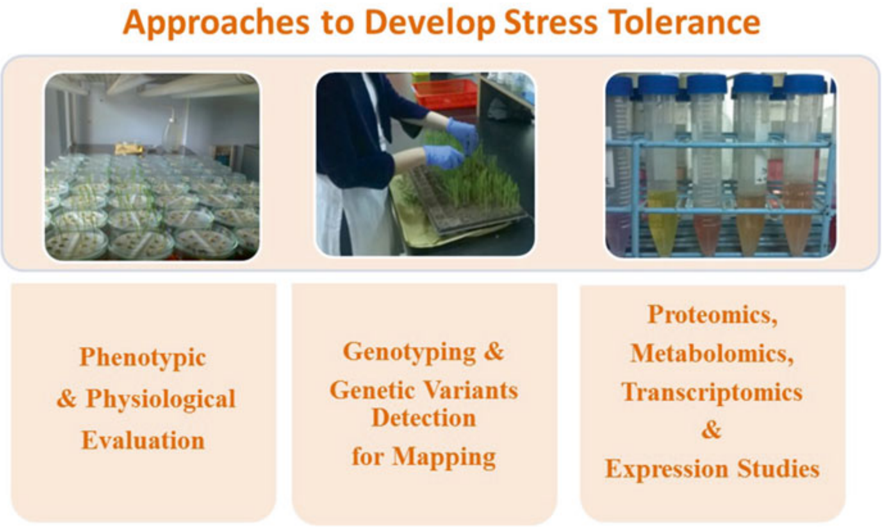

Fig. 2 Major approaches to develop stress-tolerant varieties

that will intensify output efficiency. Elucidations are the molecular sequencing developments that embrace *DArT* genotyping and also 9 K plus 90 K. These technologies shall set up class genotypic platforms and define global partnerships to target phenotypic aspects both working in tandem and in a holistic way.

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Use of Alien Diversity to Combat Some Major Biotic Stresses in *Triticum aestivum* L.

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Abstract Crop plants experience a collection of environmental stresses that involve biotic (biological) and abiotic (physical) factors. The biotic factors include pathogens including viruses, bacteria, fungi and microbes, birds, pests, weeds, insects, and invasive species. These are crucial for sessile organisms such as plants because plants cannot enhance production and even survive unless they show resistance towards undesirable changes in the surrounding environment. Both biotic and abiotic stresses negatively affect plant survival, production, and ultimately yield. Biotic stresses can deteriorate biomass at any stage of plant development by adversely affecting crop yield. Therefore, biological factors limit crop production and food security globally. The ability to adapt or tolerate these stresses by effectively countering these constraints is a very complex phenomenon. The most important biological stresses of wheat that significantly reduce yield are fungal diseases and among these the most damaging are rusts (leaf, stem, and stripe) and the emergence of new races of the pathogen that gradually cause a decline in the prevalent disease resistance of wheat cultivars. One option to combat this is the introgression of alien genes from wild and related progenitor species into common wheat. This underutilized genetic diversity can be exploited through conventional plant breeding modes utilizing diverse genetic resources across landraces, close and distant progenitor species of the recipient cultivars. Different methodologies to access alleles from the species have been practiced after first developing all the important hybrids that generate chromosome translocations, substitutions, or additions. For the identification of the chromosomal introgression, C-banding technique and genomic in situ hybridization (GISH) are ideally aided diagnostically by new molecular inputs. Although the merits of concentrating on primary and secondary gene pool genera are high, the practical contribution of *Thinopyrum curvifolium*, *Th. distichum*, and *Secale cereale* also adds credence to the continued use of a tertiary pool resource. The genetic

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diversity using a tertiary gene pool also is an added valuable resource. In order to encounter the overall wheat production challenge magnificently, plant scientists need to be cognizant of the various aspects of these stresses in view of the current development from genetic molecules to adaptive ecosystems.

Keywords Wheat • Alien gene • Genetic diversity • Biotic stresses • Rust • Wheat wild species

1 Introduction

In the context of food security, wheat (*Triticum aestivum* L.) is the largest cereal crop with a hexaploid genome ($2n=6x=42$) and plays a vital global role (Dong and Zheng 2000). Recently, a sharp loss of wheat diversity has been noticed due to the modern crop cultivation system. Thereby, genetic erosion has emerged in wheat cultivars make them gradually vulnerable to stresses (Carmona et al. 2010; Wang et al. 2011, 2012; Fu et al. 2013). Additionally, the decrease in farmland acreage and world population increase has necessitated higher wheat yields to fulfill the need of the world population. To widen the prevalent narrow genetic base, alien gene diversity is an excellent source (Ogbonnaya et al. 2013). Compared to modern cultivars, the wild progenitors of wheat are a richer source of alien genetic diversity and are abundant to address several target traits (Luan et al. 2010). The alien chromosomal fragments harboring desired genes can be introduced from the wild relatives into the modern cultivars of wheat (Song et al. 2013). The earliest and foremost example of successful utilization of alien genes is the classic spontaneous wheat–rye T1BL.1RS translocation line. These lines have remarkable resistance to wheat diseases and enhanced wheat production as well (Rajaram et al. 1983).

Globally, one of the challenging chores for researchers is to discriminate and reduce effects of the production and quality of harvested by-products such as grains on the overall performance of crops. This has distinctive significance in view of approaching climatic changes, as many new pests and weeds have evolved due to aggressive anthropogenic activities with multifaceted consequences on an economically commercial and ecologically sound agricultural system. The plant's ability to cope with these biological (biotic) and physical (abiotic) stresses is highly dependent upon the triggering of a cascade of molecular systems involved in stress recognition, signal transfer, and finally the expression of metabolites and specific stress-related genes. The expected demand for wheat for human consumption has risen at the rate of 2 % per year in the last 10 years; hence the quantity and quality of wheat have paramount influence on one's well-being and fitness around the world. Therefore, in reference to the current scenario, it is significantly important to develop wheat varieties with improved yield and good grain quality in addition to harness tolerance to biotic and abiotic stresses and thereby possess better adaptation to climatic changes (Jaradat 2011).

2 Major Biotic Constraints

Wheat is an annual crop, cultivated in a diverse climatic zone mainly in the temperate region. Due to narrowing down of the genetic makeup of modern wheat cultivars, various biological and physical factors are now the cause of a decline in wheat yield. The most damaging physical stresses for a wheat crop are extreme high and low temperatures, salinity, nutrient deficiency, and waterlogging. Among the biotic factors the most detrimental are rusts in addition to some minor constraints: karnal bunt, barley yellow dwarf virus (BYDV), spot blotch, and powdery mildew. Rust is the most emerging and paramount fungal disease limiting wheat yield globally and called stem, stripe, and leaf rust. The distinctive features of these rusts are mentioned in Table 1.

2.1 Leaf or Brown Rust

Among all rusts, leaf or brown rust is the leading disease caused by the fungus, *Puccinia triticina* (heteroecious basidiomycete), and has the capacity to be epidemic and cause substantial production losses (German et al. 2007; Riar et al. 2012) and spread very effectively in many parts of the globe. The losses due to leaf rust are low compared to other rusts. Brown rust is the most widespread and damaging disease of wheat and harvest losses range between 30–50 % (McIntosh et al. 1995). The foremost section of plant protection is genetic shielding from these biotic constraints over the globe. Most recently, more than 60 leaf rust resistance (*Lr*) genes have been identified in the common wheat at the chromosomal location that controls brown rust resistance (McIntosh et al. 2007; Adonina et al. 2012).

Table 1 Distinguishing features of wheat rust disease

Characteristic features of symptoms	Symptom color	Spore morphology	Locality on wheat surface
Leaf rust	Brownish orange	Randomly present on leaf in circular to oval form	Mostly located on upper surface of leaf and also found on leaf sheath
Stripe rust	Yellow	In young plant leaf, circular, small, and tightly packed. In old plant leaf, running as yellow stripes	Mainly reside on upper surface of leaf but also present on awn, leaf sheath, and inside glumes
Stem rust	Reddish brown	Randomly on leaf with slightly round to elongated having tatty edges	Chiefly present on lower and upper leaf surface, also observed on leaf sheath, stem, and on the outer coat of head

2.2 Stem or Black Rust

Stem or black rust along with foliar diseases is a harmful pathogen causing heavy yield declines worldwide. Resistant cultivars provide a competent way for wheat growers to avoid yield losses. Stem rust caused by *P. graminis* currently is a very dangerous disease of wheat (Singh et al. 2011). The disease bears the ability to make a healthy looking crop just weeks away from harvest, into nothing more than a maze of black stems and shrunken grain at harvest. Yield losses of 70 % or more can emerge under favorable conditions. Wheat stem rust is highly spreading expeditiously over sizable voluminous distances by wind or via fortuitous human transmission (infected apparel or plant material).

Rust pathogens change expeditiously, often by mutation. Ug99 (*P. graminis* f. sp. *tritici*) is a lineage of stem rusts that potentially causes wheat production adversity leading to problems with food security worldwide. The first novel race of Ug99 is designated as "TTKSK" according to the North American nomenclature system, and was initially characterized in Uganda in 1999 (hence the name Ug99) and has since migrated to South Africa, Kenya, Eritrea, Sudan, Ethiopia, Yemen, Mozambique, Zimbabwe, Tanzania, and Iran. Eight variant forms (TTKSK, PTKSK, PTKST, TTKSF, TTKST, TTTSK, TTKSP, and TTKSF+) are now identified in the Ug99 ancestry. All have similar DNA fingerprints, but vary in acridity designs. All of these are considered to be evolved from single-step mutations. Supplemental paramount stem rust resistance (*Sr*) genes are the most used approach to combat diseases and are known in many countries; Kenya, for instance, *Sr36* and *Sr24*, South Africa (*Sr24*), Ethiopia (*Sr24*), and Tanzania (*Sr24*, *Sr36*) are now subjugated by different versions of the Ug99 fungal race. This Ug99 race or its variants are quantified to be the major threat to global wheat production.

2.3 Stripe or Yellow Rust

Stripe or yellow rust, is chiefly a foliar fungal wheat disease that can also taint spikes and stem tissues. If the pathogen taints the spike it causes extensive quality and grain loss. The disease is caused by *P. striiformis*. The fungus infects wheat and it grows from one season to the next on an alternate host plant. Mild winters and a cooler damp climate in the spring and untimely summer sustain the propagation of the disease spores. Plant resistance is the chief source of managing the disease; consequently, planting resistant cultivars is globally suggested. Conversely, dissimilar races of the fungus capable of arising from one year to the next can potentially surmount the resistance (Bux et al. 2012). Several (48) stripe rust with resistance genes (*Yr*) have been categorized (McIntosh et al. 2008, 2010). The brown and yellow rust resistance genes have been identified in accordance with hypersensitive reaction and the gene for gene interrelation with with pathogen.

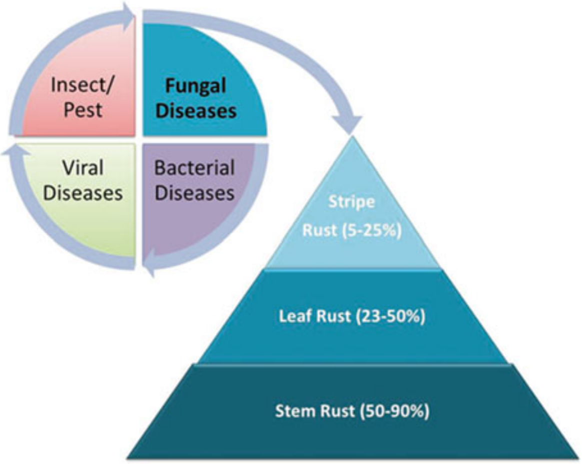

Fig. 1 Different biological stresses in wheat and fungal diseases yield losses in wheat

The resistance of most of these genes has deployed with the passage of time either an increase of virulence in the pathogen races or emergence of new pathotype. Therefore, there is a constant demand for searching and transferring novel and efficient sources for rust resistance. In this context, the genetic diversity in the wild progenitors and nonprogenitor species of modern wheat cultivars is an excellent source of alien genes for the transfer of useful traits together with disease resistance practiced in wheat improvement programs (Riar et al. 2012). The range of yield losses in wheat due to stripe, stem, and leaf rust diseases are 5–25 % (Wellings 2011), 50–90 % (Ejaz et al. 2012), and 23–50 % (Kassem et al. 2011), respectively (Fig. 1).

3 Improvement Strategy

The improvement strategy for the introduction of new and different genes (*Vg*) is an important step in a wheat breeding program. This has mainly focused on the availability of diversity and its exploitation to establish a superior cultivar. Conventional breeding is the foremost leading approach globally for the improvement of wheat germplasms and for the introduction of genetic diversity through alien sources over mutation breeding.

3.1 Mutation Breeding

Several decades ago mutation breeding was a well-known means to address all wheat improvement targets. However, now the mutation breeding approach has become very limited in wheat breeding programs owing to the crop polyploidy nature ($2n=6x=42$; AABBDD). One of the limiting factors of mutation breeding is that induced mutation is undirected and unpredictable. Therefore, more plant breeders are inclined to conventional breeding to improve wheat germplasms.

3.2 Conventional Breeding

With conventional breeding the paramount approach is hybridization breeding. Hybridization is the dominant breeding method for the introgression of alien diversity in modern wheat cultivars. There are three main modes of transferring alien genetic diversity in the elite cultivars: intraspecific, interspecific, and intergeneric hybridizations. The intraspecific hybrids are the product resulting from the cross of two different subspecies within the same species, for instance, a cross between *T. aestivum* and *T. monococum*. The hybrids produced from the cross of two different species within the same genera are called interspecific hybrids, exemplified as a cross between *T. aestivum* and *Aegilops tauschii*. However, the intergeneric hybrids are those that emerge as a result of a cross between two different genera, such as a cross between *T. aestivum* and *Hordeum chilense*.

Intergeneric hybridization emerged on the scene with the classic work of Kruse in the late 1960s and the recognized contribution that he made by publishing on wheat/barley hybrids that were followed by other groups (Kruse 1973; Barclay 1975; Dewey 1984). This focused on the tertiary gene pool and proved basic in significance. In the ongoing process Harlan (1975) reported on the generation of hybrids from the tertiary gene pool. According to him, such hybrids would be lethal, anomalous, or completely nonreproducible. The allocation of genes in the hybrids would be troublesome to generate as required, needing highly extreme and crucial conditions. However, scientific creativity and progress was substantial through the efforts of a few research groups and their output led to the compilation of results and a discourse by Sharma (1995) when he published the paper, "How Wide Can a Wide Cross Be?" Reported were impacts of intergeneric hybridization that elucidated how diverse genera were readily combined and derivatives were realized with great potential of exploitation for agricultural gains. These involved briefly the genera *Agropyron* spp., *Th. curvifolium*, *S. cereale*, *E. giganteus*, *P. juncea*, *Th. distichum*, and *Th. intermedium* across valued traits including spot blotch, head scab, salinity, drought, rusts, and powdery mildew culminating in yield maximization. In general gains from intergeneric combinations are long term due to the complexity of alien chromosomal introgressions and selection of good agronomic plant types during breeding. Thus utilizing landraces or close wild relatives has gained prominence over recent years and in particular the diploid species *Aegilops tauschii* contributing the D genome to modern wheat has attained greater importance and has enriched wheat with numerous resistances/tolerances to various stresses (Mujeeb-Kazi et al. 2013).

4 Gene Pools in Triticeae

More than 500 species are included in the 26 genera of the Triticeae tribe (http://www.ncbi.nlm.nih.gov/Taxonomy/Browser/wwwtax.cgi). Around 75 % of these species in the tribe are perennials and the remaining are annuals that include the principal cereal crops such as wheat, rye, and barley (Dewey 1984). The modern cultivated species are related to these species of the tribe and are considered to be included in any primary, secondary, or tertiary gene pool conditional to how similar they are at the genome level (Fig. 2). The species arrange genome components in a diploid hybrid that are recognized by their characteristic meiotic pairing.

4.1 Primary Gene Pool (GP1)

Landraces, wild, and initial domesticated species are placed in the primary pool of the Triticeae tribe and are compatible to hybridize with the modern cultivars. Homologous recombination is detected when these species are crossed with cultivated crops in breeding and selection programs as contributing homologous chromosomes. Thereby, this is the best genetic pool that has been efficiently exploited for crop improvement. The examples of a primary gene pool in wheat are *Triticum turgidum*, (AABB; 2*n* = 28), the polyploidy, and *T. urartu* (AA; 2*n* = 14) and *T. tauschii* (DD; 2*n* = 14), the diploid donors of the A and D genomes. On the other hand,

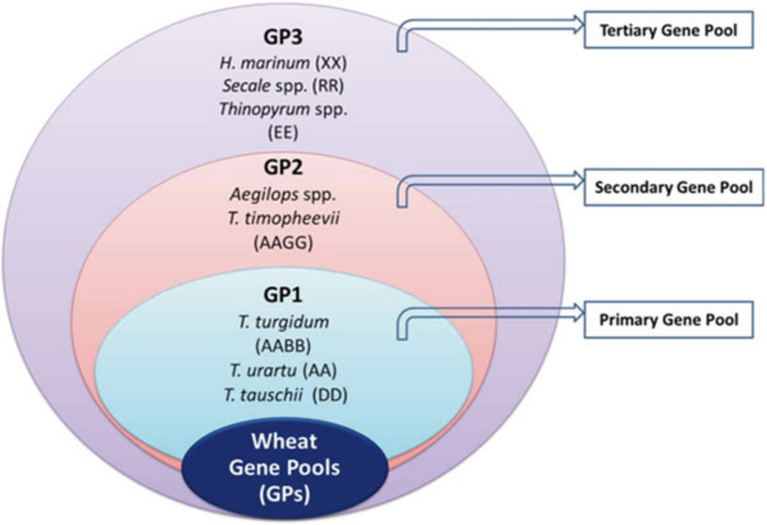

Fig. 2 Wheat gene pools; primary gene pool GP1, secondary gene pool GP2, and tertiary gene pool GP3

highly diverse and widely distributed but sexually compatible progenitors of barley and rye such as *H. spontaneum*, *S. montanum*, and *S. vavilovii*, respectively, are included in the primary gene pool (Feuillet et al. 2007).

4.2 Secondary Gene Pool (GP2)

The polyploid species of wheat are considered in the secondary gene pool that share with a similar homologous genome at least one locus with the cultivated species. These species can only be utilized for gene transfer through homologous recombination if the desired gene is present on the homologous genome. The polyploidy examples of this genetic pool are *Triticum* and *Aegilops* species, for instance, *T. timopheevii* (AAGG; $2n=28$), whereas the diploid S-genome species (resembling the B genome) is from *Aegilops* section *Sitopsis*.

4.3 Tertiary Gene Pool (GP3)

In the tertiary gene pool distantly linked diploid and polyploidy species are involved. These species lack the genome combination of cultivated species. Therefore, special approaches such as irradiation and gametocidal chromosomes can be employed for gene transfer for homologous recombination. The members of Triticeae other than those of the primary or secondary gene pool are placed in this group. Mainly perennial species are present in the group. The important species for wheat in the group are *H. marinum* (XX), *Secale* (RR), and *Thinopyrum* (EE), for rye, *Triticum* and *Aegilops* species, and for barley, *H. bogdanii* and wild barley are gathered in this gene pool (Feuillet et al. 2007).

5 Methods for Transfer of Alien Genes

The procedure for crop genetic improvement in crop manipulation usually involves conventional methods in order to accomplish desired crossing outputs giving rise to useful derivatives. The selection of elite parents is the prerequisite for releasing improved varieties after hybridization. The breeding methodologies involve different approaches briefly described here: selection of two parental materials, recipient with elite genotypes and donor with a target gene, then the hybridization cross (intraspecific, interspecific, and intergeneric), embryo culture to rescue hybrid embryos, plantlet germination, hybrid validation, massive clonal propagation, backcrossing for seed production on the F1 hybrid or the induced amphiploid, prebreeding and applied breeding techniques (Mujeeb-Kazi and Rodriguez 1984; Mujeeb-Kazi and Kimber 1985; Mujeeb-Kazi and Miranda 1985; Mujeeb-Kazi and

Hettel 1995). This methodology is commonly applied to both interspecific and intergeneric hybrid crosses.

Chromosome engineering is the cytogenetic methodology that can be used to engineer the genetic material of modern cultivated wheat employing alien gene segments by combining chromosomal translocation, chromosomal deletion, and chromosomal inversion for decades. The varied gene pools of the Triticeae species are relatively close to cultivated wheat and are easily utilized through this approach. The wild relatives and progenitor species significantly broaden the genetic base of wheat by introgression of target genes and thereby provide an opportunity for the wheat cultivars to perform better in the present and future scenarios of environmental and socially economical facets of agriculture (Ceoloni et al. 2005).

In reference to disease resistance, the alien gene transfer into a wheat crop is a paramount approach for improving agronomic characters and enlarging the gene pool. In some cases, chromosomes in interspecific or intergeneric hybrids can pair up during meiosis thus allowing the introduction of a free alien gene. But a chromosome pairing in meiosis rarely happens in hybrids of distantly similar species and this creates the difficulty of introducing the allocation of even a small chromosomal segment of alien resource in hybrids (Masoudi-Nejad et al. 2002).

6 Validation of Transfer of Alien Gene

Most of the resistance genes related to various diseases can easily be induced from distant species into wheat cultivars through chromosome translocation, substitution, or additions. It is the translocation forms that are most in demand and have applied output potential. The wheat crop is protected from the potential yield loss from diseases by utilizing these alien genes' reservoir. A comprehensive study of genomic composition of any wheat germplasm is equally beneficial for genetic understanding and for parental selection in breeding systems. The techniques mostly used for the identification of the alien gene segment in the wheat hybrid are molecular cytology (GISH and C-banding), immunocytology (FISH), molecular markers (RFLP, RAPD, SCAR), and biochemical markers (Isozymes).

Chromosome banding or C-banding (Gill et al. 1991; Jiang et al. 1993) and GISH, genomic in situ hybridization (Ahmad et al. 2000), are the molecular cytological analyses in which the biotin-labeled total genomic DNA of the donor specie previously extracted is taken as a probe to identify the alien chromosomal segment integrated into the unlabeled total genome of the recipient modern wheat genome as a blocking DNA (Friebe et al. 1992). However, molecular marker approaches are more popular and efficiently applied to identify alien chromatin in the wheat genome using different markers such as restriction fragment length polymorphism (RFLP), sequenced characterized amplified region (SCAR), random amplified polymorphic DNA (RAPD), and many others (Francis et al. 1995). Moreover, the identification of an introgressed segment of wheat can also be performed through biochemical markers using isozyme markers (Li et al. 2004). Fluorescent in situ hybridization

(FISH) is an immune-cytological analysis for the detection of alien genetic diversity in the recipient wheat genome in which the alien source is fluorescently labeled (Zhang et al. 2001). The FISH and GISH analyses follow the same procedures; however, FISH analysis is more realistic and efficient and potentially identifies repeated DNA sequences, single copy genes, and even low copy sequences (Miller et al. 1996).

7 Contribution Regarding Biotic Stresses

Rusts are the most emerging and paramount biotic stresses that limit wheat yields globally. The cultivars with a wide range of rust resistance are the only stable materials that can cope with related yield losses. In this situation, the process of identification and introduction of novel and alien genes harboring resistance to combat these spreading pathogens is a consistent process.

For the introgression of alien genes into wheat cultivars the crop evolutionary relationships of various species are a major factor as that allows recombinations to occur and transfers to take place. Recently many schemes have been analyzed for transferring genes from the tertiary gene pool (Qi et al. 2007). In these schemes the transfer of foreign genes via wheat–alien translocations is the most significant step of gene transfer. This transfer can be approachable for the desired chromosomes through the process of centric breakage and fusion (Robertsonian) during meiosis or interstitial transfers, but in general the transfers have terminal events.

7.1 Wild Species Contributing to Alien Diversity

7.1.1 Wild Emmer

The wild wheat emmer is renowned as an efficient source of target genes for desired traits, for instance, genes for grain size, tall spike, large grain, and protein production such as required storage proteins, herbicidal response, amount of photosynthate, drought and salinity tolerance, resistance to diseases including rusts, soilborne mosaic virus, powdery mildew, abundant tillering, and other quantitative trait genes (Jaradat 2011).

7.1.2 *Aegilops* Species

Ae. tauschii (Goat grass; $2n=2x=14$; DD) is the progenitor contributing genome D in bread wheat (hexaploid). This wild species contains many genes of valuable agronomic interest and resistance to pests/insects, diseases, and extreme abiotic factors. The substitution lines of wheat-*Aegilops* have been developed utilizing

Ae. speltoides ($2n=2x=14$; SS), *Ae. umbellulata* Zhuk ($2n=2x=14$; UU), *Ae. longissima* Schw. and Musch. ($2n=2x=14$, S^lS^l), *Ae. caudata* ($2n=2x=14$; CC), *Ae. geniculata* ($2n=4x=28$; MMUU), and *Ae. tauschii* and *Ae. sharonensis* Eig. ($2n=2x=14$, S^lS^l). Thus useful agronomic characters have been transferred into common wheat from *Ae. umbellulata*, *Ae. longissima*, *Ae. comosa* ($2n=2x=14$; MM), *Ae. ventricosa* Tausch ($2n=4x=28$; DvDvNvNv), *Ae. geniculata*, and *Ae. speltoides*. Due to this potential of possessing valuable practical traits interest remains high in exploiting these resources. However, the focus is more on *Ae. tauschii* because the excellent homologous pairing of its D genome chromosomes allows for rapid production of improved wheat varieties either by bridge or by direct crossing. The range of attributes that can be transferred is huge and covers almost all major stresses including powdery mildew, yellow rust, brown rust, black rust, insects/pests such as cereal cyst nematode, Hessian fly, greenbug, and root knot nematode (Schneider et al. 2008). The abiotic stresses such as drought, salinity, sodicity, heat, cold, and waterlogging also fall in its arsenal of valued genes and are being exploited by groups that face these constraints.

7.2 *Interspecific Wheat Hybrids*

On a commercial basis, the genetic materials introduced into common wheat genotypes from related species are catalogued into two groups. The primary and some secondary gene pools contain hybrids with many introgressions. Their complexities and instability has been discussed by Adonina et al. (2012). The merit of such strategies of which pentaploid breeding is only one is phenomenal. Modern wheat cultivars have been hybridized with many donors for valued traits generating remarkable derivatives that have allowed yield increases to continue over the past few decades and also successfully captured needed resistance against many stresses both biological and physical (Fig. 3). A lot of work has been done with regard to creating tolerance to diseases and the most epidemic diseases of wheat that are widespread and prevalent are rusts. Some specifics follow below.

7.2.1 Contribution of Alien Species to Leaf Rust (Brown Rust)

Leaf rust genes from natural common wheat relatives have been introduced into modern wheat genotypes through interspecific hybridization practices. It has been reported that various *Aegilops* species possess several resistance genes for diseases responsible for wheat yield declines (Schneider et al. 2008).

Species of *Aegilops* carrying genomes C, U, and M are considered valuable sources of disease resistance including stripe and leaf rusts (Singh et al. 2000). The nonprogenitor species *Aegilops* with its large volume of variable genomes has been utilized to a limited extent. Riar et al. (2012) have investigated inheritance, molecular gene mapping, and introgression of leaf rust tolerant genes from *Ae. caudata* into

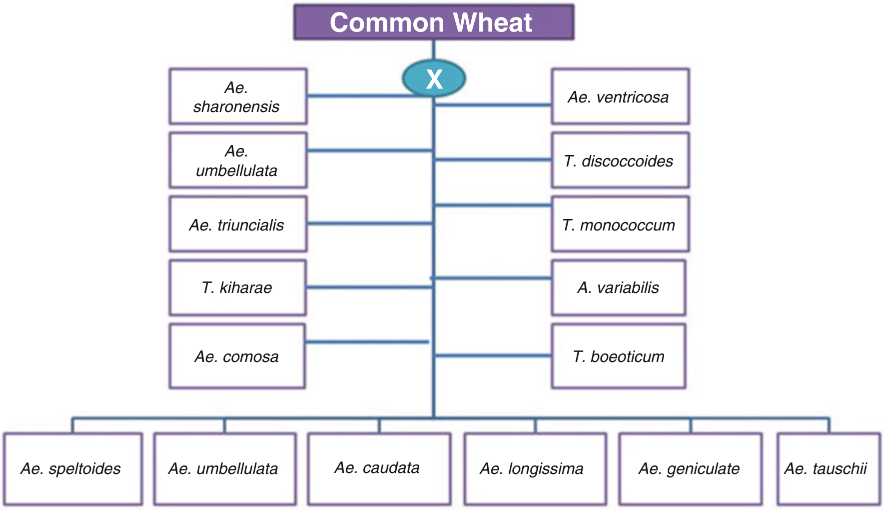

Fig. 3 Interspecific crosses of common wheat with related species for rust resistance

common wheat. The F2 generation developed from the cross of *Ae. caudate*/*T. aestivum* and the resulting introgression lines with wheat cultivars have been separated for individual dominant genes for leaf rust both at seedling and adult phases.

A number of wheat/*Aegilops* hybrids have been established through addition, translocation, and substitution lines that have many valuable genes regulating agronomic traits (Friebe et al. 2000). Ling and his colleagues screened more than 200 experimental samples of *Ae. tauschii* for leaf rust tolerant genes on the basis of the *Lr1* leaf rust gene. It was recognized that the resistance found in these accessions was regulated by an individual *Lr1* gene that mapped a similar chromosomal fragment as that in wheat (Ling et al. 2004). Thereby, numerous leaf and stripe rust resistance genes had been introduced into planted wheat genotypes from *Thinopyrum* and *Aegilops* species and commercially utilized, for instance, *Th. intermedium* (*Lr38*); *Th. ponticum* spp. (*Lr19*, *Lr24* and *Lr29*); *Ae. umbellulata* (*Lr9*); *Ae. ventricosa* (*Lr37*, *Yr17*); *Ae. speltoides* (*Lr28*, *Lr51*, *Lr36*, *Lr35* and *Lr66*); *Ae. tauschii* (*Lr21*, *Lr32*, *Lr22a*, *Lr41*, *Lr39*, *Lr40* and *Yr28*); *Ae. geniculata* (*Lr57*, *Yr40*); *T. dicoccoides* (*Lr53*, *Yr15*, *Yr35*, *Yr36*); *Ae. triuncialis* (*Lr58*); and *Ae. longissima* (McIntosh et al. 2008, 2010). Nonprogenitor species, *Ae. caudata* (diploid) with the CC genome additionally contains several genes to combat wheat diseases including powdery mildew and rusts with high lysine and protein genes (Riar et al. 2012).

The efficient way to improve and preserve the yield of common wheat grain is to reduce damage related to diseases and to increase production. Many studies have been reported on the transfer of several *Lr* genes from the wild and closely related species of wheat into the genome of modern wheat cultivars. For example, the leaf rust resistance genes such as *Lr28*, *Lr35*, *Lr26*, *Lr47*, and *Lr51* are located within the genome of *Ae. speltoides* Tausch (Schneider et al. 2005, 2008; Todorovska et al.

2009). Unfortunately, the efficacy of the individual *Lr* gene may be declining with the passage of time because of the emergence of new races of virulent pathogen (Adonina et al. 2012).

The collections of common wheat lines developed by the cross of *T. aestivum*/*Ae. speltoides* displayed resistance to leaf rust for many years (Dzhenin et al. 2009). These lines were established by exposure of ionizing radiation to the pollen of *Ae. speltoides* that originate chromosomal breakages and facilitate manifold translocations. Later monotranslocation lines were identified using molecular markers and the location and size of the genetic segment of *Ae. speltoides* introgressed into wheat lines were determined by the fluorescence in situ hybridization technique. The translocations were detected in the long arm of 5 and 6 chromosomes of genome B and the short arm of chromosome 1B. As the translocation occurred in different chromosomal segments from the identified leaf resistance genes, it was suggested that new fragments of genes were transferred from *Ae. speltoides* into developed common wheat lines (Adonina et al. 2012).

Similarly, wheat accessions have been collected by the cross of hexaploid wheat with alien genetic stock of *T. kiharae*, *Ae. speltoides*, and *Ae. triuncialis* ($2n = 4x = 28$; CCC^uC^u). The accessions of wheat carry alien genes including resistance to yellow spot, leaf rust, septoriosis, powdery mildew, and some other diseases (Gajnullin et al. 2007). Similarly, rust resistance genes *Sr38*, *Yr17*, and *Lr37* are derived from *Ae. ventricosa* and are translocated in western European wheat genotypes and the resulting hybrids were analyzed by molecular marker (Bartoš et al. 2004). Genes can be transferred from *Ae. variabilis* ($2n = 4x = 28$, UUSS) for resistance to leaf rust (Marais et al. 2008), powdery mildew (Spetsov et al. 1997), root knot nematode (Coriton et al. 2009), and karnal bunt (Williams and Mujeeb-Kazi 1996).

Alien resistance genes in the wild progenitors are a good source for wheat breeding programs. On the basis of transfer, evaluation, and molecular analysis, many leaf rust confrontation genes (*Lr1*, *Lr15*, *Lr2*, *Lr32*, *Lr21*, *Lr39*, *Lr22*, *Lr34*, and *Lr42*) have been positioned in *Ae. tauschii* (diploid; genome D). There have been 12 resistance genes for leaf rust documented located in the *Ae. tauschii* genome. Recently, ambiguous entry of *Lr57*/*Yr40* and *Lr58* from two species, *Ae. geniculata* and *Ae. triuncialis*, respectively, have been documented as offering possibilities for the shifting of alien genes without any hindrance in linkages. The resistance genes encoding leaf rust are situated at the tip of wheat chromosome arms. These segments are identified to be recombined rapidly and explain the phenomenon of the high rate of evolution (Gill et al. 2008).

7.2.2 Contribution of Alien Species to Stem Rust (Black Rust)

The global wheat yield is threatened by stem rust and its variant Ug99 and associated strains. Almost 50 resistance genes of stem rust are being recognized and mapped to definite chromosomal positions (McIntosh et al. 2008). But few are successful in resistance to Ug99 (Singh et al. 2008) and mostly are connected with surplus impact on the agronomic character (McIntosh et al. 1995). The gene *Sr2* is a broadly used stem rust resistance gene (McIntosh et al. 1995). *Sr2* was being transplanted from *T. turgidum* hooked on bread wheat during the nineteenth century. The *Sr2* gene has been sent out and used in wheat breeding projects globally and has given sturdy mature wheat plant rust resistance for more than 50 years. Moreover, it merely gives limited mature plant confrontation and is related to the pseudo black chaff trait. The gene *Sr22* was initially recognized in the bread wheat variety *T. monococcum* spp. *boeoticum* with accession number G-21 and *T. monococcum* L. ($2n=2x=14$, AmAm) accession line RL5244. Interspecific hybridizations are used to transfer *Sr22* in tetraploid and hexaploid. In Australia, *Sr22* is efficient beside all pathotypes of the stem rust variants. Moreover, its use becomes limited by a yield consequence related to the *T. monococcum* spp. *boeoticum* segment of the chromosome containing the *Sr22* gene. Some lines recently produced with *Sr22* have reduced *T. monococcum* fragments (Olson et al. 2010). Resistance genes for stem and leaf rusts are being transferred from *Ae. geniculata* (*Lr57* and *Yr40*), *Ae. triuncialis* (*Lr58*), and *Ae. umbellulata* (*LrU1*, *LrU2*, *YrU1*) (Chhuneja et al. 2007).

7.2.3 Contribution of Alien Species to Stripe Rust (Yellow Rust)

Damage cause by stripe rust can be decreased by resistance breeding which is a quite inexpensive and ecologically friendly method. Hence, in southwestern China production of resistant cultivars is the primary breeding goal where stem rust is the main problem. Globally, a chain of *Yr* genes *Yr1*, *Yr41*, and many conditionally selected genes are being recognized (McIntosh et al. 2008). In China some genes are effective including *Yr5*, *Yr10*, *Yr11*, *Yr15*, *Yr12*, *Yr26*, *Yr13*, *Yr14*, *Yr24*, and *YrZH84* whereas additional genes have depleted their resistance such as *Yr1*, *Yr2*, *Yr3*, *Yr4*, *Yr6*, *Yr7*, *Yr8*, and *Yr9* (Wan et al. 2007). The stripe rust resistant genes are being determined. A large pool of variability present in a wild relative of wheat might be utilized for enhancement of wheat (Mujeeb-Kazi 2006). *Ae. variabilis* is a species that had been used efficiently in the past. Dhaliwal and his group (1993) discovered that resistance to stripe rust can be brought about by definite *Ae. variabilis* accessions; thus far the *Yr* relocation to bread wheat has not yet been recorded. The important source of a resistance gene is a wild progenitor and nonprogenitor species of wheat (Singh et al. 2007). Two new resistance genes for stripe rust from *T. boeoticum* and *T. monococcum* have been mapped and transplanted to cultivated wheat (Chhuneja et al. 2008).

7.3 Wild or Nonrelative Species Contributing Alien Diversity

7.3.1 *Triticum ventricosum*

Wheat breeders from all over the world are developing hybrids with high rust resistance utilizing alien species, for instance, *T. ventricosum* ($2n=4x=28$; genome DvDvMvMv) crossed with common wheat. Therefore, rust resistance genes *Lr37*, *Sr38*, *and Yr17* have been introduced from *T. ventricosum* chromosomal segment 2NS into the wheat cultivars (Mumtaz et al. 2007).

7.3.2 *Thinopyrum intermedium* and *Th. ponticum*

An allo-hexaploid specie *Th. intermedium*(($2n=6x=42$; E1E1E2E2XX) is perennial and has a potential resource of plenty of useful genes for common wheat yield enhancement. For instance, rust resistance (Larkin et al. 1995), barley yellow dwarf virus resistance (Larkin et al. 1995), and common wheat with resistance against bunt and powdery mildew in addition to wheat curl mite and wheat streak mosaic virus resistances. This specie has high crossing compatibility with common wheat and transferred many useful genes into the wheat genome and made it possible to produce many commercial wheat cultivars. These wheat cultivars are partially amphiploids and some are substitutional, additional, and translocation lines (Tang et al. 2000).

7.3.3 *Hordeum* Species

The wild barley (diploid), *Hordeum chilense* Roem. et Schult ($2n=2x=14$), is exclusively polymorphic in nature and occurs widely in Argentina and Chile. This polymorphic specie has the highest potential after *H. bulbosum* ($2n=2x=14$) and *H. vulgare/spontaneum* ($2n=4x=28$) for cereal breeding systems as it has shown high compatibility to cross with other species of the tribe Triticeae such as *Secale*, *Hordeum*, *Triticum*, and *Agropyron* (Martin et al. 2000). Plant breeders have been performing different techniques to successfully develop hybrids from the cross of wheat and barley for more than decades but with little achievement. On the other hand, hybrids produced with *H. chilense* are usually amphiploids and fertile. *H. chilense* possesses resistance against the diseases wheat and barley brown rusts caused by fungi, *P. hordei* and *P. triticina*, respectively (Rubiales et al. 2001).

7.3.4 *Secale cereale*

Rye (*S. cereale* L.; $2n=2x=14$), another specie in tribe Triticeae, is enriched with a potential source of increasing genetic diversity and transferring resource in cultivated wheat. The chromosomal arm 1RS of rye has been exclusively used in wheat improvement programs all over the world. The wheat–rye translocation harboring 1BL.1RS has been released globally and numerous wheat cultivars have been produced. The most widely used of this T1BL.1RS segment of chromosome may carry the genes for resistance *Lr26* against leaf rust, *Sr31* to stem rust, and *Pm8* to powdery mildew (Ko et al. 2002).

7.3.5 *Dasypyrum villosum* or *Haynaldia villosa*

D. villosum ($2n = 2x = 14$; VV) is a diploid wild relative of bread wheat dweller of the Mediterranean region. Some of the genes that had been transplanted from the *D. villosum* consist of the *Pm21* gene associated with resistance against powdery mildew in the conformation of T6AL.6VS transformation and the gene *Wss1* associated with wheat spindle band for mosaic virus in the conformation of a T4DL.4VS transformation (Zhang et al. 2005a, b). The translocation T6AL-6VS also has a gene providing resistance to wheat curl mite colonization (Chen et al. 1996). Various transfers have shown that T6AL-6VS harboring *Pm21* have been distressed in crop production. Resident of the region around the Mediterranean Sea and South and Western Asia is *Haynaldia villosa*, a wild grass specie of the subtribe Triticeae. *H. villosa* has resistance against biotic and abiotic stresses exemplified by stem rust (*P. graminis*), powdery mildew (*Blumeria graminis*), leaf rust (*P. triticina*), stripe rust (*P. striiformis*), and yellow mosaic virus (*Bymovirus*), elevated seed protein amount, and drought tolerance (Blanco et al. 1996).

7.4 *Intergeneric Wheat Hybrids*

The tribe Triticeae is a group of unusual plants. This accounts collectively for about one third of the world cereal production. It comprises many diverse species including tetraploids (durum wheat; $2n = 28$), diploids (barley and rye), hexaploids (spelts, bread wheat, and Triticale), and even certain octaploid Triticales. All the members of this Triticeae tribe are very closely related and therefore, hybrids developed between them are fertile. Most of the species in Triticeae are self-pollinated and rye is the only cross-pollinated crop. High strategic approaches are being practiced in improving cereal crops globally to strengthen a link between the cultivated gene pools and the desired alleles or genes from wild progenitors or nonprogenitors (Feuillet et al. 2007). The crosses between common wheat with tertiary and some secondary gene pool species are the result of intergeneric hybrids (Fig. 4). Many researchers from all over the globe have been practicing to generate hybrids of

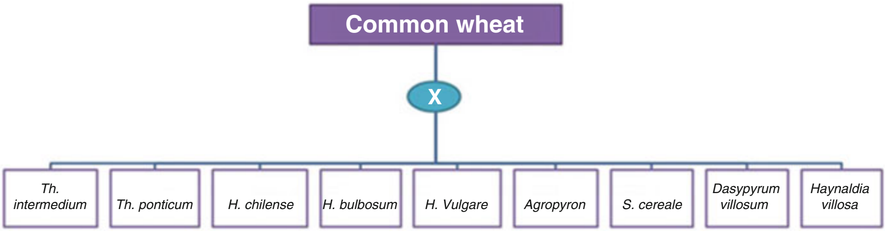

Fig. 4 Intergeneric cross of common wheat with closely related species for rust resistance

wheat via crossing common wheat cultivars with nonprogenitors spp. and they successfully developed remarkable varieties.

7.4.1 Contribution of Alien Species to Leaf Rust (Brown Rust)

Barley provides a novel resource of important genes in wheat breeding systems. For instance, barley chromosome region 1H contains genes involved in resistance to leaf and strip rust (Islam and Shepherd 1992) and powdery mildew (Wei et al. 1999), chromosomes 6H and 7H controlling genes to combat common bunt, and chromosome 5H harbors genes for resistance to stem rust. In the addition of useful genes from barley into wheat, the generation of plants carrying a recombinant chromosomal segment is a prerequisite. However, the chromosomal pairing frequency in the hybrids of wheat and barley rarely occurs in the pairing of chromosomes during meiosis division (Malysheva et al. 2003).

Rye is a paramount source of alien genes conferring resistance to abiotic and biotic stresses (Mater et al. 2004). In the attempt to produce hybrids from the cross of wheat–rye, the rye chromatins 1R (1RS.1BL, 1RS.1AL, 1RS.1DL) and 2R (2RS.2BL, 2AS.2RL, 2BS.2RL) have been substituted with equivalent chromatin of the wheat genome (Hysing et al. 2007). Among these the most successful translocation line is 1BL.1RS. In the practice of generating wheat–rye hybrids, 2RL chromatin from the parental line of rye harbors tolerant genes for leaf rust and powdery mildew translocated in hybrids. These 2RL translocated hybrids have enhanced tolerance to biological and physical stresses such as heat shock and dehydration-induced proteins by altering protein expressions (Kim et al. 2011).

The translocation T1BL.1RS between rye and common wheat is broadly exploited in the bread wheat breeding approaches, but because of this translocation in modern wheat some genetic weaknesses are experienced, for instance, in Petkus, a German cultivar (Zeller 1973). In this context, Ko and his colleges developed the new translocation line of T1BL.1RS as a result of backcrossing hybrids produced in the F1 generation of wheat–rye. The presence of new rye-chromatin was identified by the GISH technique in the selected lines and obtained one line with somatic chromosomes ($2n=42$). Later on, C-banding analysis confirmed that the chromosome had theT1BL.1RS translocation (Ko et al. 2002).

7.4.2 Contribution of Alien Species to Stem Rust (Black Rust)

All around the world, the wheat crop is susceptible to stem rust and many vital stem rust tolerant genes exploited and located in common wheat have been overcome by race Ug99 which is also known as TTKSK and its derivatives (Jin et al. 2007, 2009). The center for Wheat Genetic and Genomic Resources (WGGRC) functions for the making of Ug99-resistant wheat crops; for this reason they screened a collection of about 95 accessions in *D. villosum* against stem rust races of North American (a mixture of RKQQC, TPMKC, and QFCSC). It was observed that infection types ranged from “0” to “0” as all accessions were immune. A subset of *D. villosum* disomic integration reservoirs in the background of the vulnerable cultivar, “Chinese Spring” (Sears and Miller 1985) was prepared that discovered chromosome 6 V contains at least a single stem rust confronting gene, selected as *Sr52*. In replicating seedling tests *Sr52* provided resistance to TTKSK with ITS 1–2 which depends on TA7682 testing.

Th. intermedium has been exploited as an excellent source of resistance against many diseases. In one such study, two partial amphiploids were produced from the hybridization of *Th. intermedium*-durum wheat. Meiotic analysis of these partial amphiploids suggested that they are cytologically stable. These partial amphiploids were the potential source of disease resistance including leaf, stem rusts for race Ug99 and fusarium head blight. Thereby, these novel hybrids could be used as multiple disease resistance sources in durum and bread wheat (Zeng et al. 2013).

Th. ponticum ($2n=10x=70$) and Dewey are the sources of *Sr25* and *Sr26* and these were transferred into wheat which showed thriving resistance against stem rust such as Ug99 and correlated exertions. The long arm of the chromosome 7D in wheat and chromosome 7A in wheat (Zhang et al. 2005a, b) had been translocated by the *Sr25* gene and the attached leaf rust tolerance gene *Lr19*. The limited use of germplasm having *Sr25*/*Lrl9* was done because linkage was developed with an additional *Th. ponticum* consequent gene that causes deplorably yellow flour. A new mutant line Agatha-28 had been introduced by Knott (1980) which contained *Sr25*/*Lr19* with less yellow color because of *PSY-E1* gene modification (Zhang and Dubcovsky 2008). In Australia during the 1960s *Sr26* was used as a resource of resistance and in 1971 a new and first cultivar, Eagle, was introduced (Martin 1971). Afterward, other varieties Kite, Jabiru, and Avocet were introduced that have *Sr26*.

The *Th. ponticum* segment has rarely been used in breeding programs because it is associated with a yield penalty. To surmount the yield consequence associated with lines possessing *Sr26*, small alien segments were introduced in new lines (Dundas et al. 2007). A gene from *T. timopheevii*, *Sr40*, was introduced but it was not broadly established in current cultivars, however, to determine its effects on agronomical traits, this was transplanted into common wheat.

Many genes have been transferred into common wheat; these genes includes *Sr13*, *Sr35*, *Sr32*, *Sr45*, *Sr39*, *Sr44*, *Sr46*, and a small number of anonymous genes but these were not introduced in commercial varieties. The above-mentioned genes efficiently combat Ug99 (Jin et al. 2007) and are functional with additional stem rust resistance genes for efficient rust tolerant cultivars. Two genes, *Sr24* and *Sr36*, commencing alien diversity had been introduced in bread wheat and were broadly utilized by wheat agriculturists. In the past it was considered that wheat varieties having *Sr24* and *Sr36* genes were efficient in combatting Ug99 but recently it has been found that after screening for stem rust in Kenya a vulnerable disease type revealed that *Sr24* and *Sr36* are inefficient beside variants of Ug99, mainly for two races TTKST and TTTSK (Jin et al. 2009).

Sr24 and *Sr36* genes were equally and broadly recognized as commercial resistance genes and are even very thriving against a larger number of stem rust types; they might even be constructive for other genes to get rust-tolerant varieties of wheat. The rye gene *SrR* was introduced for stem rust onto either chromosome 1BL or 1DL of wheat by the chromosomal interchange of 1RS of *S. cereal* (Koebner et al. 1986). All stem rust phenotypes in Australia are being provided with resistance by *SrR*. 1RS is usually coupled with the harmful feature of “sticky dough” so 1RS has not been broadly used in wheat varieties. Molecular markers that were previously identified as using wheat rye recombinants in the region having the *SrR* gene additionally revealed markers at the powdery mildew confrontation Mla allele locus in the map of barley in the *SrR* section of rye (Mago et al. 2002). Suppressed translocation at the *SrR* gene locus provided a few studies in earlier experiments based on mapping; thus, with a goal of studying the organization of the *SrR* region, a molecular analysis of the locus has been undertaken with a mutation-based approach (Kim et al. 2004).

7.4.3 Contribution of Alien Species to Stripe Rust (Yellow Rust)

The rye genome carries a 1RS segment located at the short arm of the chromosome responsible to confer resistance to many diseases including rusts and powdery mildew. Many wheat cultivars carrying 1RS translocation have been successfully generated including “Veery” lines–spring bread wheat for many environments, produced at CIMMYT (Rajaram et al. 1983). This 1B/1R translocation of rye carries many genes *Yr9*, *Lr26*, *Pm8*, and *Sr31* that have race-specific resistance against stripe and leaf rusts, powdery mildew, and stem rust, respectively. Therefore, rye chromosome 1 short arm has been widely exploited in the wheat breeding program to obtain new cultivars incorporated with new disease resistance genes. Moreover, molecular markers were identified and mapped in the 1RS chromosomal regions harboring resistance alleles for *Lr26*, *Yr9*, *Sr31*, and *SrR* from varieties Petkus and Imperial (white rye), respectively (Mago et al. 2002).

In the practice of producing efficient hybrids through intergeneric crosses, a partial amphiploid Zhong 5 ($2n=56$), developed by a Chinese group, is a cross between *T. aestivum–Th. intermedium* and comprises seven chromosomal pairs from a specie *Th. intermedium* supplement to the complete complementary chromosome of *T. aestivum* with tolerance against barley yellow dwarf virus, in addition to stem, stripe, and leaf rust resistance (Tang et al. 2000).

It has been reported that there are about 53 permanently named and more than 40 provisionally designated stripe rust resistance genes or quantitative trait loci (QTL) (Cheng 2008; McIntosh et al. 2009, 2010, 2011; Ren et al. 2012; Xu et al. 2013). Along with the permanently named resistance genes, *Yr11*, *Yr12*, *Yr16*, *Yr13*, *Yr29*,*Yr14*, *Yr18*, *Yr30*, *Yr39*, *Yr34*, *Yr36*, *Yr46*, *Yr48*, and *Yr52* confer adult plant or high temperature adult plant (HTAP) resistance genes, whereas the others confer all-stage resistance (Xu et al. 2013). The *Yr* genes that were permanently named and identified from wild parents include, *Yr5*, *Yr15*, *Yr8*, *Yr9*, *Yr17*, *Yr19*, *Yr35*,*Yr26*, *Yr28*, *Yr36*, *Yr40*, *Yr37*, *Yr38*, and *Yr42* (McIntosh et al. 2009, 2010; Wang et al. 2008; Li et al. 2012). Chinese *P. striiformis* races have been made resistant by *Yr15* and *Yr5* genes (Yang et al. 2003).

Previous studies on tolerance inheritance against stripe rust in *Haynaldia villosa* L. *Schur* and a few translocation lines showed that *Haynaldia villosa* has important genes for disease resistance that can be greatly expressed in a wheat background. From translocation lines V9128-1 (Zhou et al. 2008), one dominant *YrV1* gene that provides tolerance to *P. striiformis* f. sp. *tritici* race CYR30 was identified and positioned on wheat chromosome 3BS. For translocation line V9128-3 (Hou et al. 2009), also having the dominant *YrHV* gene which shows resistance to *P. striiformis* f. sp. *tritici* pathotype Sun11-4, was identified and positioned on wheat chromosome 2AL. Wang (2011) identified the one dominant gene (*YrHV*) derived from translocation line V9125-2 and positioned this gene in 7DS using the flanking markers Xwmc463 and Xwmc405.

7.4.4 Alien Diversity Contributes to Some Minor Stresses

Many translocation lines have been made from *T. aestivum* and *H. villosa* translocation 6VS/6AL and these lines include 92R89, 92R149, 92R90, 92R137, and 92R178 by Nanjing Agricultural University, The Cytogenetics Institute. These lines provide resistance to powdery mildew and yellow rust; on chromosome 6VS a gene *Pm21* was present with resistance to powdery mildew. In China, a group of high-quality wheat varieties such as Nannong 9918 (Chen et al. 2002), Neimai 8, Neimai 9 (Huang et al. 2007), Neimai 10, and Yuanfeng 175 (Ji et al. 2006) etc., were selected and developed by *T. aestivum–H. villosa* translocation lines, substitution lines, or addition lines.

"Salmon" wheat is another source of T1BL.1RS (Zeller 1973), but seldom used in wheat breeding because it was less characterized. The translocation 1AL.1RS with 1RS from rye variety Insave, the wheat cultivars such as Amigo, and accession line GRS1201 both contain a T1AL.1RS, which was genetically heterogeneous. The Amigo cultivar with 1RS is tolerant to green bug confrontation gene Gb2, whereas 1RS in GRS1201 has Gb6 which provides tolerance to biotypes including I, E, and K green bugs (Porter et al. 1994). After the successful performance of 1RS in wheat variety, the wheat–rye interchanges participated in consequential roles in various wheat breeding projects. Approximately 25 % of ingressions in wheat recital test experiments in the region of the Great Plains in the United States, hold whether T1BL.1RS and/or T1AL.1RS wheat–rye interchange (Graybosch 2006). Similarly, about 54 % of cultivated wheat varieties harbor T1BL.1RS translocations in different parts of Bulgaria (Landjeva et al. 2006) and in China, almost 38 % of the modern wheat cultivars since 1980 confined similar translocations (Zhou et al. 2004).

The techniques used for the recognition of a genetically changed chromosomal segment such as T1AL.1RS or T1BL.1RS in wheat breeding programs are the primary approach. A rapid and realistic marker system that enables recognition of the most important translocation sources of wheat–rye relating 1RS would be very supportive for an efficient cull of intrigued ranks in wheat propagation. Thus for many rye categorical molecular markers, the described systemic assessment of their effectiveness for markers is quite weak (Nagy and Lelley 2003).

8 Challenges of Using Alien Genes to Improve Wheat Crop

In the progress of developing wheat hybrids using wild progenitor and nonprogenitor species, the major bottleneck is the introgression of alien genes that link chromosomal segments carrying genes of negative impact within useful traits in the selected elite wheat cultivars. This phenomenon is referred to as “linkage drag” and is responsible for limiting the use of alien genes in the breeding programs. The procedure to eliminate the deleterious effect of negative alleles is not only time consuming but also tiresome. This recombination barrier challenge can be overcome by using the emerging field of chromosome engineering (CE) that prompts donor chromosome fragmentation and enhanced recombination within the genome of recipient (Endo 2007). The gametocidal chromosomes and ionization of radiation have been employed to make chromosomal breakages that are later rejoined and emerge in the substitutions and translocations between receipt and alien gene genome (donor).

CE allows the transfer of alien genes that were previously not available in modern wheat from other members of the Triticeae tribe such as *Aegilops*, *Secale*, *Agropyron*, *Thinopyrum*, *T. urartu*, *T. turgidum*, and *T. monococcum* (Islam et al. 2007). The linkage drag can be reduced through sequence-specific recombination of homologues by exploiting the strategies’ “allele replacement” with a better understanding of regulation, recombination distribution, and structure in the genome of Triticeae (Feuillet et al. 2007).

Moreover, the discovery of the *Ph1/ph1* locus in wheat is very significant. This locus involves homoeologous chromosomal pairing and recombination. The efficient use of homoeologous chromosomes in the wheat–alien translocation can be achieved by eliminating the 5B wheat chromosome (Sears 1972), exploiting the *phlb* mutant (Koebner and Shepherd 1985), or by deterring the expression of the *Phl* gene (Riley et al. 1968). The dominant *Ph*^{I} gene refered as high pairing gene derived from *Aegilops speltoides* (Chen et al. 1994) lowers the expression of the *PhI* gene and allows homoeologous pairing (Riley et al. 1958). Therefore, wheat–alien translocation can be established without the removal of *Phl*. The *Phl* locus characterization has been broadly utilized in wheat cultivars to induce homologous recombination and its molecular structure has recently been defined (Griffiths et al. 2006). Relatively recently Mujeeb-Kazi(2003) initiated an integrated protocol that exploits the *Ph1b* gene for inducing wheat–alien translocations and the scheme has been studied in depth by Kazi(2011) and reviewed by Mujeeb-Kazi et al. 2013. This scheme has the potential for all existing amphiploids to be manipulated for agricultural advantage around practicality targets. Spontaneous exchanges (rather rare) also are beneficial and here the recombination between homologous chromosomes allows segmental introgression as exemplified by the famous spontaneous wheat–rye chromosomal translocation 1BL.1RS. This translocation increases yield as well as provides rust disease resistance (*Lr29*/*Yr26*) with improved stress tolerance and adaptation (Zarco-Hernandez et al. 2005), but has a negative impact on wheat with poor gluten strength (Lukaszewski 2006).

Alien species may give a response of hypersensitive disease reaction owing to major gene effect, hence the alien diversity has to be carefully examined before alien genes/alleles exchange. The more advanced trend of combatting stresses has moved towards minor gene from major gene effect as the latter has short-lived resistance. Adult plant resistance (APR) is preferable as it has durable resistance and the potential to develop the disease gradually. Fortunately, the excessive alien chromatin is present in the Robertsonian translocation 1AL.1RS and T1BL.1RS that deal massively in practical agriculture. However, this alien contribution is reduced in the germplasm with the trait of target genes as *Lr25* and *Bdv2*. The gene pyramiding with major genes can be incorporated with minor genes to obtain highly desirable germplasms with durable resistance and tolerance associated with food security parameters (Mujeeb-Kazi et al. 2013).

More recently, the high-throughput approaches in genotyping have been helpful in the discovery of genes with high proficiency and understanding of alleles/genes functions. Likewise, RFLP and C-banding base techniques are laborious and time consuming to detect the translocation in the crossing of wheat with an alien source specie. However, the advancement in sequence-based marker technology facilitates a rapid and cost-effective approach to identify the alien segment established on sequence polymorphism. In the past few years, the development of SNP-based assay has been focused on the study of the complex wheat genome, however, SNP assay highly depends on study objectives and genotyping.

Another more advanced approach in addition to utilization of Triticeae tribe gene pools that has recently been applied and successful is the genetic transformation in wheat. There are established efficient protocols and methodology to transfer the novel genes into the wheat genome harboring resistance to biological and physical stresses and agronomical traits with improved quality.

9 Conclusion and Future Prospects

In the present scenario, the chief issue related to plant yield and production is to manage plant diseases that daily are involved vigorously in the decline of crop plant yield. In wheat, the most damaging biotic stress factors regarding to yield are the rust diseases. Although much research and experimentation have been performed in this context to cope with the prevalent diseases, there still remains a gap that prevents superior cultivars from giving high yields and possessing multiple disease resistance. The main reason for this failure is the emergence of new races of pathogens with the passage of time that reduces the productivity span of cultivars to be the most demanding and remarkable.

The wheat breeders' community has already determined that several genes regulate simple as well as complex traits through genetic approaches. Marker-assisted selection has been widely exploited to incorporate these useful genes (Reece and Haribabu 2007). The sources of alien genes have been long identified as have been the procedures of introducing these useful genes into elite cultivars. Both these facets still remain viable in wheat-breeding approaches. Extensive efforts have attempted to incorporate desired genes controlling various disease resistance including the major three rusts (stem, stripe, leaf) from the wild wheat relatives into common wheat cultivars. Hence, different progenitor and nonprogenitor species have been identified that have provided beneficial alleles and have yielded derivatives tolerant to order biological and physical stresses. Being a dynamic area, gene transfer today is not the end of breeding efforts as new races of the pathogens evolve with the passage of time. Therefore, novel genes controlling these diseases with new races of pathogens should be discovered within various wild and related species. To add efficiency to realize swift outputs new methodologies also play a vital part and have been continuously evolving.

During the past few decades, several targeted genes were introgressed into modern wheat genomes from the wild relatives via intraspecific, interspecific, and intergeneric hybridization that have relied upon homologous and homoeologous wheat/alien chromosome exchanges. For the way forward we suggest that the most preferable and desired gene pool for the homologous pairing during genetic exchange is the primary gene pool exploiting the diploid accession of the A and D genome progenitors and the AABB genomic profile.

Greater efficiency prevails from the high-throughput approaches and advances in genomics that will facilitate opportunities for further effective chromosome engineering. Although the resistance to different stresses to combat is the foremost objective for food security, yield maximization is the major universal alternate goal for our way forward to the year 2050 food security vision that has to combat several climatic change factors, keeping sight of the large population projections of about 9.2 billion people. For the achievement of high yields, the genetic material of common wheat has to be diversified by the exploitation of under-utilized genomic diversity using all possible genetic resources. The awareness of the common breeder must also ensure that monoculture does not prevail for maximizing yield.

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Sulfur Nutrition of Oil Palm for Enhancing Oil Yield in Tropics

Muhammad Sabir, Mohamed M. Hanafi, and Khalid Rehman Hakeem

Abstract Globally, the demand for vegetable oil is increasing due to tremendous growth in the world population. Among vegetable oils, palm oil contributes a major share (33 %) in annual consumption of vegetable oil around the world. The yield of palm oil has witnessed an unprecedented increase in the last few decades, mainly due to the increase in area under oil palm plantation. However, the prospects for increasing palm oil yield due to the increase in area under oil palm cultivation are very bleak as possible areas have already been brought under oil palm plantation. Moreover, palm oil yield per unit area has been stagnant over the last decade. Mainly, oil palm is grown in Oxisols and Ultisols which are highly weathered soils having inherently low fertility status. Soil fertility management is therefore prerequisite to realizing the maximum yield potential of oil palm in such low fertility soils. Sulfur is an essential macronutrient that has a very crucial role in oil biosynthesis in oil seed crops. Sulfur is generally deficient in Oxisols and Ultisols and thus needs proper consideration for enhancing the oil yield of oil palm. But sulfur is least considered in soil fertility and nutrient management programs of oil palm plantations. We have reviewed the literature to highlight the role of sulfur in the biosynthesis of oil in oil seed crops in general and oil palm in particular and have suggested some suitable measures for sulfur management of oil palm plantations for enhancing oil yield in highly weathered soils of Oxisols and Ultisols.

Keywords Vegetable oil • Oil biosynthesis • Sulfur • Palm oil • Oxisols and Ultisols

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1 Introduction

The demand for vegetable oil is increasing tremendously throughout the world due to rapid growth in world population. The world consumption of vegetable oil was 150 million tons during 2011–2012 and oil palm contributed a major share (33 %) of vegetable oil consumed worldwide (www.statista.com). Globally, oil palm (*Elaeis guineensis, Jaq*) is grown on approximately 15 million ha (UNEP 2010), mainly in tropical regions located within 10° north and 10° south of the equator (Goh 2000) with Malaysia and Indonesia occupying more than 85 % of the total area under oil palm plantation (www.worldgrowth.org). Being the major contributor in world vegetable oil supplies, palm oil production has increased tremendously mainly due to expansion in the area under oil palm plantation.

Over time, it is now well recognized that the possibility of bringing more area under oil palm plantation is poor due to the limited availability of suitable land as well as emerging environmental and biodiversity concerns. The only viable option to meet the growing need for vegetable oil is to increase yield per unit area, which seems a daunting challenge against the backdrop of yield stagnancy over the last 20 years (Ooi 2004). Yield stagnancy is due to different soil and plant factors, which need proper consideration for yield enhancement (Cristancho et al. 2011) More than 95 % of oil palm is grown in highly weathered soils having low pH and low cation retention capacity (Davies 1997; Mutert 1999). The majority of these soils (>43 %) belong to Ultisols and Oxisols which are characterized as low fertility soils (Richter and Babbar 1991; Sanchez and Logan 1992; Fageria and Stone 1999; Mutert 1999). Presently, inherently low fertile soils derived from granite and Pleistocene sediments and deep peat soils are being planted in oil palm expansion areas throughout Southeast Asia. Such soils are characterized by a deficiency of micro and macro nutrients, particularly sulfur (S) (Weil and Mughogho 2000).

Sulfur is an essential nutrient for plant growth due to its presence in proteins, glutathione, phytochelatins, thioredoxins, chloroplast membrane lipids, and certain coenzymes and vitamins (Takahashi et al. 2011). For many plants, S also has an important ecological role in defense against herbivores and pathogens (Falk et al. 2008).

Sulfur is very important for oil seed crops due to the higher requirements of oil seed crops than cereal crops; for example, cereals, legumes, and oil seed crops require 3–4, 8, and 12 kg S to produce one ton of seed, respectively (Jamal et al. 2010). Generally, oil seed crops need S in a quantity almost equal to P for high yield and good quality of oil (Jamal et al. 2010). It has been reported that different oil seed crops responded to S application and the role of S in oil synthesis is well documented (Pasricha and Aulakh 1991). In intensive crop rotations including oil seed crops, S uptake can be very high, especially when the crop residue is removed from the field along with the product (Jez 2008) which could lead to considerable S depletion in the soil if the corresponding amount of S is not applied through fertilizers. Now, areas of S deficiency are becoming widespread throughout the world due to the use of high-analysis fertilizers having less contamination of S, low S returns with farmyard manure, high-yielding varieties and intensive agriculture, declining use of S-containing fungicides, and reduced atmospheric input caused by strict emission regulation (Abrol and Ahmad 2003).

The S requirement of oil palms is almost equal to Mg but its role and requirement for oil palm is not studied considerably (Gerendas et al. 2009). In oil palm, major losses of S are attributed to nutrient export by fresh fruit bunches (FFB) and leaching of sulfate (Gerendas et al. 2009). Leaching losses are governed by soil texture (high losses in sandy soils) and water balance (high losses in high rainfall areas) (McGrath et al. 1996; Biswas et al. 2003). In oil palm plantations, urea has been the major source of nitrogen (N) for decades, which is creating an imbalance in the N:S ratio adversely affecting protein synthesis and oil production (Gerendas et al. 2009). Both N and S are essential components of proteins and availability of these in sufficient amounts is necessary for economic crop yield. Application of N at higher rates with a limited supply of S restricted protein synthesis and the oilseed yield of rapeseed (Janzen and Bettany 1984). Similar reports are common in S-deficient soils where N fertilizers are applied (Brennan and Bolland 2008). Decreases in the yield of rapeseed had been recorded with application of N in S-deficient soils without application of S (Malhi and Gill 2007). In fact, as early as the 1980s several publications already addressed the issue and predicted more widespread occurrence of S deficiency, as the trend towards using fertilizers low in S and increasing yields continues (Sumbak et al. 1983; Ng et al. 1988). Keeping in view the importance of S in increasing quality and quantity of oil and limited use of S in oil palm, we have reviewed the S status of tropical soils, the role of S in oilseed crops, particularly oil palm, occurrence of S deficiency, and different management strategies to address S deficiency in oil palm to enhance the yield and quality of palm oil.

2 Sulfur in the Soils

Sulfur is the tenth most abundant element in the universe and thirteenth most abundant in the Earth's crust; its average concentration in the Earth's crust ranges between 0.06 and 0.15 % (Stevenson 1986). The sulfur status of agricultural mineral soils is variable and may range from <20 mg kg^{-1} in sandy soils to >600 mg kg^{-1} in heavy textured soils, whereas organic soils may contain up to 0.5 % S (Tabatabai 1984). Sulfur in the soils exists in organic and inorganic forms and the major fraction (>90 %) of total S in the soil exists in organic form in the humus and recent crop residues (Freney 1986). In the humus, S is present as organic sulfates in the form of sulfate esters, thioglucosides, and sulfamates (Tabatabai 1984). This form of organic S is easily mineralized and thus considered to be a labile form of organic S and constitutes between 30 and 70 % of total organic S (Stanko-Golden and Fitzgerald 1991). The remaining organic S in the soils is directly linked with carbon in the form of amino acids, sulfonic acids, and complex hetrocyclic compounds (Schoenau et al. 2008). Inorganic S is generally present as pyrite (FeS_2), other metal sulfides, gypsum ($CaSO_4{\cdot}2H_2O$), elemental S, and SO_4^{2-} (Zhao et al. 1996). The soils of tropical regions are diversified due to great variation in the age and characters of parent material (Blair et al. 1980). In tropical regions, such as Malaysia and other oil palm-growing countries, >50 % soils belong to Oxisols, Ultisols, and Entisols (Davies 1997). These soils are characterized by intensive weathering and thus contain high contents of hyro-oxides of Fe and Al. These soils contain high amounts of 1:1 type silicate clays (kaolinite and halloysite) having low cation exchange capacity and abundance of oxides (Davies 1997). As these soils are formed under high rainfall conditions, most of the basic cations (Ca, Mg, K, Na) are removed from the soil profile due to leaching and thus such soils are characterized by low pH (Davies 1997). Generally, tropical soils are low in S due to low content in the parent material, low organic matter, and leaching losses (Olson and Engelstad 1972 ; Rego et al. 2007). The average content of S in tropical soils was reported to be 106 mg kg^{-1}, which is well below the S content in temperate soils (Jordan and Reinsenaur 1957). The typical range of S in agricultural soils of humid and semi-humid regions is 0.01–0.05 % (Stevenson 1986).

3 Sources of Sulfur in Soils

3.1 Natural Emissions

Sulfur originates in the environment, both from natural as well as anthropogenic sources (Haneklaus et al. 2003; Song et al. 2009). The major sources of S are natural biogenic sources contributing the major share of total S in the environment (Gui-Peng et al. 1996; Watts 2000). Biomass burning of plants is an important source of the natural emission of S into the atmosphere in tropical areas. Plant material contains about 0.25 % S on a dry matter basis and 50 % of the total S is released on burning, whereas the rest of S remains in the ash (Maynard et al. 1986; Smith et al. 2001). Oceans are the other major natural source of S in the troposphere and the major contribution is from sea-spray. Sulfur deposition from seawater is more near the coast and decreases when moving away from the coast (Delmas and Servant 1988). Dimethylsulfide [$(CH_3)_2S$ or DMS] is another source of S, which is generated due to the decomposition of dimethylsulfoniopropionate (DMSP) from dying phytoplankton cells in the shallow levels of the ocean (Quinn and Bates 2011; Delmas and Servant 1988). Sulfur is also released to the atmosphere directly from living plants in the form of carbon disulfide (CS_2) (Haines 1991; Watts 2000). But this has a very short residence time in the atmosphere and is redeposited in the sea. Volcanic emissions and man-made pollution are other potential sources of S compounds in the intertropical zones (Carn and Bluth 2003). A survey of about 100 sites in the United States of America and Canada showed deposition of 0.5–10 kg S ha^{-1} annually from atmospheric sources (Tabatabai 1984). Sulfur from the soil is released into the atmosphere in the form of hydrogen sulfide, organic sulfides, or as sulfur dioxide, which oxidize into sulfuric acid and are deposited on the soil by precipitation (Delmas and Servant 1988).

3.2 Parent Material

The parent material is another major source of S in all types of soils and it ranges between 0.026 and 1.0 %. Different types of parent materials contain varying amounts of S following the increasing trend in igneous rocks < metamorphic rocks < magmatic rocks ≪ limestone < sedimentary rocks (sulphides) < shales < sedimentary rocks (sulphates) ≪ coal (Bowen 1966; Friend 1973). The different of types of primary and secondary minerals bearing S are present in the soil, but major S-bearing minerals include gypsum, anhydrite, epsomite, mirbilite, pyrite, and marcasite. Generally, silicate minerals contain less than 0.01 % S (Tisdale et al. 1993). Igneous rocks, such as pyrite (FeS_2) comprised the original pool of S on Earth. Owing to the S cycle, the amount of mobile S has been continuously increasing through volcanic activity as well as weathering of the crust in an oxygenated atmosphere. The majority of S is found in seawater or sedimentary rocks, especially pyrite-rich shales and evaporite rocks (anhydrite and baryte). These minerals on weathering release the S in SO_4^{2-} form, which is available to plants. Sulfate adsorbed on exchange sites and present in the soil solution represents an available pool to plants (Tisdale et al. 1993). In the atmosphere, S mainly comes as a spray or windblown S-rich dust (Reheis and Kihl 1995) that remains in the atmosphere only for a short time. Another major source of S includes the burning of coal and other fossil fuels.

4 Forms of S in Tropical Soils

Sulfur exists in different oxidation states ranging from a highly oxidized state +6 (SO_4^{2-}) to a highly reduced state −2 (H_2S) (Murphy 2009). Sulfur in tropical soils exists both in organic and inorganic forms, but the organic form is the dominant form of S in all the soils (Möller et al. 2002). Inorganic S in the soils can be divided into sulfate-S, sulfide–S, and other nonsulfate inorganic S, such as elemental S, thiosulfates, and sulfites (Landers et al. 1983; Barber 1995). Water-soluble and adsorbed inorganic SO_4^{2-}-S are dominant fractions of soil S in addition to organic S. Adsorbed inorganic S fraction (SO_4^{2-}) is generally associated with hydrous oxide of iron and aluminum (Harward and Reisenauer 1966) and is reported to be 16 % of total S in the soil (Nor 1981). The amount of inorganic S is generally less than that of organic S in most of the soils (Bohn et al. 2001). Sulfate S is the dominant form of inorganic S in soil solutions of well-drained aerated soils having neutral to alkaline pH (Schoenau and Germida 1992) but in acidic tropical soils, inorganic sulfate is adsorbed to surfaces of amorphous iron and aluminum oxides and hydroxides and positively charged sites of edges of clay minerals and humus functional groups (Williams 1975). Total S contents of tropical soils are much less than other soils due to low organic matter, high mineralization rate, adsorption, and leaching losses (Davies 1997). Organic S may constitute up to 98 % of total soil S, which is present in plant residues, animals, and soil microorganisms (Jamal et al. 2010). The amount of organic S in the soil generally varies with organic matter (Probert 1980). Organic S in the soils can be divided into two groups: one containing oxidized S, and the other containing reduced S (Stevenson 1986). For the organic S to become available for plants, it has to be mineralized by microorganisms by a relatively slow process and the amount of S mineralized by this process may be insufficient to meet crop requirements (Nor 1981). Analysis of soil samples from tropical forest soils indicated that a major fraction of soil S is present in organic form (Stanko-Golden and Fitzgerald 1991). Organic S is present in the form of ester sulfate–S, C-bonded S, and nonreducible organic S (Schoenau et al. 2008).

5 Sulfur Deficiencies in Soil

Sulfur deficiency is widespread in crops around the world in temperate and tropical soils as atmospheric and anthropogenic deposition of S into soils has decreased remarkably (Scherer 2001; Wilhelm Scherer 2009). Sulfur deficiency is quite common in the areas of intensive cropping involving oilseed crops due to higher S uptake by oilseed crops (Jamal et al. 2010). It has been reported that S deficiency is a common growth-limiting factor in acid soils and most crops responded positively to S application in soils, when available S was <10 mg kg^{-1} (Fageria and Baligar 2001). In the past, adequate S was added to fulfill crop requirements through the use of N and P fertilizers, such as ammonium sulfate and single superphosphate (Eriksen et al. 2004). Coal combustion in several industrial activities also contributed substantial amounts of S for plant needs by aerial deposition. However, in the recent past, a paradigm shift towards S deficiency in the agricultural system has been observed (Wilhelm Scherer 2009) due to the use of high analysis N and P fertilizers, which decreased incidental S addition to the soils. The situation is further aggravated with the introduction of high-yield crop varieties with increased nutrient mining, including S from soils (Scherer 2001). Generally, crops removed 15–25 kg S/ha and requirements for S are almost equal to P (Eriksen et al. 2004) but oil seed crops required more S than P for optimal yield and quality (FAN 2007). Sulfur deficiency is dependent on soil type, the crops grown on the soil, and the manuring history of field and organic matter in the soil (Johnson et al. 1979).

The major reasons for S deficiency in soils include use of high-analysis fertilizers having low S, the cultivation of high-yielding crop varieties, limited use of sulfur-containing pesticides and fungicides, and decreased emission of sulfur dioxide from industries (Blair 2002). Globally, the S deficit is 9.6 million tons annually, which is expected to reach 11.9 million tons by the year 2012 and the incidence of S deficiency is widespread in Asia (FAN 2007).

The soils of tropical regions are generally deficient in nutrients and S deficiency is widely reported (Cochrane et al. 1980; Weil and Mughogho 2000). In tropical regions, Oxisols and Ultisols are the dominant soil orders and such soils are generally deficient in S (Davies 1997; Buol and Eswaran 1999). Several researchers have reported that different crops responded to S application in Oxisols and Ultisols of tropical areas (Blair et al. 1980; Malavolta et al. 1987). The supply of S has been reported to increase the crop yields from a few percent to 1000 % in the United States and up to 280 % in Indonesia (Nor 1981).

5.1 Causes of S Deficiency in Tropical Soils

Different factors are responsible for S deficiency in tropical soils, including adsorption of SO_4^{2-} to the positive charge on the soils, leaching losses due to high rainfall, high mineralization rate, and low organic matter content in such soils (Buri et al. 2000).

5.1.1 Sulfur Adsorption

Adsorption is a key process controlling plant availability of S in acidic, highly weathered soils (Fox et al. 1986). Sulfate adsorption is controlled predominantly by pH and anion and cation concentration, in soil solution and the character of the colloidal surfaces present (Harward and Reisenauer 1966). Adsorption is not a simple exchange process and is affected by many other physical, chemical, and biological factors (Bohn et al. 2001). Sulfate is retained by soil constituents having an amphoteric nature like oxides of Al and Fe (Karltun et al. 2000; Biswas et al. 2003; Alves and Lavorenti 2004). The amorphous nature of Fe and Al minerals provides preferred sites for the adsorption of SO_4^{2-} (Parfitt and Smart 1978; Rajan 1979). Sulfate is adsorbed on goethite, kaolinite, and hydrous alumina by forming a six-member ring with two surface metal atoms (Rajan 1978; Rao and Sridharan 1984). Investigation on SO_4^{2-} adsorption in six different tropical soils of Malaysia indicated that adsorption of SO_4^{2-} increased in the soils with increasing SO_4^{2-} concentration in the soil solution and adsorption of SO_4^{2-} in tropical soils is controlled by high levels of hydrous oxides of Fe and Al, type of clay, and soil pH (Nor 1981). Sulfate in the soil solution has always been in equilibrium with the solid phase form (Mengel and Kirkby 2001) and adsorption of SO_4^{2-} is very strong under acidic conditions (Scherer 2001). Adsorption of SO_4^{2-} occurred with the number of edge adsorption sites of the silicate clay minerals, and generally SO_4^{2-} adsorption on silicate clays in acidic soils follows the order: kaolinite > illite > montmorillonite (Kparmwang et al. 2004). Such types of soils are common in tropical regions such as Malaysia and other oil palm growing countries and thus confronted with S deficiency due to high adsorption. More than 50 % of soils in tropical regions belong to Oxisols, Ultisols, and Entisols (Davies 1997), which are characterized by intensive weathering and thus contain a high content of oxides of Fe and Al and thus high SO_4^{2-} adsorption. Sulfate adsorption increases with decreasing pH and is always greater in soils with high iron and aluminum content (Biswas et al. 2003). With changing fertilizer practices towards the use of high-analysis fertilizer such as urea and triple superphosphate, sulfur deficiency could become a dominant limiting factor in crop productivity in tropical areas, particularly Malaysia (Nor 1981).

5.1.2 High Rainfall

Sulfur is lost in the tropical soils due to leaching as SO_4^{2-}. It is highly mobile in soils having low retention capacity (Biswas et al. 2003). Sulfur losses due to leaching are common in high rainfall areas (greater than 800 mm annual average) due to leaching of sulfate-S below the root zone (Edwards 1998). Leaching losses are common in uniform deep sands or in sandy topsoils with low capacity to adsorb SO_4^{2-} (Wilhelm Scherer 2009). Although soils of tropical regions carry a positive charge, these have very low anion retention capacity and thus leaching losses of anions particularly SO_4^{2-} are high. Leaching is affected by different soil factors, including clay content, content of Fe and Al oxides, and pH. Leaching losses of SO_4^{2-} are more common in sandy soils as compared to heavy textured soils (Scherer 2001) due to lower SO_4^{2-} adsorption and/or less charged sites in sandy soils and a higher downward water movement (Eriksen and Thorup-Kristensen 2002).

5.1.3 Mineralization Rate

Organic S formation is known to be a biotic process that is time, temperature, and moisture dependent (Fitzgerald et al. 1983; Strickland et al. 1986). Generally, it seems that tropical climates may favor mineralization of S. This may be the reason why some claim that tropical soils usually contain lower levels of total S than non-tropical soils, due to the high mineralization rate of the organic forms (Nor 1981; Itanna 2005). In an incubation study of two months, tropical soils of Malaysia released 20–150 mg kg^{-1} SO_4^{2-} compared to <20 mg kg^{-1} released from temperate soils of Iowa (United States; Nor 1981). He concluded that an average of 16 % of total mineralized S is adsorbed due to the coarse texture of the soils and the rest may be present in soil solution, which could be due to the low organic matter content, lower exchange capacities, and high rainfall in the humid tropics (McCune 1981).

6 Sulfur in Plants

Sulfur is an essential macro nutrient for plant growth as it is the constituent of cysteine, and methionine, which ultimately constitute proteins (Leustek et al. 2000; Mengel and Kirkby 2001). Sulfur is a structural component of many coenzymes, glutathione, phytochelatins, thioredoxins, and chloroplast membrane lipids, and it may act as a functional group involved in many metabolic reactions (Falk et al. 2008; Jez 2008). Sulfur increases chlorophyll formation and photosynthesis, activates various enzymes, and forms nucleic acids and vitamins such as biotin and thiamine. In fruit crops, it is known to increase the ascorbic acid content in the fruit as well as the total soluble solids. Sulfur plays a very important role in the defense system of plants against herbivores and pathogens (Williams and Cooper 2003; Falk et al. 2008). It is an essential component of different defense compounds, including antimicrobial peptides called defensins and thionins and glucosinolate (Broekaert et al. 1995; Dubuis et al. 2005; Falk et al. 2008). Sulfur is known to decrease leaf spot caused by Pyrenopeziza in oilseed rape and stem canker caused by *Rhizoctonia solani* in potato (Haneklaus et al. 2007). The role of S against diseases in perennial plants of tropical regions is not well investigated. However, S accumulation in the xylem of cocoa plants has been reported in response to infection with *Verticillium dahliae* (Cooper and Williams 2004). Elemental S is toxic to some fungal pathogens and may be considered to be a phytoalexin in its own right (Resende et al. 1996). Glucosinolates are another group of compounds involved in plant defense mechanisms and their concentration is increased due to S application (Zhao et al. 1997; Egesel et al. 2009).

6.1 Sulfur Absorption and Content in Plants

Plants absorb S from the soil in the form of SO_4^{2-} through the roots or as sulfur dioxide (SO_2) and hydrogen sulfide (H_2S) directly from the atmosphere (Blake-Kalff et al. 1998; Dubuis et al. 2005). After absorption of S as SO_4^{2-}, its assimilation in plants can follow two pathways: assimilation as sulfate, which is known as sulfation, and reduction of SO_4^{2-} into sulfide which is the substrate for cysteine synthesis (Varin et al. 1997). Root plastids contain SO_4^{2-} reduction enzymes but mainly reduction of SO_4^{2-} to sulfide and its subsequent incorporation into cysteine takes place in the chloroplast in the shoots. Different S containing biomolecules in the plants have crucial roles in various metabolic reactions including redox reactions, detoxification of metals and xenobiotics, and metabolism of secondary metabolites (Saito 2000; Nikiforova et al. 2003). Cysteine contains reduced S, which serves as a donor for most of the other organic sulfur compounds in plants. Sulfur contents in the plants vary depending on the species ranging from 0.1 to 0.6 % of the dry weight (De Kok et al. 2002) but some scientists have reported the S contents as low as 0.05 % to as high as 0.9 % (Generally, S concentrations in plant parts follow the order: grains > shoots > roots and these differences are wider in the case of crucifers as compared to legume crops.

6.2 Role of Sulfur in Oil Seed Crops

Sulfur plays an important role in biosynthesis of oil in oilseed crops as it promotes the formation of saturated fatty acids and is an essential component of oil storage organs (Chandel et al. 2003; Raja et al. 2007). The oilseed crops have three times more S requirement than that of cereals and such plants store S as organic S rather than SO_4^{2-}-S, which necessitates the relationship between S supply and oil content (Aulakh and Pasricha 1988). For example, the amount of S required to produce one ton of seed is about 3–4 kg S for cereals, 8 kg S for legume crops, and 12 kg S for

Table 1 Effect of S on seed yield and oil content of different oilseed crops

Crop	Increase over control (%)		Rate of S (kg ha^{-1})	References	Experiment
	Seed yield	Oil content			
Canola	34	13	60	Mansoori (2012)	Field
Rapeseed	05	—	40	Khalid et al. (2009)	Field experiment
Sunflower	45	7	60	Hussain and Tarance (2010)	Field experiment
Sesame	42	34	60	Raja et al. (2007)	Field experiment
		—			
Oilseed rape	6	1	80	Asare and Scarisbrick (1995)	Field
Soybean	24	5	40	Farhad et al. (2010)	Field

Tandon and Messick (2002), Aulakh and Pasricha (1988), Tiwari et al. (2002)

oil crops (Jamal et al. 2010). Each kilogram of S applied can increase oil content by 3.0–3.5 kg, which emphasizes the importance of S as a key factor in oil production (Jez 2008). Several researchers have recorded a significant increase in seed yield and oil content of different oilseed crops due to S application (Tandon and Messick 2002; Aulakh 2003; Chandel et al. 2003). The higher oil yield is due to higher seed yield caused by proper partitioning of photosynthates from source to sink due to S application (Tisdale et al. 1993). Increase in oil yield due to S application has been reported in sunflower and groundnut (Tandon and Messick 2002), in rapeseed-mustard (Chandel et al. 2003), in canola (Mansoori 2012; Sattar et al. 2011), and in sesame (Raja et al. 2007). The effect of S on increase in seed yield and oil content of different oilseed crops is presented in Table 1.

7 Sulfur Nutrition and Production of Palm Oil

The oil palm is native to West Africa but now is being grown commercially in 43 countries including Indonesia, Malaysia, Thailand, and Nigeria as major oil palm growing countries. Oil palm is mainly grown in tropical regions of world with Indonesia and Malaysia having a major share in global area under cultivation, producing 85 % of global palm oil and contributing about 94 % in world palm oil exports (Donough et al. 2009). Malaysia was the largest palm oil producer until 2000, when Indonesia took over as the largest producer of palm oil mainly due to expansion in area under oil palm plantation. Palm oil production has experienced unprecedented growth (>300 %) during the period from 1985 to 2008 but expansion in area under oil palm cultivation is the major contributing factor to this growth, and yield per unit area remains stagnant (Murphy 2009). The role of S in oil palm is not widely investigated with regard to its effect on growth and oil production.

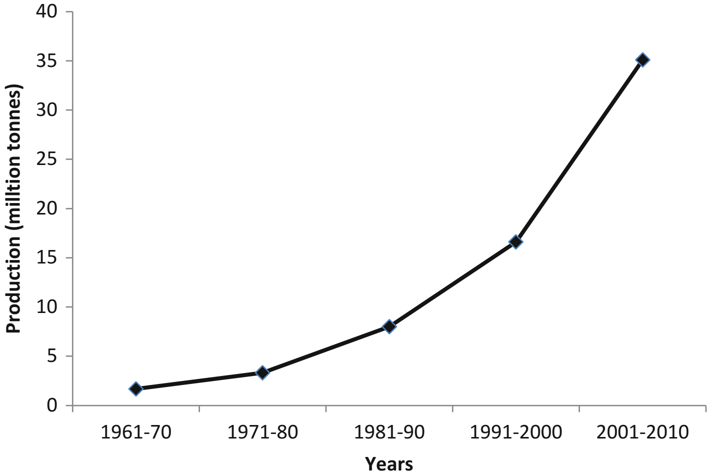

Fig. 1 Historical perspective of global palm oil production (http://faostat3.fao.org/home/index.html#DOWNLOAD)

Sulfur plays important functions in plant metabolism in general and in oil synthesis particularly in oilseed crops and a strong response of oil-producing crops to S supply has been reported (Pasricha and Aulakh 1991). Sulfur is a structural element of coenzymes required for the formation of long-chain fatty acids and thus for the synthesis of mesocarp and kernel oil in oil palm and increased growth of oil palm seedlings). Global area and production of oil palm increased tremendously since 1970 particularly in the Southeast Asian countries of Indonesia and Malaysia (Donough et al. 2009). The potential productivity of oil palm is several times greater than that of other oil-producing crops and much less land is required to produce the equivalent amount of oil produced by other oil-producing crops. Globally, palm oil production has increased tremendously from 1.47 million tons in 1961 to 43.57 million tons in 2010 (Fig. 1). The maximum reported oil yield is 8 tons/ha with an average yield of 6 tons/ha against the estimated commercial potential of 10 to 11 tons/ha (Fairhurst and Haerdter 2003; Donough et al. 2009).

8 Sulfur Status and Deficiency in Oil Palm

Oil palm requires S in an amount equal to the amount of Ca and Mg (Gerendas et al. 2009). Several researchers have reported different ranges of S concentration in the oil palm and frond 17 is considered to be representative for the study of concentration of different nutrients and physiological parameters (Gerendas et al. 2009). The critical concentration of S in frond 17 was found to be 0.2 % with average value ranging between 0.17 and 0.36 % (Ng et al. 1988; Fairhurst and Haerdter 2003), whereas the reported optimum range is between 0.20 and 0.23 % in frond 17

(Ollagnier and Ochs 1972). More recently, Gerendas et al. (2009) observed a very low concentration of S (0.12–0.13 %) in frond 17 of oil palm and concluded that if S concentration in frond 17 was found to be less than 0.15 %, then S should immediately be applied to avoid any significant loss of yield. Sulfur deficiency is most likely to occur where plantations are located far from S emission points (i.e., industrial and coastal zones). Sulfur deficiency in early growth stages of oil palm resembles N deficiency, which leads to stunted and pale-colored pinnae. Severe S deficiency causes brown necrotic spots on leaves and increased incidence of Cercospora disease (Calvez et al. 1976). Incidence of the disease due to S deficiency is widespread in young palms grown on poorly drained soils, with low soil organic matter, and formerly covered by savannah vegetation (Calvez et al. 1976).

9 Assessment of S Requirements of Oil Palm

The fertilizer requirement of oil palm is affected by different factors including planting material, target yield, soil type, and, most important, environmental conditions (Foster 2003). The most common way to assess the fertilizer requirement of oil palm is through fertilizer response trials but practically it is a difficult task to conduct such trials on vast areas where oil palm is being grown. Alternatively, other methods could be used for assessment of nutrient requirements, which are based on the principle of soil fertility and plant nutrition. These methods include soil analysis, leaf analysis, and nutrient balance approach or a combination of these methods.

9.1 Soil Analysis

This includes the use of physical, chemical, and mineralogical properties of soil to group different types of soils and their potential to supply nutrients to oil palm (Hew and Ng 1968). This approach is based on soil analysis and nutrient balance and also on the concept that the soil can continuously supply a proportion of nutrients to the palms with negligible depletion of soil nutrients and nutrients which are assumed to be replenished due to soil weathering and biological activity (Foster et al. 1988). In addition to these considerations, fertilizer rate is determined by palm age, soil type, terrain, soil moisture status, and expected nutrient loss. This is a subjective approach and those who use this approach always take help from field response trials. It usually falls back to fertilizer response trials and experience for further guidance and in general, not used in the first instance to decide on fertilizer rates in an existing plantation (Corley and Tinker 2008). Due to variation in fertility status among the soil types and the area within oil palm plantations and sampling error, this approach is relatively unreliable and interpretation of the soil analysis for fertilizer recommendations is a difficult task (Foster and Chang 1977; Law and Tan 1977; Goh et al. 1995).

9.2 Leaf Analysis

Leaf analysis is the most commonly used method to assess nutritional status of oil palm plantations and to recommend appropriate fertilizer rates (Gerendas et al. 2009). Although leaf analysis is an entirely empirical system (Foster 2003) it is commonly used due to the significant relationship between leaf nutrient concentration and fresh fruit bunch yields for oil palm (Foster and Chang 1977). The major problem of using leaf analysis data for fertilizer recommendation is the variation in optimum concentration of nutrient, which changes with soil types, terrain, palm age, climate, season, frond age, sampling methods, and so on (Teoh and Chew 1987; Foster 2003). To overcome this difficulty, the leaf sampling method, the choice of frond, sampling unit, choice of palms, and time of sampling have been standardized. Different researchers have developed various interpretation methods for using leaf analysis as a basis for fertilizer recommendations. These include single nutrient critical level, nutrient ratios, DRIS, and total S.

9.3 Nutrient Balance Approach

This method is based on balancing the nutrient demand of plants with the nutrient supply to the plants. In the oil palm agro-ecosystem, nutrient demand includes nutrient uptake for growth and production, nutrient losses through soil processes such as runoff and leaching (environmental losses), and nutrient immobilization. The nutrient supply includes precipitation, pruned fronds, and applied by-products, such as empty fruit bunches. Any shortfall between nutrient supply and demand is met by fertilizer input. Plant nutrient demand is the requirement for essential elements by a growing plant (Corley and Tinker 2008). It can be separated into two processes: growth demand and deficiency demand (Tinker and Nye 2000).

10 Fertility Management and S Nutrition of Oil Palm

Adequate nutrition is essential during the growth and development stages of the oil palm because nutrient uptake establishes the plant's production potential. The nutrient requirement of oil palm depends on target yield, palm spacing, palm age, soil type, type of planting material, ground cover, and climatic and other environmental conditions. Nutrients in oil palm plantations are generally removed/depleted because of (1) harvesting of fresh fruit bunches, (2) pruning fronds and male inflorescences, and (3) nutrients immobilized in the palm biomass. To avoid fertility depletion of the soil, removed nutrients should be recycled by returning the empty fruit bunches to the soil and by applying suitable fertilizers (Tinker 1976). For good yields to be sustained, fertilizer inputs are necessary and typically constitute 40–50 % of the total field upkeep cost. The S losses from soils under oil palm plantation is through fresh fruit bunches and leaching of SO_4^{2-} (Gerendas et al. 2009). Among various nutrients required for realizing economical yield of oil palm plantations, S is an important nutrient that received little attention in different nutrient management programs of oil palm plantations. Oil palm is dominantly grown in Oxisols and Ultisols, which are highly weathered soils with a very poor inherent fertility level, very low pH, and very low ion retention capacity. Consequently, fertilizers are essential for economic production as attested by ample field experiments and growth in fertilizer usage in the oil palm sector (Goh et al. 1995). Different reasons could be assigned to this poor performance of oil palm in terms of yield per unit area, but imbalanced fertilizer use is the most important. Sulfur is a neglected nutrient in oil palm nutrient management due to the use of N fertilizers containing S. In addition, soil organic matter, organic fertilizers, S deposition from natural (volcanic eruption, fires) and man-made resources (industrial pollution), and groundwater contribute to the S availability to a crop (Pasricha and Fox 1993). Traditionally, the use of urea as a source of N in oil palm plantations, dolomite in place of kieserite ($MgSO_4{\cdot}H_2O$), limited use of other S-containing fertilizers, and controlled burning of forests has further escalated the situation. All these practices resulted in a decrease in incidental input of S to oil palm plantations (Gerendas et al. 2009). Due to the limited possibilities of expanding the area under oil palm plantation, the growing requirement of vegetable oil and oil palm as a major contributor in global vegetable oil supplies, it is of utmost importance to enhance the yield per unit area of oil palm. Sulfur fertilization of oil palm could be a promising approach to enhance yield per unit area due to the well-established role of S in oil synthesis in the case of other oil seed crops (Jez 2008). Different approaches can be used for S management of oil palm plantations which could include (1) crop residue management, (2) fertilizer management, and (3) use of animal manures.

11 Sulfur Management Strategies for Oil Palm

11.1 Crop Residue Management

Sulfur status of the soils is influenced by the type of crop grown (annual or perennial) and its S requirements. The net amount of S required is normally determined by counting S input and S loss from the soil in the form of plant products and crop residues (Blair et al. 1980). Plant removal of S depends on the rooting system of plants. Deep-rooted plants can absorb the S from deeper layers, where it is deposited through leaching. In the case of oil palm, 20 kg ha^{-1} S is removed in palm oil and oil palm cannot absorb the S from deeper layers as it has a shallow root system that cannot penetrate into deeper layers. In addition to this a considerable amount of S is also removed in empty fruit bunches. Burning of plant materials leads to considerable loss of S from the soils. About 0.05–0.25 kg S ha^{-1} is added through ash, which may be subjected to losses due to leaching in the rainy season if not adsorbed or taken up by the plants (Bromfield 1974; Singh et al. 2005). A proper return of crop residues, particularly empty fruit bunches, would be helpful for the S fertility status of soil under oil palm plantation.

11.2 Fertilizer Management

Sulfur addition through chemical fertilizers remains the most important input of S to the soils. Historically, S was added as a secondary component of fertilizers such as ammonium sulphate, single superphosphate, potassium sulfate, or compound fertilizers of NPK. But during the last few decades, the use of such fertilizers containing S as a secondary element has decreased significantly. Concurrently, use of non-S–containing phosphatic and nitrogenous fertilizers has increased. As adsorbed SO_4^{2-} in tropical soils is the major S source for the plants (Nor 1981), application of fertilizers containing phosphate and nitrates could aggravate the S problem by replacing adsorbed SO_4^{2-} into the soil solution (Barrow 1969; Alves and Lavorenti 2004), which may be subjected to leaching due to high rainfall.

11.3 Use of Animal Manures

Globally, S excreted from domestic animals is estimated to be around 8 million tonnes per annum, which is equal to 80 % of fertilizers S used worldwide annually (Eriksen 2004). Sulfur content of animal manures is variable depending upon the age of the animal and type feed given to animals which could be a very good input of S to the soils. Use of animal manures must be included in fertility management programs of oil palm plantations to reduce the chances of S deficiency.

12 Summary and Future Prospect

Oil palm contributed more than 85 % of the global vegetable oil supply which necessitates its importance as a major contributor to fulfill human nutritional requirements. The role of S in synthesis of oil is well established, but S nutrition of oil palm remained neglected for the different reasons already elaborated. This situation is further aggravated due to poor fertility status, particularly S of the highly weathered soils of Oxisol and Ultisol soil orders in the areas under oil palm plantation. With very bleak chances of bringing more area under oil palm plantation, it is pertinent to enhance the yield of palm oil per unit area by adopting different soil and plant management strategies. Use of S fertilizers, inclusion of animal manures in fertility management of oil palm plantations, return of crop residues such as empty fruit bunches and waste of palm oil mills should be promoted to decrease the chances of S deficiency and enhancing the yield per unit area of oil palm plantation. In addition to this existence of genetic variation among different oil palm progenies for efficient utilization of S should be used to select such progenies that have high S utilization efficiency and give economical yield under low S conditions. As interaction of S with N is very important, application of nitrogenous fertilizers without considering S status of soils is creating an imbalance in the N:S ratio which is very important in oil synthesis. Nitrogenous fertilizers should be applied while considering S status of soil and plants to maintain the required N:S ratio in plant tissues for economical oil yield. Management of S fertilizer sources should consider both the short- and long-term impacts on crop yield, seed quality, and economics of production. Soil testing to determine the requirements for S fertilizer is challenging due to the spatial and temporal variability in sulfate availability. Improved assessment of S availability needs to consider both the release of S from organic matter and the site-specific distribution of sulfate across the landscape.

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Genetic Modification of Crop Plants: Issues and Challenges

Faheema Khan and Khalid Rehman Hakeem

Abstract The growing area of genetically modified (GM) crops has significantly expanded since they were first commercialized in 1996. Currently 400 million acres of the fertile land worldwide are used to cultivate genetic engineering (GE) crops such as rice, corn, cotton, and soybeans. Genetically modified crops are increasingly gaining acceptance and their adoption has brought huge economic and environmental benefits. In the past 17 years, these achievements have been primarily supported by two simple traits of herbicide tolerant and insect resistant crops. Concurrently GM crops generated intense consumer debate in many parts of the world. The issues under debate include the costs and benefits of the GM crops and the inherent safety concerns. It is widely claimed, however, that biotechnology, particularly genetically engineered food offers dramatic promise for meeting some of the twenty-first century's greatest challenges; as do all new technologies, it also poses certain apprehensions and risks, both known and unknown. The introduction of *Bacillus thuringiensis* (Bt) genes into the plants has raised issues related to its risk assessment and biosafety. The chapter presents an overview of the production of GM crops, their adequacy, detection strategies, biosafety issues, and potential impact on society. Furthermore, the future prospects of the GM crops are also highlighted.

Keywords GM crops • *Bacillus thuringiensis* • Biotechnology • Crop resistance

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1 Introduction

In the present scenario of a growing population, global warming and diminishing biodiversity have a remarkable influence on our environment. The world population has increased by 2.3 billion people in the past 40 years (Hakeem et al. 2012). It is likely by the year 2050, there will be 9.3 billion people living on Earth and 50 years in the future the world population is expected to surge by three billion. The biggest challenge is to feed this enormous number which leads to extensive modifications in the production, dispersal, and constancy of crop yield. Inopportunely, the cultivable land and population are not equivalently dispersed. The main factors are decreasing cropland due to soil erosion, water scarcity, fewer renewable resources, and insufficient manpower. Moreover, the devastation of wilderness, afforestation, and constant usage of fuel resources have immensely increased carbon dioxide levels, resulting in global warming. Based on numerous studies covering an extensive range of regions and crops, it has been reported that negative impacts of climate change on crop production have been more common than positive impacts; moreover, global climate change at rates slower than the current anthropogenic climate change caused significant ecosystem shifts and species extinctions during the past millions of years. Change in climate can drastically modify rainfall patterns and consequently require the relocation of people and changes in agricultural and production practices. Conventionally agriculture production has been supported by technological advancement, mostly in the field of genetic crop improvement. For several years, the agriculture industry has been searching and exploiting the genetic traits of seeds in search of healthy and productive varieties. There are several ways that can enhance agricultural productivity in a sustainable way, including the use of fertilizers, improved pest control, soil conservation, and by selecting better plant seeds, produced by both traditional and biotechnological means. Among these methods, biotechnological applications, particularly production of transgenic plant varieties and future functional genomic projects, possibly hold the potential to extend agricultural productivity when suitably incorporated into conventional methods. Genetically modified seeds are a major step in advancing the agricultural production.

Genetically modified organisms (GMOs) are the ones in which the genomic material, DNA (deoxyribonucleic acid), has been transferred from a bacterium or a plant, or even an animal, into a different plant species to obtain the desired and improved quality. Genetic engineering modifies the genetic material of crops to display specific traits (Fernandez-Cornejo and Caswell 2006). This technology is often recognized as "recombinant DNA technology" or "genetic engineering" and the resultant organism is said to be "genetically engineered," "genetically modified," or "transgenic." Presently GM products include foods and food ingredients, feeds and fiber, medicines, and vaccines. Although it is extensively claimed that biotechnology, mainly genetically engineered crops offers strong promise for meeting some of the twenty-first century's utmost challenges, it also poses certain risks and apprehensions both known and unknown. It is, therefore, paramount in this perspective, to know the basic procedures involved in genetic modification for suitable appreciation of the related issues and challenges.

1.1 Genetic Engineering: The Technique

All living entities from plants, animals, and human beings are made up of cells. The nucleus comprises a unique set of information concerning their size, shapes, and qualities. These instructions are found on a DNA fragment, which is divided into sections called genes. The sequence of genes on DNA determines the characteristics of an organism. The complete set of genetic material of an organism is known as the genome. The method of isolating genes from the genome of one organism and inserting them into the genome of another organism in order to modify it for the desired trait is known as genetic engineering (Vert et al. 2012). Plants, animals, or microorganisms that have transformed through genetic engineering are termed genetically modified organisms. The modified organism carries the new genes to its progeny. The methodology is now in practice to produce GM plants of desired growth and quality. The main purpose is to produce the varieties with high yield, disease/pest resistance, and other such assets for better durability and market value. This process is different from modifying crop plants through customary mutation breeding or selective breeding by farming activities (Kavitha et al. 2007). By the year 2012, the most successful GM plant has gene transformation that provides defense against herbicides and insects (James 2012). Gene isolation is carried out by using restriction enzymes to cut the DNA into small fragments followed by gel electrophoresis to separate them out according to their length and size (Alberts et al. 2002). A polymerase chain reaction (PCR) is used to amplify gene segments, which can then be isolated through gel electrophoresis (Kaufman and Nixon 1996). If the selected gene or the donor organism's genome has been studied, it may possibly be available in a genetic library, but if the DNA sequence is unknown, it can be synthesized artificially (Liang et al. 2013). In order to work properly the selected gene to be inserted into the genetically modified organism must be combined with other genetic elements. The gene can also be altered at this stage for effectiveness and better expression; for this the constructs contain a promoter and terminator region as well as a selectable marker gene. The promoter region initiates transcription of the gene and can be used to regulate the site and level of gene expression, whereas the terminator region finishes transcription. The constructs are prepared using recombinant DNA techniques, such as restriction digestion, ligations, and molecular cloning (Berg and Mertz 2010).

1.2 Genetically Modified Crops

The first genetically modified crop was produced in 1982, utilizing the antibiotic-resistant tobacco plant (Fraley 1983). In 1986 the first trial of genetically modified plants occurred in the fields of the United States and France, where tobacco plants were engineered for resistance against herbicides (James 1996). In 1987, Plant Genetic Systems (Ghent, Belgium), established by Marc Van Montagu and Jeff Schell, was the pioneer company to grow genetically modified tobacco plants with insect resistance by expressing genes encoding for insecticidal proteins from *Bacillus thuringiensis* (Bt; Vaeck 1987). In 1992, China was the first country to allow commercialized transgenic plants (virus-resistant tobacco; James 1997) which was later withdrawn from the market in 1997 (Conner et al. 2003). The first genetically modified crop permitted for sale in the United States, in 1994, was the tomato called FlavrSavr which is modified to ripen without softening by a California company, Calgene (Bruening and Lyons 2000). In 1994, the European Union allowed the tobacco plant engineered to be herbicide resistant, bromoxynil, making it the first commercial genetically modified crop in the European market (MacKenzie 1994). In 1995, Bt Potato was approved safe by the Environmental Protection Agency, making it the first pesticide-producing crop to be permitted in the United States (USDA 2000).

In 2012, more than 420 million acres of GE crops were cultivated in 28 countries contributing approximately 10 % of global cropland (ISAA 2012). Several food crops have been modified to increase production and durability; the examples are cotton, sugarcane, tomatoes, soybean, Hawaiian papaya, potatoes, rice, rapeseed, sugar beet, field corn, and sweet corn. Plant geneticists are also investigating other crops they expect will be beneficial for the commercial industry, such as oil-producing plants for cosmetics, crops with traits to provide nutritional fortification, and even crops that produce pharmaceutical drugs (Fernandez-Cornejo 2006). The major transgenic crop-producing countries are the United States, Canada, India, South Africa, China, Argentina, and Brazil. Most genetically engineered crops are transformed to be either herbicide tolerant, to destroy weeds without damaging crops, or insect resistant, to shield plants from harmful pests. After nearly 20 years, only one high-yield GE seed has been considered for approval (USDA 2013).

2 Benefits of Genetically Modified Food

2.1 Increased Crop Yields

It is widely expected by those in crop production that genetically engineered seeds will increase the yields of farmers who implement the technology in the fields. Although there is not much research available regarding the impact of genetic engineering in increasing crop production, available research supports these expectations. In 1997, the Economic Research Service (ERS) found a statistically significant association between improved crop yields and increased adoption of pesticide and herbicide resistant crop seeds (ERS 2000). The ERS study also reported that crop yields significantly increased when farmers adopted herbicide-tolerant cotton and Bt cotton. Another study performed by Iowa State University (USA) reported Bt crops had higher yield over non-Bt crops. The university studied 377 cultivated fields and calculated that crops grown from GM seeds yielded 160.4 bushels of Bt corn per field, whereas crops grown from non-GM seeds yielded 147.7 per field.

2.2 *Herbicide Tolerant and Pest Resistant Crops*

Eradicating weeds in physical ways such as tilling is not cost effective. To destroy weeds, farmers often spray large quantities of different herbicides, which are an expensive and laborious process involving caution so the herbicide doesn't harm the crops and environment. Herbicide-tolerant crops are aimed to resist specific herbicides. Herbicides are designed to work with particular herbicide-tolerant seeds that can kill weeds without causing any detrimental effect on genetically engineered crops. Most of these crops are resistant to the herbicide glyphosate commercially sold as Roundup (manufactured by the agrichemical company Monsanto) (Fernandez-Cornejo 2004a, b). In 2012, Monsanto's Roundup was present in 86 % of the US GE cotton market and 98 % of the US GE corn market. Monsanto has created a genetically modified soybean strain that is unaffected by their herbicide product Roundup. Farmers cultivate these soybeans, which then only require one application of herbicides instead of several applications, dropping production cost and minimizing the hazards of agricultural waste (USDA 2013). Other known herbicide resistant crops include Calgene's BXN cotton and Bayer's Liberty Link corn (USDA, ERS 2013a, b). Crop losses from insects and pests can be surprising, causing an immense economic loss for farmers and food shortages in developing countries. To overcome this loss farmers annually apply several tons of chemical pesticides. Due to the potential health hazards of pesticides, consumers hesitate to eat food that has been treated with chemicals, also agronomic wastes from extreme use of pesticides and fertilizers can contaminate the water supply and cause detrimental effects to the environment. Growing genetically modified crops such as Bt corn can reduce the application of chemical pesticides and reduce the cost of crop production (US Patent 6313378 2001). The *Bacillus thuringiensis* soil bacterium gene is designed to resist the European corn borer and numerous cotton bollworms (Fernandez-Cornejo 2004a, b). An entomologist from the University of Missouri found that corn rootworms could pass on Bt resistance to their offspring. University of Arizona scientists found that within seven years of Bt cotton introduction, cotton bollworms developed Bt resistance which they later passed on to offspring, signifying that the resistance was dominant and could evolve quickly.

2.3 *Disease Resistance*

There are many microorganisms and entities such as bacteria, fungi, and viruses that cause plant diseases. Researchers are working on several projects to construct genetically modified plants that show resistance to these diseases (Dahleen 2001). Fungi cause a range of severe plant diseases such as grey mould, blight, powdery mildew, and downy mildew. Fungal plant diseases are generally coped with by the use of chemical fungicides. Moreover, combating yield losses and avoiding fungal infection saves crops from various mycotoxins produced by pathogenic fungi. Mycotoxins can affect the immune system and interrupt the hormone balance; a few of them are also carcinogenic. Genetic engineering facilitates novel means of managing fungal infections by transferring genes from other bacteria or plants encoding enzymes such as glucanase or chitinase. These enzymes further break down glucan and chitin, which are vital constituents of fungal cell walls. Some other approaches include provoking a hypersensitive response. The spread of most viruses is very difficult to control. Once the infection is established, no chemical treatment or methods are available to stop the same. Genetic engineering can also be used to develop virus resistant plants. The most common method to exploit this technique is by inserting a plant with a viral gene encoding the virus coat protein. The plant can then produce this viral protein before the virus infects the plant. Papaya ring spot potyvirus is a severe viral disease of papaya, which inhibits photosynthesis in plants and stunts growth. Genetic engineering proved to be successful in producing virus resistant GM papayas.

2.4 Drought and Salinity Tolerance

Creating drought or salinity tolerant crops was a great task, but improvements were made through a stepwise methodology. Recent inventions in biotechnology are conveying a better understanding of the pathways and mechanisms involved in drought and salinity tolerance. Developing crops that can resist extensive durations of drought or salinity in soil and groundwater will encourage people to cultivate crops in earlier inhospitable areas (Tang 2000; Zhang and Blumwald 2001). Several drought and salt tolerant genes have been recognized. Identification of these salt regulated genes has allowed a better understanding of the complexity of higher plants (Hasegawa et al. 2000). Research institutes such as ICARDA developed drought and salt tolerant wheat and barley exploiting genetic engineering.

2.5 Pharmaceutical Crops

GE crops comprise genes that are beneficial for pharmaceutical industries. Medicines are often expensive to produce and generally need special storage conditions not freely accessible in developing countries. Scientists are working to produce edible vaccines in potatoes and tomatoes (Daniell et al. 2001; Qingxian et al. 2001). These vaccines will be considerably easier to transport, store, and manage than conventional injectable vaccines. The USDA has permitted field trials for a safflower variety that is genetically modified to produce a precursor to human insulin that can be used for diabetes treatment (SemBioSys 2010).

2.6 Nutrition-Added Crops

Various GE crops can modify the nutritional value of a food and are therefore encouraged by biotech industries as a promising solution against diseases. Malnutrition is one of the biggest threats in third-world countries. Underprivileged people mainly depend on rice as a staple food. Rice, however, does not have sufficient quantities of all required nutrients to prevent malnutrition. Giving significance to malnutrition, rice has been genetically modified to contain surplus vitamins and additional minerals in order to alleviate the nutritional value. “Golden Rice” is a variety boosted with an organic compound, carotene. The rice has been modified to decrease the occurrence of vitamin A deficiency in the developing world (Xudong 2003). Similarly, GE soybean and canola oil are engineered to ensure lesser polyunsaturated fatty acid content and higher monounsaturated fatty acid levels (oleic acid) (WHO 2008). In 2010 the USDA permitted a novel soybean brand that is modified to produce more oleic acid (75Fed. Reg. 32356).

3 Important GE Crops

3.1 Safflower

The USDA in 2007 permitted a field trial of a safflower variety engineered by the Canadian company SemBioSys. It was tested to produce proinsulin, a precursor to insulin in humans (73Fed. Reg. 8847-8848; 2008). Although safflower self-pollinates, some insects can still cross-pollinate safflower plants with genetically engineered pharmacological qualities (USDA 2007). Regardless of the contamination threat, SemBioSys has a pending application to bring the GE pharmaceutical to market (USDA 2011a, b, c, d).

3.2 Soybean

Soybean is among the two most extensively grown GE crops. The USDA has released two soybean varieties engineered to have healthier oil profiles (Shoemaker 2001). Furthermore in December 2011, the USDA approved a novel soybean genotype that was lower in saturated fat, and in July 2012 it approved a soybean with higher level omega-3 fatty acids (USDA 2011a, b, c, d).

3.3 Sugar Beet

In 2005, after determining that genetically modified production posed no threats to other plants and the environment, the USDA approved Monsanto’s Roundup Ready sugar beet (70 Fed Reg 13007-13008; 2005). In 2008, the Center for the Food

Security Club confronted this approval in law court on the basis that the USDA's environmental assessment overlooked significant economic and environmental impacts (69 N.D. Cal 2010). In July 2012, the USDA finally approved GE sugar beets.

3.4 Sweet Corn

Monsanto in 2011 announced that Roundup Ready sweet corn would be engineered for implanting (Gilliam 2011). Sweet corn is Monsanto's first commercialized GE vegetable crop approved by the USDA.

3.5 Tomato

In 1991, DNA Plant Technology Corporation transferred a gene from the flat fish winter flounder to produce a cold-tolerant tomato (USDA 2011a, b, c, d). It was later approved for field testing, but was never approved for commercialization (USDA 2011a, b, c, d). In 1992, Calgene engineered the tomato called Flavr Savr having a longer shelf life and was the first GE crop on the market. Later it was withdrawn from the market due to harvesting difficulties and lower demand (USDA, ERS 2013a, b).

3.6 Wheat

In 2002, Monsanto appealed the USDA for the approval of Roundup Ready red spring wheat. It was the first GE crop modification for human food consumption other than livestock feed. In 2004, an Iowa State study predicted that allowing genetically modified wheat could decrease US wheat exports by 30–50 % and reduce costs for both GE and conventional wheat (USDA 2013). Monsanto abandoned GE wheat field tests before getting commercial agreement, although the company continued research in 2009.

3.7 Alfalfa

Alfalfa is an important feed crop for livestock. The USDA permitted Monsanto's Roundup Ready alfalfa in 2005. In 2007, non-GE alfalfa producers challenged the USDA's permit on the basis that GE alfalfa might contaminate organic alfalfa (CRBNo. C06-01075; 2007). In 2010 a USDA environmental impact statement confirmed the possible harmful impacts of organic and conventional alfalfa growers, including lower demand in the market due to adulteration (USDA 2010). Nevertheless, in 2011 the USDA approved genetically engineered alfalfa deprived of any planting restrictions (76. Fed. Reg. 8708; 2011).

3.8 Corn

The USDA in 2011 allowed Syngenta's amylase corn with distinctiveness to produce an enzyme that accelerates the production of ethanol. The USD assured that it was harmless for food and livestock feed and allowed it for field trials (USDA 2011a, b, c, d).

3.9 Papaya

In 1999, the EPA approved two varieties of papaya that are resistant to the papaya ring spot virus (Fernandez 2006). Genetically engineered papayas contributed 30 % of Hawaii's papaya production in 1999 increasing to 77 % by 2009. Moreover, the third ring spot-resistant papaya was approved by the USDA in 2009 (74. Fed. Reg. 45163; 2009).

3.10 Potato

The EPA and FDA in 1995 permitted Monsanto's Colorado potato beetle resistant New leaf potato (Monsanto 2010). Later in 2001, Monsanto withdrew the potato commercialization, but in 2010, the European Union approved the Amflora potato for farming which is a product of the German chemical company BASF, although the crop is intended for industrial use only such as paper and textiles (BASF 2010). The USDA is seeking for the approval of a low-acrylamide and reduced-bruising potato created by McDonald's main supplier J. R. Simplot (BSPR 2013).

3.11 Rice

The Rockefeller Foundation in 1982 launched a modified variety called Golden Rice to combat a deficiency of vitamin A. In the first field test of golden rice the strain was found unsuccessful in providing enough beta carotene to meet the Vitamin A deficiency (Brown 2001). In 2004 Syngenta tested 2-Golden Rice in fields at Louisiana State University.

4 Concern Against GM Foods

Scientists, environmentalists, professional associations, public interest groups, and other government representatives have all raised concerns about genetically modified food and criticized the agro industry for earning profits without concern for potential health hazards. Critics also pointed to government for failing to implement adequate regulatory measures. Utmost concerns about GM foods are human health risks, environmental safety, and economic issues.

4.1 Environmental Safety

4.1.1 Effect of GE Pesticides

The US Environmental Protection Agency set a regulation of pesticides and herbicides, together with GE crops that are modified to be insect resistant. The EPA also sets tolerable levels of pesticide and herbicide remains in food, including GE insect tolerant crops. During the year 1995–2008 the EPA listed 29 GE pesticides modified into cotton, corn, and potatoes. In 1947, bioengineered insecticides were regulated under the Federal Insecticides, Fungicide, and Rodenticide Act (FIFRA 1998). Pesticide and insecticide resistance GE crops need to prove they do not cause any adverse effects on the environment or public health. The biotech industries must conduct field trials for insect tolerant GE crops, create tolerable pesticide characteristics, and record the pesticide trait for commercial production (CFR 2001). A study showed that pollen from Bt corn caused high mortality rates in monarch butterfly caterpillars (John et al. 1999). Unfortunately Bt toxins destroy several species of insect larvae indiscriminately. It is impossible to design a Bt toxin that would only target crop damaging pests and remain harmless to all other insects. This study has been later investigated by the EPA and other nongovernmental research agencies; the initial data from new findings propose that the original study may have been flawed (Niiler 1999). This topic is highly debatable and both sides are defending their data strongly. Presently, there is no conclusion about the Bt studies and the potential risk of harm to nontarget organisms requires further evaluation.

4.1.2 Reduced Efficacy of Pesticides

Farmers are concerned that usage of GM seeds may reduce efficiency of pesticides. Several populations of mosquitoes developed resistance to the currently banned pesticide DDT.A study reported a decreased susceptibility in pests to the use of Bt as a sprayed pesticide (www.colostate.edu).

4.2 *Development of Resistant Weeds and Insects*

When the crop is grown nearby a closely related weed species, gene transfer from GE crop to weed through pollen transfer has been verified (www.colostate.edu). The crossbreeding transfer of the herbicide resistant genes will create superweeds or superbugs that may possibly develop a resistance to GM crops and insecticides.

5 Effect on Consumers

5.1 *Ambiguous Safety*

The effects of GM crops on human health are not yet identified. GE food like non-GE food can carry hazards to consumers such as potent allergens and toxins. Evidence proves that human reaction to allergens will be similar when it is transferred to GE organisms. A study found that persons allergic to nuts responded in a similar way to genetically engineered soybeans in which a protein from a Brazil nut was introduced. However, very little evidence supports a significant health hazard of GM crops to consumers. The Centers for Disease Control also found no evidence between a processed food that contained a GM product and claimed to be allergic (Bonalume 1999). Moreover the GM industry identified that the local market consumers of GM products for years have no associated health hazards (Hodgson 1999). Corn and soybeans are the major GE food crop of the industrial food supply, from vegetable oils to high-fructose corn syrup to livestock feed. Safety studies on GE food are insufficient as biotech companies prohibit production for research purposes in their seed licensing contract. A toxicologist reported in a study that rats fed on GE corn over two years had deteriorated liver and kidney functioning and also had high chances for tumor development (Gilles-erec 2011). Another study reported impaired embryonic development and abnormalities in the livers of mice as well as in rats fed GE soybean (Malatesta et al. 2002). In 2007 a study found liver damage and kidney impairment of rats that were fed insect tolerant Bt corn (Gilles-erec 2007).

Studies indicate that the Roundup Ready attribute lowers the nutritional content of engineered crops by constraining the absorption of nutrients such as iron, calcium, zinc, and magnesium making plants more disease vulnerable (Huber 2010). A study reported that fusarium, a pathogenic fungi that infects plant roots, becomes more dominant over Roundup-treated crops (Johal and Huber 2009).

5.2 *Identity Preservation in Field and Markets*

Labeling of GM foods and food products is also an important issue. For consumers to have the opportunity to make selections about their food, all GE foods should be labeled. The agro-industry considers that food labeling should be voluntary and subject to the requirements of the free market. Consumer interest groups are also demanding obligatory labeling on GM food. The FDA's recent status for food labeling is administered by the Food, Drug and Cosmetic Act. The FDA is only concerned with food additives, not whole foods that are considered "GRAS," generally recognized as safe. There are some other queries that need to be responded to if the labeling of GM foods becomes obligatory. Firstly, the agronomist will absorb the cost of such an initiative in order to save GM crops and non-GM crops from mixing during harvesting and shipping. It is almost assured that manufacturers will pass along these added expenses to consumers in the form of higher prices. Secondly, the suitable limits of GM adulteration in non-GM products, where the acceptable limit of cross-contamination is 1 % is determined by the EC, yet several consumer groups debated that only 0 % is adequate. Researchers concluded that present technology is incompetent to identify minute amounts of contamination, so safeguarding 0 % contamination is not guaranteed. Finally, the utmost challenge confronted by a new food labeling policy is to educate and notify consumers without damaging the public trust and causing alarm or fear of GM food products.

6 Economic Concerns of GM Products

Bringing a GM food from field to the local market is an extensive and expensive process and agro companies wish to ensure a commercial profit on their investment. Unions combined with patent restrictions have increased the economic power of biotechnology companies. Consumers are concerned that patenting improved plant varieties will increase the price of seeds which will be unaffordable for farmers and third-world countries. Biotech corn seed prices rose by an average of 13 % annually between 2002 and 2012, and soybean seed prices increased by an average of 11 % annually. Between 1996 and 2007, Monsanto acquired more than a dozen seed companies. Strict patents preserve genetically engineered varieties and violation of such patents is of great concern for an agro-industry. The patent holder controls how partnering companies utilize the combined traits. Therefore, there are several seed companies; most of the accessible soybean, cotton, and corn seeds contain Monsanto-patented traits that have been cross-licensed to other seed-producing companies (David 2004) Agriculturalists pay patent tolls and sign a bond for limited authorization to plant GE seeds. Growers need to purchase new seeds every year due to patent infringement. However, this would be financially disastrous for farmers in third-world countries who cannot afford to buy seed each year and traditionally set aside a portion of their harvest to plant in the next growing season.

7 Global Trade

GM crops and GM products are not universally accepted in the global market. The United States has eagerly permitted GE crops, whereas consumers in Japan and Italy are doubtful about the safety of GE foods. The European Union has banned the import of crops with inserted genes, referring to concerns about the environment and human health hazard. Presently some EU countries prohibit GE cultivation altogether: France, Germany, Austria, Luxembourg, Greece, and Hungary. Nations that prohibit GE food normally enforce strict rules to avoid illegal GE imports which blocks US exports of soybean and corn that are major GE food crops. Japan does not produce GE crops and needs obligatory labeling of all GE food. In spite of the modern grain-handling arrangement in the United States, GE grains have contaminated non-GE shipments. The Government Accountability Office recognized six known unlicensed releases of GE crops between 2000 and 2008. In 2000, Japan noticed GE StarLink corn which was not allowed as fit for the human diet.

After the Star Link exposure, Europe banned all US corn shipments, costing crop producers $300 million. In August 2006, non-licensed GE Liberty Link rice was found to have contaminated conventional rice stocks. Europe and Japan enforced heavy restrictions and ceased all US rice imports costing the US rice producers $1.2 billion. In recent years, the US Trade Representative has been pushing transaction partners to eliminate unnecessary import prohibitions and limitations to US GE crops and GE products and is even insisting countries remove GE labeling necessities (USTR 2010). Moreover the US State Department has pressured governments all over the world to lift GE restrictions (U.S. (DoS) 2007).

8 Future Prospects and Conclusion

There are many potential reasons to believe that current and future GM crops have the greatest potential to benefit economic, ecological, and evolutionary components of sustainable crop production in the future. Increasingly, the use of GM crops will require agronomists, ecologists, farmers, and policy makers alike to take more of a systems perspective that considers the broader evolutionary consequence of the traits in question. However, engineering crops with complex traits such as abiotic stress tolerance, nutrition use efficiency, and yield potential remains difficult, although they are highly desirable in agricultural production. A great number of genes have proven effective under well-controlled conditions, but are generally not good enough when tested in the field. More and more research is needed through the integration of GM crops as the basic strategy for successful management of pests, diseases, and weeds in an agro-ecosystem. The safety assessment of foods derived from GM crops conferring nutritional benefits may in some cases require the development of improved in vivo dietary studies of whole foods. It is important to develop animal models that are very sensitive to the detection of toxic and antinutritive effects and intended positive nutritive effects. Toxicological tests should be considered on a case-by-case basis, for example, proliferative changes in tissues during the 90-day study may indicate the need for a long-term toxicity study. In addition to animal studies designed specifically for safety evaluation, nutritional or wholesomeness testing may be performed to determine whether the food or feed product of the GM crop poses any nutritional problems in comparison with the unmodified parent crop (Hammond 1996). There are many challenges ahead for biotech companies and government mainly in the areas of human health hazard, food labeling, safety trials, and international policies. There are opinions of the scientists that genetic engineering is an inevitable movement and we cannot afford to overlook a technology that has such enormous potential benefits. However, we need to progress with caution to escape unintentional impairment to human health and the environment as a consequence of our interest in this influential technology.

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Plant Responses and Tolerance to High Temperature Stress: Role of Exogenous Phytoprotectants

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Abstract Among the abiotic stresses high temperature stress is one of the most detrimental stresses threatening higher plant productivity and survival throughout the world. Each degree Celsius increase of average growing season temperature may decrease crop yield and affect plant distribution. On the other hand, global average temperatures are supposed to increase from 1.8 to 4.0 °C or higher by 2100 as compared to the 1980–2000 average. Plants are intimidated by adverse effects of high temperature stresses. Protein denaturation, inactivation of enzymes, production of reactive oxygen species, and disruption of membrane structure are some of the primary damage effects of high temperature that are also responsible for damage of ultrastructural cellular components. These anomalies hamper plant growth and development. Although higher plants develop their own defense strategies to overcome the high temperature stress effects, these often are not enough, therefore

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substantial damage is observed. The metabolism in plants is altered in response to high temperature stress. The antioxidants, secondary metabolites, hormones, osmoprotectants, and many other essential biomolecules are modulated, which help to defend against high temperature impacts. Moreover, numerous studies have proved that as protectants the exogenously applied hormones, osmoregulators, antioxidants, signaling molecules, polyamines, and trace elements confer high temperature stress tolerance in the organisms. This chapter presents the responses of plants to high temperature stress and evaluates the role of exogenous protectants under high temperature stress.

Keywords Phytoprotectants • Thermotolerance • Abiotic stress • Climate change

1 Introduction

Temperature is one of the major factors responsible for natural distribution of living beings in particular, plants. The success and timing of agricultural crops too is controlled by this factor. Habitats occupied by the plants growing in differing habitats differ in their endurance to the temperatures as well, ranging from freezing to over 60 °C. We also come across seasonal variations in the same individuals in many habitats due to seasonal as well as diurnal fluctuations in temperature. These affect the molecular events in different ways that are currently well understood. However, an interpretation of all these developments in plants is difficult, because the significant observations in plants are related to temperature involvement in the rate of physiological activities, plant growth, or the timing of some important developmental events such as seed germination, flowering, or the breaking of dormancy. Even greater understanding is needed to interpret the distribution of plants in various natural communities or competition among species in relation to the temperature.

The stresses in the natural surroundings of living beings lead to various physical and chemical interactions, which result in a loss of different functions. Many features in living beings allow them to live under a wide temperature range, either through modifications in the structure or function via natural selection or through phenotypic modifications. These modifications and adaptations help them to mitigate the stresses. In general the effects of temperature are around the optimum range, but why high temperatures result in the death of some organisms needs to be studied at length. The high temperature stresses above the optimum range lasting for days or weeks are regarded as chronic exposures, whereas those lasting for shorter durations are accepted as acute ones. The injuries resulting from these vary to a great extent (Kappen 1981; Berry and Raison 1981; Steponkus 1981).

High temperature (HT) stands for temperatures high enough to damage metabolic processes and affecting the growth and developmental processes of plants (Balla et al. 2009). Among the abiotic stresses HT stress is one of the most detrimental stresses threatening higher plant productivity and survival throughout the world.

According to the global climate change scenario, average temperatures are expected to increase from 1.8 to 4.0 °C or higher by 2100 as compared to the 1980–2000 average (IPCC 2007). Each degree Celsius increase of the average growing season temperature may decrease crop yield up to 17 % and plants at lower altitudes will escape towards higher altitudes (Lobell and Asner 2003; Ozturk et al. 2015), because plants are intimidated by adverse effects of HT stresses. Protein denaturation, inactivation of enzymes, production of reactive oxygen species, and disruption of membrane structure are some primary damage effects of HT which are also responsible for the damage of ultrastructural cellular components. These anomalies hamper growth and development of plants (Howarth 2005; Hemantaranjan et al. 2014). Mild HT reduces cell expansion and division; on the other hand, severe HT results in programmed cell death. Scorching of leaves and twigs, sunburn on plant organs, and leaf senescence and abscission are visual HT damage symptoms. Delayed seed germination, a loss of vigor, abnormal seedling development, reduced and altered vegetative growth pattern, male sterility, infertile female gametophyte, abortion of fertilized embryos, fruit abscission, and distorted fruit are common effects of HT stress. Physiological processes such as water and nutrient transportation, photosynthesis, respiration, transpiration, and dry matter partitioning—none is devoid of HT induced damage effects (Kappen 1981; Berry and Raison 1981; Steponkus 1981; Ozturk and Szaniawiski 1981; Ozturk et al. 1981; Vertovec et al. 2001; Howarth 2005; Ismail and Hall 1999; Egli et al. 2005; Wahid et al. 2007; Hasanuzzaman and Fujita 2011; Hakeem et al. 2012; Turkyilmaz et al. 2013; Hasanuzzaman et al. 2011, 2013, 2014; Hasanuzzaman and Fujita 2013; Brestic et al. 2014; Nahar et al. 2015). Thus HT severely reduces the yield of cultivated and wild plant species (Ozturk et al. 2009). Extreme temperature stress accelerates the generation and reactions of ROS [such as, singlet oxygen ($^1O_2$), superoxide radical ($O_2^{\bullet -}$), hydrogen peroxide (H_2O_2), and hydroxyl radical ($OH^{\bullet}$)], thereby inducing oxidative stress (Mittler 2002; Yin et al. 2008). The pattern of HT effects on plants depends on the temperature factor and plant factor. The temperature factor may include the degree of HT stress, duration of HT stress, and frequency of temperature exposure. The susceptibility to HT in plants varies with plant developmental stages. The effects also depend on the species and genotype, and may vary according to inter- and intraspecific variations of plants (Kappen 1981; Berry and Raison 1981; Steponkus 1981; Barnabás et al. 2008; Sakata and Higashitani 2008). Although higher plants develop their own defense strategies to struggle against HT stress, often these are not enough and thus result in substantial damage. In response to HT stress plant metabolisms are altered; antioxidants, secondary metabolites, hormones, osmoprotectants, and many other essential biomolecules are modulated, which help to defend against stresses. Moreover, numerous studies have proved that exogenously applied hormones, osmoregulators, antioxidants, signaling molecules, polyamines, and trace elements as protectants confer HT stress tolerance. This chapter presents the responses of higher plants to HT stress and summarizes the latest views focusing on the role of exogenous protectants under HT stress and also the information on the links between the effects of high temperatures at different levels (Kappen 1981; Berry and Raison 1981; Steponkus 1981).

2 Biogeography of Plants in Relation to Temperature

Many investigations have been undertaken on the formation of ecads or ecotypes at different altitudes in order to uncover the physiological parameters responsible for the formation of ecotypes, but the findings were not very encouraging (Ozturk 1980). The plausible reason for the ecotypes and ecad formation on the basis of seasonal variations related to the growth behavior of plants appears to come down to the differences in tissue temperatures instead of habitat temperatures (Ozturk 1980; Ozturk et al. 2015). In general, it is difficult to learn the physiological differences between plants without carrying out detailed experimental investigations on the interactions of plant responses to temperature. Comparative studies of the physiology of C_3 and C_4 plants have shown large differences in the response to temperature and water relations and C_4 plants are regarded to favor dry and hot environments (Ozturk et al. 1981).

In spite of these studies no definite findings have been recorded related to the gradientwise replacement of the species on the basis of a single environmental factor. We come across large seasonal changes in plant growth behavior in temperate environments, even plants with different physiological characteristics might coexist in the same habitat in different seasons (Berry and Raison 1981).

The elevational gradients on different mountain ranges face more stable environmental conditions. There is always a replacement of plant taxa when we move from lower to higher elevations, which can take place over a narrow elevational band of about 600 m. The investigators always interpret elevational gradients as temperature gradients, but the complications arise from changes in other factors with altitude such as changes in water relations and the herbivores. The same situation is met with geographically different gradients depicting that temperature plays a major role in determining the success plant taxa. The reasons for all these replacements are that some plants are probably superior at low temperatures explaining the fact that some steps in photosynthesis are sensitive to high temperatures, although some case studies discredit the idea. Another explanation is that the efficiency of light utilization in photosynthesis in some plants increases at lower temperatures. In the meantime not much work has been published on the influence of lower atmospheric pressures. Similarly the nitrogen content of some species is reported to decrease whereas that of other species, stays constant as the temperature for growth increases, reflecting a lower requirement for nitrogen in order to fulfill the photosynthetic functions (Hakeem et al. 2011a, b). A lower requirement of nitrogen allows some plants to allocate more growth to the aboveground parts than belowground. The lower water requirement also plays a role in this connection (Ozturk et al. 1981). No doubt the exact physiological basis for the replacement of species is not yet fully understood, but it is clear that temperature plays a major role. The biogeographical and seasonal variations probably interplay between the thermal regime of a habitat and the physiological features of plants naturally occupying the habitat.

3 Response of Higher Plants to High Temperatures in Different Growth Stages

Heat as a stress factor limiting the survival of plants has been recognized for some time, and reports about plants in hot environments have been critically discussed. These were treated as a physiological problem, but later studies showed that ecological evidence related to the heat resistance of plants is very important. On the basis of thermal regime ecologically there are two types of environments, either characterized by permanently high or low temperatures, or a range of temperature variations including extreme heat stress. The adaptations here depend either on the physiological properties of the cytoplasm or on the extent to which plants can endure occasional heat stress. Major natural sources of thermal stress on our globe are solar radiation, geothermic heat, and fire. A metabolic heating is also observed in compost, hay, or stored fruits. Very little information is available on the vegetation of hot volcanic soils. Some plants are able to live next to hot springs, even in the effluents of hot springs; the algal populations change from thermophilic to thermotolerant. Solar radiation can strongly heat the rocky substrata or the soil surfaces, leading to extreme thermal stress, particularly for plants living close to the soil surface (Kappen 1981; Berry and Raison 1981; Steponkus 1981). Soil temperature extremes can vary between 65 and 75 °C on bare soils, but forest soils do not get heated up beyond 40–50 °C. Desert soils reach up to 70–80 °C. In plants the thermal load also depends on the mass and conductivity of irradiated organs, their area as well as transpiration intensity, and the nature of the plant surface. Fruits and succulent plants are subjected to high thermal stress (Ozturk and Secmen 1999). There are two types of thermal response, an “overtemperature” and “undertemperature.” The intermediate types maintain their leaf temperatures close to air temperatures with the help of small assimilatory organs, leaf color, and a cover of dust or chemicals on leaves or fruits (Kappen 1981; Berry and Raison 1981; Steponkus 1981; Ozturk and Secmen 1999). An interpretation of heat effects in field experiments is a difficult job because a combination of factors can be effective, one of these being drought. The damage due to heat can be recognized only under particular conditions. The heat damage in higher plants such as scorching of leaves and fruits, sunscald, sunburning, abscission of leaves, and growth retardation, although a result of thermal impacts, have been reported as plant diseases. The seedlings of many species especially suffer from high temperatures, and may get killed when soil temperature exceeds 40 °C. There may be a decrease in production due to extreme summer heat; even cultivated plant taxa can also show indirect effects of heat stress. The heat-induced susceptibility to infection can be attributed to biochemical or physiological changes vis-à-vis changes in the physical nature of the leaf surface. The temperature effect cannot be expected when growth is limited by some other environmental factor. The rate of photosynthesis under some conditions is fully temperature dependent; the rate of the slowest step and efficiency of that step may be limited. The differential effect of temperature upon the distribution of plants can be affiliated with the role of physiological efficiency in ecological systems. It also affects the efficiency with which water and nutrients are used for plant growth (Kappen 1981; Berry and Raison 1981; Steponkus 1981).

3.1 Germination Stage

Temperatures can control seed germination and dormancy by regulating the metabolic processes of a seed. Some seeds do not germinate even under ideal conditions until they experience a particular temperature regime after full imbibition, such as low temperature called stratification, high temperature, or alternating temperatures (Ozturk 1968, 1969; Ozturk and Vardar 1975; Kappen 1981; Berry and Raison 1981; Steponkus 1981; Ozturk et al. 2009). Stratification is the most-used temperature treatment: seeds receive a treatment of 0–5 °C for several months before they germinate at a high temperature. This condition is a simulation with seeds that fall in autumn and overwinter in the leaf litter or under a soil layer, inducing changes in seed metabolism and affecting growth. The reasons for an involvement of these changes in metabolism is still not clear; it may be due to the changes in the level of growth substances, where the temperature effect alters the balance between growth inhibitors and growth promoters in favor of the latter. Short exposure of seeds to a high temperature before left for germination at a low temperature enhances the percentage of germination. In some cases light is a precondition, during the high-temperature treatment. Alternating between high and low temperatures on a seasonal/diurnal or short-term basis also promotes germination (Kappen 1981; Berry and Raison 1981; Steponkus 1981).

A decrease in the germination percentage due to HT stress has been documented in many plant species. High temperatures also affect plant emergence, seedling vigor, and radicle and plumule growth (Kumar et al. 2011; Johkan et al. 2011; Piramila et al. 2012). The effects of HT on seed germination vary according to plant species. In *Arabidopsis*, inhibition of seed germination has been recorded due to HT stress, which occurs through the induction of abscisic acid and inhibition of gibberelic acid, which play a vital role in regulating metabolic reactions during germination (Toh et al. 2008). Carrot (*Daucus carota* L.) seed germination is reduced at HTs above 35 °C (Nascimento et al. 2008; Ozturk et al. 2009), compared to seeds exposed to 25 °C. This is supposedly due to an increase of seed respiration and metabolic activities (Nascimento and Pereira 2007) or accelerated aging (Corbineau et al. 1994) induced by HT. The carrot seeds lack the ability to tolerate HT because the seeds have low seed viability or vigor (Nascimento et al. 2005). Temperature above 40/30 °C has severely hampered germination of seeds of *Campsis radicans* (Demosthenis and Reddy 2000). For some plant species, HT also acts as beneficial as it is considered a vital agent for breaking seed dormancy which is especially true for some temperate plant species (Vandelook and Van Assche 2008).

3.2 Vegetative Stage

The effects of high temperature stress during the vegetative phase of plants generally include growth retardation, visual damage effects, anomalous growth patterns and phonological events, and reduction in the growth and developmental cycles. This type of stress shortens the life cycle and reduces plant productivity by altering photosynthesis and respiration (Barnabás et al. 2008; Ouzounidou et al. 2012). High temperature stress (28–30 °C) reduces the life cycle duration in *Triticum aestivum*, together with the germination period and days to anthesis as well as maturity (Nahar et al. 2010). The day/night alternating temperatures of 30/25 °C significantly decrease days to booting, heading, anthesis, and maturity of different wheat genotypes (Rahman et al. 2009). A reduction in total dry weight of the plant and plant growth is also observed due to a disruption in shoot net assimilation rates (Wahid et al. 2007). This type of stress may also cause scorching and sunburn of leaves and twigs, branches and stems, leaf senescence and abscission, growth reduction of shoot and root, and fruit discoloration and damage (Wahid et al. 2007; Mitra and Bhatia 2008). According to Silva et al. (2010) *Jatropha curcas* plants subjected to HT (43 °C) showed a decrease in the leaf dry weight by 10 %, compared to the control. The wheat plants subjected to HT stress at the reproductive stage hasten its development, decrease its photosynthesis and leaf area, together with the shoot and grain mass, weight and sugar content of kernels (Shah and Paulsen 2003). The net assimilation rate (NAR) in maize and millet is reduced when plants are subjected to HT effects, which in turn reduces the relative growth rate (RGR; Ashraf and Hafeez 2004). Similar findings have been reported for sugarcane (Wahid 2007). HT stress leads to yellowing, scorching of leaf-tip and margins, rolling and drying of leaves, and necrosis in the sugarcane (Srivastava et al. 2012). In the case of beans (*Phaseolus vulgaris*) it reduces the dry matter partitioning, plant–water relations, and shoot growth and extension (Omae et al. 2012). HT adversely affects wheat growth by decreasing photosynthesis and leaf area and water use efficiency, which in turn decreases the shoot and grain weight, and also the sugar content of kernels (Shah and Paulsen 2003). HT stresses also result in the alteration of nutritional flour quality (Hedhly et al. 2009). Rahman et al. (2009) have observed a reduction in the green leaf area and productive tillers per plant in wheat at 30/25 °C (day/night) temperatures. Number of tillers and shoot elongation are also reduced in these plants under HT stress (Johkan et al. 2011).

Temperature strongly affects the root/shoot growth partitioning. In experiments where root temperature was varied while shoot temperature was held constant and near optimal, there was a distinct “optimum root temperature” where the shoot growth was maximal and the root/shoot ratio was minimal (Kappen 1981; Berry and Raison 1981; Steponkus 1981; Ozturk and Szaniawiski 1981; Ozturk et al. 1986). In general, regions that may have the combination of low root temperatures and low nutrient availability tend to have higher root to shoot ratios. Subtropical pasture species produce maximum shoot growth and minimum root to shoot ratio when soil temperature is 35 °C. At lower root temperatures there is an increase in the root to shoot ratio and a decrease in the total shoot biomass accumulated at the completion of the growth period. Temperate species also show a tendency for the root/shoot to increase at low temperature; however, the root/shoot ratio is minimum at 20–30 °C and also tends to increase at high root temperature. The root/shoot ratio is minimized at a temperature optimum for root function of a particular species. The ratio increases at temperatures above or below this optimum, resulting in lower rates of shoot growth at these nonoptimal root temperatures. These changes in allocation are required to maintain a balance between root–shoot functions such that the absorption of water, uptake of nutrients, and assimilation of CO_2 occurs at a ratio appropriate for the synthesis of new plant biomass. It has been emphasized that the interaction of the nutrient status of the soil involves the effects of temperature upon root/shoot partitioning. When the nutrient status is high, the root system may not change as much with temperature (Kappen 1981; Berry and Raison 1981; Steponkus 1981).

Growth is reduced or inhibited at low as well as high root temperatures; similar root temperature dependence is observed in the nutritional status of the leaves, leaf length, and leaf numbers, as well as stem length and root numbers. The increase in shoot growth with an increase in root temperatures can partly be related to the greater portion of new growth allocated to roots at low temperature (Ozturk et al. 1986). The reason is compensatory responses, maintaining an appropriate balance between root/shoot functions with temperature change. The inhibition of water uptake at low temperatures and an immediate inhibition of leaf growth have been correlated with a turgor loss in leaf cells. Osmotic adjustment can permit the cells to regain turgor provided the rate of water uptake by the roots keeps pace with water loss via transpiration. Species from high latitudes have much greater uptake capacity (either at the rate-limiting or rate-saturating phosphate concentration) than the species from (warmer) lower latitudes (Kappen 1981; Berry and Raison 1981; Steponkus 1981; Ozturk et al. 2015).

The abrupt changes in the water conductivity of roots vary from species to species and attribute to a phase change in the membrane lipids, a general characteristic of water uptake by tropical and subtropical plants. An involvement of membrane properties in water transport still remains unclear. The water passes from the soil through the roots to the xylem, then through the cytoplasm of the cells of the endodermis; plasma membrane, endodermal cell cytoplasm, or plasmadesmata linking these cells to adjacent cells seem to act as barriers to water entry into the xylem. It is unlikely that the membrane undergoes a sharp change of phase, which would dramatically affect water permeability. Many workers have studied the effect of local temperature treatments on the rate of translocation using petiole or stem segments; it is not strongly dependent upon temperature. A sharp decrease in the rate of translocation is observed at about 10 °C in many plant taxa (Kappen 1981; Berry and Raison 1981; Steponkus 1981).

3.3 Reproductive Stage

The reproductive stage is considered the most sensitive to HT stress among the growth stages of plant and HT stress during this stage results in severe crop loss (Hedhly et al. 2009; Thakur et al. 2010). The flower bud initiation stage is very sensitive to HT; this sensitivity is maintained for 10–15 days (Hedhly et al. 2009; Nava et al. 2009). Legumes and cereals often show HT sensitivity at the flowering stage, which causes a reduction in fruit set. A similar problem is observed in tropical fruit tree species (Saha et al. 2010). The developmental stages of the male gametophyte are more sensitive to HT stress, compared to pistil and the female gametophyte (Hedhly 2011). High temperature decreases the concentration of soluble sugars in the anther walls, developing pollen grains, and in the locular fluid in the cowpea. These decreases are accompanied by a decrease in sugar concentration in the mature pollen grains, which is one of the reasons for decreased pollen viability (Ismail and Hall 1999). Decreased accumulation of carbohydrate in pollen grains and ATP in the stigmatic tissue has been observed in HT affected sorghum (Jain et al. 2007). Bita and Gerats (2013) report that HT stress adversely affects development of tomato flowers in both sensitive and tolerant lines; the sensitive line is more severely affected by HT, showing distorted anthers and less viable pollen, compared to HT-tolerant lines. High temperature stress after a successful fertilization process also hampers the development of the embryo (Barnabás et al. 2008). At the flowering and grain filling stages it decreases grain weight and grain number as observed in many temperate cereal crops (Porter and Semenov 2005; Mahmood et al. 2010). During the seed development stage, this type of stress also reduces germination and loss of vigor, and impedes emergence and seedling establishment, as has been reported in several crop plants (Akman 2009; Ren et al. 2009). High temperature above 33 °C at the heading stage of rice significantly reduces anther dehiscence and pollen fertility rate, reduces the amount of pollen upon the stigma which reduces fertilization, leading to spikelet and seed sterility (Cao et al. 2008, 2009). At reproductive and other growth stages significant reductions in crop yield have been observed under HT stress and the effect is so severe that increase in temperature for each 1.5 °C induces a gradual increase of negative effects on crop yield (Tubiello et al. 2007). This type of yield reduction has been recorded in many cultivated crops such as cereals (e.g., rice, wheat, barley, sorghum, maize), pulse (e.g., chickpea, cowpea), oil-yielding crops (mustard, canola), and in other crops also (Warland et al. 2006; Cao et al. 2008; Kalra et al. 2008; Prasad et al. 2008; Edreira and Otegui 2012; Maheswari et al. 2012). There is also a reduction in the ear length, number of spikelets per main stem, and number of fertile florets per main stem of wheat which significantly reduce yield (Ahamed et al. 2010). In maize, HT stress at flowering periods during the pre-silking and silking stages causes yield reduction by 50 and 54 %, respectively (Edreira and Otegui 2012). *Glycine max* subjected to HT shows a decrease in photosynthetic rates, abscission in flower buds, and abortion of flowers, young pods, and developing seeds, resulting in lower seed numbers and seed yield (Prasad et al. 2008). Many papers have been published that deal with temperature as one of several factors affecting flowering and documenting changes induced in flowering by high or low temperature after providing an appropriate photoperiod for induction (Ozturk and Vardar 1975). Sex expression of flowers is also influenced by temperature, but very little information is available on the mechanism of this effect. Generally high temperatures within the range of normal growth promote maleness, and low temperature favor femaleness (Ozturk and Secmen 1999). High or low temperatures can affect components of the flower bud, which is economically important. High temperature also affects flower development.

4 High Temperature-Induced Alteration of Physiological Processes

4.1 Membrane Properties

The plasma membrane and cytoplasmic membranes of plants are composed of lipids and proteins; components of cell membranes, especially the lipid may change in response to environmental conditions such as temperature. Change in physical characteristics of membrane structures is sometimes considered a necessary physiological task when environmental factors change. But changes in membrane structure beyond a certain limit result in gross structural changes that might be phase separation of the membrane constituents or disturbances of function, including the loss of selective permeability and transport processes (Quinn 1988). These phenomena might occur in all membranes, including cytoplasmic, chloroplast, and mitochondria, which results in a disruption in major and basic physiological processes. Injuries to cell membranes, organization of microtubules and cytoskeleton, and changes in membrane permeability induced by HT alter cell differentiation, elongation, and expansion (Potters et al. 2008; Rasheed 2009). Maintenance of cellular membrane function is essential for a sustained photosynthetic and respiratory performance under HT (Chen et al. 2010). High temperatures induce photosynthetic membrane damage resulting in subsequent swelling of grana stacks and aberrant stacking, which significantly increase ion leakage from leaf cells and change the energy allocation to the photosystems (Allakhverdiev et al. 2008). In *Jatropha curcas*, the leaf electrolyte leakage (EL) increases by 28 % and lipid peroxidation as measured by the accumulation of thiobarbituric acid-reactive substances increases by 50 % when subjected to HT of 43 °C (Silva et al. 2010). Hasanuzzaman et al. (2012) reported that HT (38 °C) in wheat resulted in oxidative stress which caused membrane lipid peroxidation and increased malondealdehyde (MDA) content by 76 and 144 % after 24 and 48 h, respectively, compared to control plants grown under normal conditions without stress. Homozygous near-isogenic glycinebetaine-containing (*Bet*l/*Bet*1) and -deficient (*bet*l/*bet*1) Fδ lines of maize (*Zea mays* L.) were subjected to HT. Both maize lines showed differential membrane integrity when leaves or leaf segments were subjected to temperatures above 45 °C. The *Bet*l/*Bet*1 lines showed less membrane injury compared to the near-isogenic *bet*l/*bet*1 sister lines. The average temperature difference was 2 °C between Betl/Betl and betl/betl lines, which was considered as the critical temperature threshold that triggered catastrophic membrane damage in vitro. This tolerance was due to a single gene conferring glycinebetaine accumulation (and/or a tightly linked locus) that conferred protection against HT destabilization of leaf plasma membranes (Yang et al. 1996). High-temperature-induced membrane lipid peroxidation and aggravated membrane injury were also found in cotton, sorghum and soybean (Djanaguiraman et al. 2009, 2010, 2011).

4.2 Photosynthesis

Photosynthesis plays a dominant role in plant growth and is among the most responsive of plant processes to temperature. The rates of photosynthesis and ion uptake may change with temperature. The capacity of the various growing points to act as sinks for photosynthate and nutrients will change with temperature. Comparisons of the growth responses and photosynthesis to temperature depict that species-dependent differences in the photosynthetic responses to temperature are closely linked to the response of plant growth to temperature. Also the ability of species to acclimate to contrasting growth conditions is associated with the ability to acclimate at the level of photosynthesis. Many studies give detailed information on the photosynthetic responses to temperature of species native to or grown in various environmental regimes (Kappen 1981; Berry and Raison 1981; Steponkus 1981; Ouzounidou et al. 2012). Short daylight periods induce an increase in heat tolerance in various plants in a short time; the winter peak in heat tolerance of *Rhododendrons* is due to the absence of long day influence. Herbaceous species such as *Saxifraga aizoon* and *Sempervivum montanum* also respond to short photoperiods with increasing heat tolerance. High light intensity causes an increase in heat tolerance either by compensating for a long-day-induced depression or by supporting the hardening effect of short photoperiods, accelerating heat hardening. Diversity among species in their temperature responses may be characterized according to their temperature optimum, according to their photosynthetic activities over specific temperature ranges, or according to their tolerance to extremes of high or low temperature. Species from warm habitats usually reach their optimum at a somewhat higher temperature than species from cool habitats, and the temperature optimum may shift if the species are capable of acclimating to a changing growth temperature (Kappen 1981; Berry and Raison 1981; Steponkus 1981; Ouzounidou et al. 2012). Changes in the optimum temperature do not, however, fully compensate for changes in growth temperature. Species adapted to very cold arctic and alpine environments seldom have temperature optima below 20 °C, leading some workers to suggest that plants may not have fully adapted to such cold environments. Nevertheless, the photosynthetic capacity of cold-adapted species may be quite high at low temperatures characteristic of the native habitat, and the rate of CO_2 uptake at 4 °C may be severalfold higher than the rate of a species from a more mesic environment. The temperature optima of cool-adapted species may, however, be only slightly lower than that of species which do poorly at low temperature. Enhanced photosynthetic capacity at high temperature and, especially, an enhanced capacity to tolerate high leaf temperatures without damage are important features adapting such species to hot natural habitats (Kappen 1981; Berry and Raison 1981; Steponkus 1981).

The photosynthetic apparatus appears particularly sensitive to heat stress and has been frequently investigated (Ahmad et al. 2010). The maximum upper limit around 70–73 °C of intact plant photosynthesis is found in photosynthetic bacteria and the Cyanophycea. Among the eukaryotic plants, the maximum limit of net photosynthesis ranges between 35 and 61 °C. In some cases a phytogeographical correlation between the difference in the upper limit of photosynthesis and heat tolerance seems to exist. The upper limit of positive net photosynthesis may vary with the temperature regime, particularly in hot climates, and with desert species. This photosynthetic adjustment to high temperatures is possible only in species with a wide span between the upper limit of photosynthesis and that of heat tolerance. If heat stress is sublethal the photosynthetic capacity is fully regained during a recovery period of from one to about 10 days, and even becomes adjusted to higher temperatures. The recovery of photosynthesis is not influenced by temperatures between 10 and 30 °C (Kappen 1981; Berry and Raison 1981; Steponkus 1981).

The heat tolerance limit of thermophilous organisms is frequently close to the temperature range of their highest activity. Among the very thermophilous bacteria the heterotrophic species are most resistant. Most of the eukaryotic plants are absent from environments that have temperatures permanently above 50 °C. The eukaryotes lack membranes, which are both permanently thermostable and functional. Those organisms which have been frequently found in hot springs may not be active because their viability above 47 °C is not yet established. Some algae cannot survive even short exposure to temperatures warmer than 16–20 °C. The heat tolerance of marine species has been always highest in the tropics. The maximum temperature limit for the active life of thermophilic fungi reaches 61–62 °C (Kappen 1981; Berry and Raison 1981; Steponkus 1981). Lichens only rarely exist in hot moist environments, but can grow abundantly in hot deserts if cool and moist conditions are present. The bryophytes are generally hygrophytic plants, but also occur in the deserts, and around hot spots as well as in cool freshwater habitats (Ozturk and Gokler 1988; Gokler and Ozturk 1989, 1991). These are also found on hot volcanic soils (up to 42 °C) or in close proximity to hot springs. They must exist close to their heat-tolerance limit, without any difference between liverworts and mosses. Ferns mostly grow in tropical and subtropical forests, and in hot climates. Only a few species are found in open habitats. The epiphytic species colonizing exposed rocks are very tolerant and survive high temperature stress. Heat-tolerance limits often relate well to the typical habitats of the fern species (Kappen 1981; Berry and Raison 1981; Steponkus 1981).

The heat tolerance limits of terrestrial spermatophytes coincide roughly with the climate region of their habitats. However, within restricted plant groups, differences due to local climatic conditions are obvious. The assumption that succulents are heat tolerant cannot be taken as a generalization. The plants capable of high transpiratory cooling will suffer from heat stress if transpiration is prevented. The heat tolerance of temperate, arctic, and alpine species reflects their habitat conditions. On the other hand, the higher heat tolerance of alpine plants or of the typical shade species appears unexpectedly. Several measurements demonstrate that heat tolerance differs significantly between different organs of one plant. In an ecological sense, survival depends on the resistance of those organs that maintain the existence of a plant or provide for its reproduction. In alpine dwarf shrubs, the strategy appears to be to keep the stems most resistant against heat whereas the flowers are comparatively sensitive (Kappen 1981; Berry and Raison 1981; Steponkus 1981).

According to other findings the generative plant organs are the most heat-tolerant part of a plant. Leaf injury results primarily from damage to the sensitive mesophyll, whereas the epidermis and especially the stomata are more tolerant. Heat tolerance in plants corresponds to the temperature regime of their habitat, because it is expected that heat tolerance is capable of modification. It appears very difficult to decide whether the differences are due to plant modification or to the inheritable character of ecotypes. The differences in heat tolerance in thermally different environments are due to the actual thermoadaptation of the plants. A comparison of closely related species with respect to their “primary resistance” shows correlations between heat tolerance and prevailing geographic distribution. Diurnal changes in the heat tolerance of plants show very different patterns. These are most pronounced in the leaf vertex, most sensitive to heat (Kappen 1981; Berry and Raison 1981; Steponkus 1981).

Seasonal variation in heat tolerance mostly involves changing developmental stages or aging of plants. Germinating and young plants or growing organs are generally more sensitive to heat than adult organs or plants. Annual courses of heat tolerance are recorded in most plant groups: algae, bryophytes, pteridophytes, and spermatophytes (Kappen 1981; Berry and Raison 1981; Steponkus 1981). The patterns of the annual courses of heat-tolerance limits in evergreen plants are very different and frequently do not correspond to the natural climate rhythm. Common to all investigated species is the annual minimum heat tolerance in spring when the plants are rapidly growing. Different response types are distinguished; a few species possess an almost constant low or high heat-tolerance level in addition to the spring drop in tolerance. Most species with “S-type” response (summer peak in heat tolerance) live in warm summer habitats, for example, of Mediterranean climatic regions. A larger group of species develops high heat tolerance only in winter (“W-type”), comprising typical shade plants, some alpine species, dwarf shrubs, and grasses. Most of these become very tolerant to freezing in winter. Their heat tolerance can be increased through low temperature cultivation or cold hardening. In these cases heat and freezing tolerance appear to be linked to each other. A great number of plants exhibit a combination of an adaptive increase in heat tolerance in summer and others heat tolerance peak in winter. In many cases there is an apparent tendency for species with a more pronounced heat tolerance peak in summer to grow in warm open habitats (Kappen 1981; Berry and Raison 1981; Steponkus 1981).

From an ecological viewpoint the determination of long-term heat stress tolerance best characterizes adaptation to life. Heat shock of a few minutes or even seconds are damaging mostly at very high temperatures which rarely occur under natural conditions. On the other hand, longer exposure to raised but still tolerable temperatures increases the heat tolerance of plants through adjustive processes. Heat hardening in higher plants following cultivation for 10 days at 28 °C has been demonstrated. Within a certain range hardening increases with the duration and level of the hardening temperature. The efficiency of hardening changes during the growing season in *Morus alba* (Ahmad et al. 2013). The capacity for temperature adjustment in plants is obviously of survival advantage in a varying natural environment, as revealed in the appearance of a summer peak in heat tolerance and also in the irregular appearance of a heat-tolerant peak in extremely hot summers, after the threshold temperature for hardening has been reached. Evidence of ecologically relevant hardening by short heat shocks is also known Kappen 1981; Berry and Raison 1981; Steponkus 1981; Ozturk and Secmen 1999).

The HT leads to structural alterations in chloroplast protein complexes and reduced activity of enzymes involved in the photosynthetic process (Ahmad et al. 2010). Photosynthetic enzymes of the Calvin–Benson cycle, such as ribulose 1,5-bisphosphate carboxylase (RuBisCO) and RuBisCO activase are very sensitive to increased temperature (Maestri et al. 2002; Morales et al. 2003). High temperature reduces soluble proteins, RuBisCO binding proteins (RBP), large subunits (LS), and small subunits (SS) of RuBisCO in darkness, and increases those in light which are considered as major reasons for reduced photosynthesis under HT stress (Kepova et al. 2005). Photosynthesis can be inhibited by impaired electron transport, reduced photochemical efficiency of PSII, and inhibited RuBisCO activity. Decreased RuBisCO activation is exhibited under moderate HT stress due to impaired RuBisCO activase activity and is exacerbated under HT (Liu and Huang 2008). Photochemical modifications in carbon flux of the chloroplast stroma and of the thylakoid membrane system are often considered as primary sites of HT injury (Wise et al. 2004). High temperature may reduce leaf area, increase premature leaf senescence, and reduce leaf water content which have negative impacts on photosynthesis (Djanaguiraman et al. 2009). High temperature (33 °C, 5 days) decreases the photosynthetic rate in Shuanggui 1 cultivar of rice by 16.1 % and in T219 cultivar by 15.4 % (Cao et al. 2009). In *Jatropha curcas* subjected to HT of 43 °C photosynthesis was reduced due to various reasons. Its leaf CO_2 assimilation rate (PN) decreased by 41 %, the stomatal conductance (gS) decreased by 47 %, and carboxylation efficiency (PN/CI) decreased by 35 % under HT stress. The photochemical activity parameters such as the actual quantum yield of primary photochemistry and apparent electron transport rate decreased by 56 and 83 %, respectively, under HT (Silva et al. 2010). High temperatures may be accompanied by water deficits and stomatal closure. This situation is common under field conditions. Stomatal closure and reduced stomatal movement both reduce CO_2 availability and may decrease the CO_2/O_2 ratio in chloroplasts (Foyer and Noctor 2000). Altered stomatal movement and gas exchange due to HT may reduce photosynthesis because these can affect intercellular CO_2 and CO_2 assimilation rates (Mitra and Bhatia 2008). Due to HT (45 °C) the average rates of photosynthesis of *Vitis vinifera* leaves decreases by 60 % compared to normal temperature (25 °C), and the reduction in photosynthesis was 15–30 % by stomatal closure (Greer and Weedon 2012). High temperature stress (38/28 °C) significantly reduces stomatal conductance (by 16.2 %), Fv/Fm ratio (indicates photosystem II photochemistry; by 5.3 %), and photosynthetic rate (by 19.7 %) in soybean plant (Djanaguiraman et al. 2011).

High temperature injury to thylakoid membrane is responsible for alterations in chloroplasts, structural organization of thylakoids, and cause loss of grana stacking and swelling of grana (Wahid et al. 2007; Mitra and Bhatia 2008). High temperature stress impairs biosynthesis of photosynthetic pigments and causes their destruction, making reduction in photosynthetic pigment content one of the common effects of HT (Wang et al. 2009). Hasanuzzaman et al. (2012) reported that HT induced generation of H_2O_2 rendering oxidative damage which enhances chlorophyll (chl) degradation. The reduction in chl content was observed in wheat plants subjected to HT of 38 °C (Hasanuzzaman et al. 2012). In soybean, HT stress (38/28 °C) significantly reduced total chl content (by 17.8 %), chl a content (by 7.0 %), and chl a/b ratio (by 2.5 %; Djanaguiraman et al. 2011).

High temperature reduces activity of sucrose phosphate synthase, ADP-glucose pyrophosphorylase, and invertase. Reduction of activity of these enzymes adversely affects starch and sucrose synthesis under HT (Wahid et al. 2007; Sumesh et al. 2008). Reduced photosynthesis by HT results in decreased sucrose content, reducing sugar content and leaf soluble sugar content in soybean (Djanaguiraman et al. 2011). Prolonged HT subsequently causes depletion of carbohydrate reserves and plants suffer from starvation (Sumesh et al. 2008).

Plants native to (or grown in) thermally differing habitats may have physiological differences that either improve photosynthetic performance or extend the capacity of the leaf to tolerate temperatures of the habitat. These adjustments may be genotypically fixed in which case these are termed adaptations, or environmentally induced acclimation responses. The adjustments to an extreme temperature usually result in poorer performance at a contrasting temperature, suggesting that there may be some mechanistic link which improves the performance on one side and leads to poorer performance at the other end. Lipids play a role in determining the sensitivity of chloroplast membranes to thermal denaturation and possibly also the sensitivity to low temperatures. Changing the growth temperature of fully expanded leaves from low (20 °C) to high (45 °C) or vice versa causes rapid upward or downward adjustments in the apparent thermal stability of chloroplast membranes and in the temperature optimum for photosynthesis. These changes in the chloroplast membrane performance correlated with changes in the fluidity and the fatty acid composition of the chloroplast membrane lipids. Associated with the changes in lipid properties at high temperature are corresponding changes in the temperature of onset of phase separation, which also provides an index of changes in the composition of the membrane. Inasmuch as the activity of rate-limiting enzymes of carbon metabolism may also play a role in adapting or acclimating to temperatures, the expectation may be that leaves of plants adapted to lower temperature would have more total protein than leaves adapted to a higher temperature. But there is only a minor change in total protein or RuBP carboxylase with acclimation to high or low growth temperature; however, the fructosebisphosphate phosphatase of the high temperature acclimated leaf is only 40 % of that of a low-temperature-adapted leaf. These studies emphasize the role of specific rather than general changes in protein levels with temperature.

4.3 Transpiration

Transpiration is a mechanism of the cooling plant. The transpiration pool is also important for transportation of water from root to shoot and leaf through mass flow within a vascular bundle. Under HT stress, the risk of both HT damage and water shortage to plants increases to a great extent. Transpiration significantly reduced HT damage of plants by cooling leaves and other green parts of plants through evaporation of water from stomata. *Arabidopsis* plants exposed to HT (28 °C) showed increased transpiration and enhanced leaf cooling capacity, which improved plant adaptations to HT (Crawford et al. 2012). The high temperature stress of 38 °C for 4 days significantly increased the transpiration rate of tomato plant. But after 3 days of recovery the transpiration rate decreased (Cheng et al. 2009). Water flow through the transpiration pool not only cooled the leaf temperature, but also cooled the entire plant. *Pinus ponderosa* seedlings died when the surrounding temperature was 63 °C. But some of the seedlings survived because those maintained basal stem temperatures as much as 15 °C lower than the surrounding air. This temperature reduction was due to the higher stomatal conductance, transpiration rate, and higher water transportation, which maintained leaf and seedling stems to cool the plant by the HT transferring mechanism (Kolb and Robberecht 1996). In contrast, Morales et al. (2003) demonstrated that under HT, tomato plant reduced the hydraulic conductance leading to decrease in water absorption or due to the decreased stomatal conductance.

4.4 Water Relations

Water status of the plant is one of the most important components that should be in balance under changing ambient temperatures, otherwise physiological processes will be severely affected by environmental stresses (Mazorra et al. 2002). Although plants under stress conditions try to maintain balance in their water status, it is often altered due to alteration of water relations between growing media and plant tissue or between different components of the plant under different stress conditions including HT stress. High temperature stress disrupts the balance between symplastic and apoplastic loading of the phloem. This might be the reason for reduced water transportation. Reduction of assimilating transportation might occur for the same reason that reduces carbohydrate accumulation in pollen grains and in the stigmatic tissue (Taiz and Zeiger 2006). Sugarcane leaf water potential and its components change upon exposure to HT stress. During HT stress, although soil, water supply, and relative humidity conditions are optimal, irrespective of this optimal condition HT affects the root hydraulic conductance and water status of the plant (Wahid and Close 2007). High temperature decreases water-use efficiency in wheat (Shah and Paulsen 2003). Reduced water and nutrient transport during reproductive development results in reduction of fruit set in tropical plants (Young et al. 2004). Elevated night temperatures reduce leaf water potential of *Lotus creticus* to a great extent (Bañnon et al. 2004). In tomato, HT adversely affected hydraulic conductivity due to reduced stomatal movement that significantly decreased the water status of the plant (Morales et al. 2003). High temperature stress hampered the water relation of *Phaseolus vulgaris* which severely reduced growth (Omae et al. 2012).

The vapor pressure gradient between the intercellular air spaces and the ambient uptake by the roots is required as a driving function for transpiration of water to increase in temperature to meet growth requirements. These inputs balance over the long term, but photosynthate or nutrient storage buffers short-term imbalances. The mechanism that translocates and partitions the materials within the plant may respond to temperature (Kappen 1981; Berry and Raison 1981; Steponkus 1981). The seeds as well as spores are highly tolerant of heat due to their low water content and dry seeds can even be stimulated to a higher percentage of germination following one to several hours exposure to very high temperatures. The ecological importance of heat tolerance in plants is clearly observed in terrestrial cryptogams with relatively low heat tolerance in the soaked state. Their ecological adaptation is due to their poikilohydric nature, which allows them to lose water rapidly under the sun, and their extreme tolerance to desiccation. The difference in the heat-tolerance limits of dry and soaked terrestrial cryptogams differs much; the annual amplitude of dry bryophytes is much larger than moist ones (Kappen 1981; Berry and Raison 1981; Steponkus 1981). The degree of heat tolerance in the dry state is frequently more closely related to the thermal conditions of the natural habitat than the heat tolerance of the soaked specimen as such; terrestrial cryptogams are adapted to exist in hot, but arid environments. In some hydrophytic lichens the heat tolerance reaches upto 90 °C when dry; however, wet cultivation decreases their heat resistance. The membrane stabilization resulting from thermoadaptation is different due to adaptation to desiccation. The species of some highly desiccation tolerant poikilohydric connophytes become as heat tolerant as cryptogams in the dry state. The tolerance limit strongly depends on the water deficit of the leaves and the range increases nearly constantly on an annual basis. In sclerophyllous and mesophytic plants the heat tolerance limit increases with the saturation deficit of the leaves, the reason being tolerance increases only in wilted xerophytes and not in mesophytes and 62 °C appears as the absolute upper heat tolerance limit for cormophytes (Kappen 1981; Berry and Raison 1981; Steponkus 1981; Vertovec et al. 2001; Sakcali and Ozturk 2003). Osmotic agents also increase heat tolerance, such as desiccation, although no close correlation exists between heat tolerance and desiccation tolerance.

4.5 Oxidative Damages

High temperature stress is responsible for the generation of different ROS including $^1O_2$, $O_2^{\bullet-}$, H_2O_2, and $OH^{\bullet}$. The ROS have severe damage effects to the cell and its components, causing oxidative damage. Prolonged HT stress inspires ROS accumulation and activation of calcium-induced signaling action (Mittler et al. 2012) which leads to programmed cell death (Mittler et al. 2012). In spite of ROS having negative effects on plant metabolic processes, they have also been hypothesized to have signaling action to trigger the heat shock responses vital for the development of HT tolerance in plants (Vasseur et al. 2011). ROS biochemistry is very important for plants, the chloroplast being the major site for ROS reduction. They are also generated in other organelles, including peroxisomes and mitochondria. In chloroplasts, the reaction centers photosystem I (PSI) and photosystem II (PSII) produce ROS (Asada 2006). There are several steps for the generation of ROS; high temperature stress reduces photosynthesis, therefore plants have low NADPH and ATP consumption, the $NADP^+$/NADPH ratio is decreased, and the photosynthetic electron transport chain becomes over-reduced. This circumstance facilitates electron flow to molecular oxygen (O_2) which is the reason for $O_2^{\bullet-}$ generation by the Mehler reaction. The other form of ROS can be produced from this $O_2^{\bullet-}$ through different reactions (Foyer and Noctor 2000). The Haber–Weiss reaction between H_2O_2 and $O_2^{\bullet-}$ generates $OH^{\bullet}$. The latter can also be generated through the reactions of H_2O_2 with Fe^{2+} (Fenton reaction) and decomposition of O_3 in apoplastic space (Halliwell 2006). Singlet oxygen ($^1O_2$) is generated during PS II electron transfer reactions in chloroplasts (Karuppanapandian et al. 2011a, b). The C_3 plants are more prone to ROS production and to oxidative damage compared to the C_4 plants because the photorespiration pathway may be enhanced when C_3 plants are subjected to HT stress conditions (Foyer and Noctor 2000). High temperature induced oxidative stress generally results in peroxidation of membrane lipids. Disruption of cell membrane stability by protein denaturation also results from oxidative stress (Wahid et al. 2007). The HT stress (40/30 °C, day/night) increases H_2O_2 and $O_2^{\bullet-}$ contents of sorghum by 124 and 42.6 %, respectively, compared to control which increases membrane damage and MDA content (Djanaguiraman et al. 2010). Tobacco cells subjected to HT show increased ROS generation and altered membrane fluidity (Konigshofer et al. 2008). One of the reasons for the increased ROS generation under HT stress is reduced capabilities of plant antioxidant defense systems which efficiently scavenge ROS. Hasanuzzaman et al. (2012) have reported that HT (38 °C) significantly reduces some enzymatic and nonenzymatic components of the antioxidant defense system of wheat seedlings which increases H_2O_2 content and lipid peroxidation, compared to control. High temperatures also reduce the antioxidant enzyme activities in leaves of rice, increasing MDA content (a product of lipid peroxidation; Cao et al. 2009). Wheat root growth is inhibited under HT because of severe oxidative stress created by 68 % increase of $O_2^{\bullet-}$ production in root cells, which then results in lipid peroxidation (Savicka and Škute 2010). *Lolium perenne* subjected to moderate (36 °C) or HT stress (40 °C) shows oxidative stress with higher damage effects under HT. The higher H_2O_2 level is observed under HT. Oxidative stress causes severe physiological damage of maximal efficiency of photosystem II. Cell membrane stability is disrupted under HT and membrane lipid peroxidation increases (Soliman et al. 2011). Djanaguiraman et al. (2009) have reported that ROS produced by HT stress are involved in proteolysis or degradation of polymeric protein into simple soluble protein in cotton leaf, resulting in leaf senescence at the premature stage.

The influence of ions on heat tolerance has been investigated primarily from the aspect of effects on the physiological state of the cytoplasm, however, it can also be of ecological importance as an edaphic effect. Calcium ions have been repeatedly shown to increase the heat tolerance of algae, bryophytes, and tissues of terrestrial and water plants, or to stabilize thermophilic bacteria, whereas this is not due to its osmotic effect. Apparently because of its lyophilic nature, Ca^{2+} causes a shrinking of the membranes, which counteracts heat-induced leakage and thus prevents injury. Univalent alkali ions and nitrate cause swelling of the cytoplasm, and consequently decrease heat tolerance. Thus, it is evident that high nutrient levels increase sensitivity to heat stress. The halophytic taxa including *Kochia*, *Arthrocnemum*, *Tamarix*, and *Nitraria* also display very high heat tolerance (Kappen 1981; Berry and Raison 1981; Steponkus 1981; Ozturk et al. 2008).

Even though temperature is the most commonly measured environmental variable, the thermal regime of plants is often not adequately characterized. It is most frequently used to characterize an environment with air in a standard meteorological enclosure. Plant tissue temperature may differ quite significantly from that of air. Leaves exposed to radiant heat exchange may experience larger extremes of temperatures than air. Roots, owing to the large thermal mass of their substrate, are buffered from the diurnal extremes of temperatures and are nearer to the mean daily temperature. Other plant parts may fall between these extremes. The plant temperature is determined by purely physical interactions with the environment, however, direct metabolic control of plant tissue temperature does occur in some plants. The heat produced by rapid uncoupled respiration of stored carbohydrate causes the inflorescence of eastern skunk cabbage to be significantly warmer than air temperature during a period of rapid development in late winter. In a hot desert environment stem succulents reach temperatures 10–15 °C above the air temperature. The respiratory production of heat is regulated in a way that it compensates for the changes in ambient temperature. In some members of the Arum family respiratory heat production attracts pollinators with the help of volatilizing odoriferous substances. Only few plant organs such as rapidly developing shoot apices thermoregulate via metabolic means, a rare phenomenon. The rapidly transpiring leaves of desert ephemerals try to maintain leaf temperatures below air temperatures; the same is the case with some alpine taxa or winter annuals. Generally leaf temperatures are more favorable for physiological activity than air temperatures. The morphology of a plant enables it to maintain a favorable temperature, which represents an evolutionary alternative to physiological adaptations. These include formation of reflective leaf surfaces, light-controlled leaf movements, and rosette or cushion growth form (Kappen 1981; Berry and Raison 1981; Steponkus 1981; Ozturk and Secmen 1999).

5 Exogenous Phytoprotectants Confer High Temperature Stress Tolerance in Higher Plants

5.1 Osmoprotectants

5.1.1 Proline

Proline (Pro) is an osmoprotectant and its accumulation has adaptive roles in plant stress tolerance. It acts as a store of carbon and nitrogen (Hare and Cress 1997), is a ROS scavenger, and a molecular chaperone stabilizing the structure of proteins and protects cells from stress-induced damage (Ashraf and Foolad 2007; Verbruggen and Hermans 2008; Szabados and Savoure 2010). Studies of HT stress with different plant species has proved that Pro has various physiological roles by which it prevents HT damage and enhances tolerance. Some studies have also proved the negative correlation between Pro and very high/extreme temperature tolerance.

Proline imparts HT tolerance to *Cicer arietinum* by reducing cellular injury and protecting vital enzymes of carbon and oxidative metabolism (Ozturk et al. 1986). Exogenous application of Pro has certain beneficial roles under HT stress. High temperature (40/35 °C and 45/40 °C) inhibits shoot and root growth of chickpea and causes physiological disorders, such as increase of oxidative damage, MDA level, hydrogen peroxide content and membrane injury; reduction of cellular respiration, chl content, and relative leaf water content. Inhibition of antioxidant components (the activities of superoxide dismutase, SOD; catalase, CAT; ascorbate peroxidase, APX; glutathione reductase, GR; and levels of ascorbate, AsA; and glutathione, GSH), enzymes for carbon fixation (RuBisCO), sucrose synthesis (sucrose phosphate synthase), and sucrose hydrolysis (invertase) have been affirmed by the HT. *Cicer arietinum* plants growing in the presence of 10 μM Pro have shown an increase in the endogenous Pro level, improved shoot and root growth, less injury to the membranes, improved content of chl and water content, reduced oxidative injury, coupled with enhanced antioxidant system and activities of enzymes of carbon metabolism (Kaushal et al. 2011). High temperature stress tolerant wheat genotypes (Bijoy, Sufi, Kanchan, Fang 60, BAW 1059, BL 1883, BL 1022, IVT 7, IVT 8, IVT 9, IVT 10, and BAW 917) show <50 % membrane injury, compared to HT sensitive genotypes. At HT (35 °C), the HT tolerant genotypes produce more than double (>200 %) Pro than those at 25 °C. In contrast, HT-sensitive genotypes produce a smaller quantity of Pro at 35 °C, compared to HT tolerant genotypes (Ahmed and Hasan 2011). The effect of HT (40 °C) on the accumulation of Pro in tobacco plants has been investigated. It overexpressed a modified gene for the Pro biosynthetic enzyme Δ1-pyrroline-5-carboxylate synthetase (*P5CSF129A*). After 2 h HT, the amount of Pro in the upper leaves and roots of the wild type increased by 33 and 25 %, respectively, compared to control. Whereas, after 6 h of HT stress, the amount of Pro in the lower leaves of both the wild type and the transformants increased highly (Cvikrová et al. 2012). Transgenic *Arabidopsis thaliana* plants expressing the Δ(1)-pyrroline-5-carboxylate synthetase 1 gene (*AtP5CS1*) under the control of a heat shock protein 17.6II gene promoter accumulates Pro under HT stress. Pro accumulation under HT stress (50 °C for 4 h) decreases the thermotolerance of *Arabidopsis* by increasing ROS production via the Pro/P5C cycle and by inhibiting ABA and ethylene biosynthesis (Lv et al. 2011). Pro accumulation at HT has also been reported in barley leaves (Chu et al. 1974), in flag leaves of wheat (Hasan et al. 2007), in radish leaves (Chu et al. 1974), in tomato floral buds and leaves (Kou et al. 1986), in cabbage and in the leaves of *Brassica* vegetables (Takeda et al. 1999); in cotton leaves (Ronde et al. 2001), and in apple (Park et al. 2001).

5.1.2 Betaine

Betaines (*N*-methylated amino acid derivatives) are osmoprotectants. The compatible solute glycine betaine (GB; a quaternary ammonium compound) is one of the most efficient and compatible, protecting plants by acting as an osmolyte, maintaining water balance between the plant cells and the environment, and stabilizing macromolecules under stress condition (Papageorgiou and Murata 1995). GB is important in protecting plants against the damaging effects of abiotic stresses. Genetically engineered plants containing genes of the GB biosynthetic pathway confer enhanced tolerance to a range of abiotic stresses (Khan et al. 2009). Exogenous GB improves HT tolerance of Yunyan 85 tobacco cultivar plants by improving its physiological activities; and exogenous GB significantly increased the biomass, chl content, antioxidant enzymes SOD and POD (peroxidase) activities, and maintains higher free Pro content under HT stress, compared to non-GB treated plants. GB application also maintains membrane permeability and reduced MDA content in tobacco under HT (Lu et al. 2011). The enhanced HT (25–45 °C) tolerance of transgenic tobacco is due to the efficiency of PSII, enhanced CO_2 assimilation rate, and RuBisCO activase-mediated activation of RuBisCO induced by GB (compared to the wild type tobacco; Yang et al. 2005). Moreover, in a recent study Yang et al. (2007) demonstrated that the accumulation of GB in BADH-transgenic tobacco increased the tolerance of PSII to extreme HT ranges, even up to 50 °C. This transgenic tobacco improved the thermostability of the oxygen-evolving complex and action center of PSII which prevented HT-induced photoinhibition of PSII.

Protection of enzymes and protein complexes has been demonstrated to occur by GB against HT stress (Gorham 1995). GB plays vital roles in photosynthesis under HT stress, and protects PSII complex during photoinhibition and complex proteins against HT-induced inactivation (Allakhverdiev et al. 2007). High temperature stress (40 °C) adversely affected different physiological attributes of wheat, with a significant decrease of relative water content, chl content, net photosynthetic rate, carboxylation efficiency and apparent quantum yield, transpiration rate, stomatal conductance, and intercellular CO_2 concentration. A transgenic wheat T6 line was developed that possesses a gene encoding betaine aldehyde dehydrogenase (BADH) and GB overaccumulation in this wheat line improved those parameters and enhanced its HT tolerance, compared to wild-type wheat (Wang et al. 2010b). High temperature damages the cell membranes, including the chloroplast membrane and thylakoid lamellae (Wang et al. 2010a, b), but accumulation of GB in transgenic wheat improves membrane properties. This prevention is done by reducing or scavenging ROS through the enhancement of antioxidant components AsA and GSH together with increased activities of SOD and APX by GB (Wang et al. 2010b). Accumulation of GB and GB induced metabolite soluble sugars and Pro-decreased osmotic potential of the plant cell enhances the absorbance of water into the plant cells and induces opening of stomata and improved water stress of wheat plant cells (Wang et al. 2010a). The COD-transgenic *Arabidopsis* accumulated GB, protected RuBisCO activase, and showed enhanced tolerance to HT during the seedling growth stage (Alia et al. 1998).

5.1.3 Trehalose

Trehalose (α-D-glucopyranosyl-1,1-α-D-glucopyranoside, Tre) occurs in a large variety of organisms and serves as an energy source or stress protectant (Wingler 2002). Trehalose may act as a signaling molecule; both Tre and trehalose-6-phosphate can affect levels of genes involved in abiotic stress (Schluepmann et al. 2004; Bae et al. 2005). Trehalose is an appropriate membrane and molecule stabilizer, and replaces water by establishing hydrogen bonds with membranes, macromolecules, or biomolecule, under stress condition (Crowe 2007). The role of Tre under HT stress was not studied extensively. Trehalose is known as a stress protectant, but stress induces both its synthesis and degradation pathways which show differential responses under different stress conditions (Singer and Lindquist 1998; Miranda et al. 2007; Luo et al. 2014).

Transformation of tobacco with an *Arabidopsis thaliana* gene involved in Tre biosynthesis (heterologous expression of TPS1 gene) increased HT tolerance. At the temperature of 24 °C, all most all the seeds (100 %) germinated from control wild-type and transgenic lines. But at 35 °C, germination in wild-type tobacco showed less than 20 % germination. In contrast, the germination rate of transgenic tobacco lines was 80 and 90 % (Almeida et al. 2005). Trehalose pretreated wheat (*Triticum aestivum* L.) seedlings before HT (40 °C) stress ameliorated some adverse effects of HT. Exogenous Tre partially promotes HT recovery of wheat by the increase of nonphotochemical quenching, β-carotene content, and degree of de-epoxidation. Without these, Tre played roles in the increase of dry mass and leaf water content after recovery from the HT stress (Luo et al. 2014). *Arabidopsis* plants (engineered with yeast TPS1 gene) under the control of either 35S promoter or a yeast TPS1–TPS2 fused-genes construct under the control of a stress regulated promoter accumulated Tre at low levels and showed enhanced resistance to HT stress. Aberrant growth, color, and shapes were observed in plants transformed with the first construct. But the plants transformed with the second construct were better, without any morphological or growth abnormalities (Miranda et al. 2007). The effects of Tre on the activities of antioxidant enzymes were studied in wheat (*Triticum aestivum* L.) under HT stress. The activities of SOD, CAT, and APX and the ability of Tre to scavenge different ROS including H_2O_2 and $O_2^{\bullet -}$ were examined. Trehalose protected SOD activity slightly. But Tre did not significantly protect CAT and APX activities under HT stress,however, Tre scavenged H_2O_2 and $O_2^{\bullet-}$ in a concentration-dependent manner. The highest amount of H_2O_2 scavenging rate (95 %) and $O_2^{\bullet-}$ rate (78 %), were documented for 50 mM Tre application (Luo et al. 2008). Pretreatment with Tre decreased electrolyte leakage in *Arabidopsis thaliana* that was under HT which is supposed to occur by scavenging of reactive oxygen species (Stolker 2010).

5.2 Phytohormones

5.2.1 Abscisic Acid

Abscisic acid (ABA) is a plant hormone. ABA functions in many plant developmental processes such as germination, lateral root development, seedling growth, seed development, seed dormancy, and transition from vegetative to reproductive phase. Diverse plant processes are regulated by ABA under normal growth conditions as well as under abiotic stress conditions. Diverse roles of ABA in plants suggest the existence of multiple receptors and signal transduction pathways (Chinnusamy et al. 2008).

In *Arabidopsis thaliana*, suppression of seed germination at supraoptimal HT was associated with an increase of ABA content. High temperature stimulated ABA synthesis in *Arabidopsis* seeds by regulating ABA biosynthesis and metabolic genes which have signaling roles during germination of seeds (Toh et al. 2008). The roles of endogenous and exogenous ABA on pollen germination of HT tolerant and sensitive tomato varieties were investigated. Under normal temperature the endogenous ABA level was similar irrespective of tolerant or sensitive variety. But under HT stress the endogenous ABA level was higher in the tolerant cultivar, compared to the sensitive cultivar. Moreover, application of exogenous ABA could partly alleviate inhibition effects of HT stress on pollen germination (Shengli et al. 2005). High temperature stress (45 °C, 2 h) resulted in elevated H_2O_2 and MDA content and increased ion leakage, and HT also inhibited growth and decreased cell viability in the calli of reed (*Phragmites communis* Trin.) ecotypes (dune reed and swamp reed) where dune reed showed better HT tolerance. Exogenous application of ABA alleviated the HT stress symptoms through the enhancement of activities of SOD, CAT, APX, and POD which by the antioxidant properties reduced H_2O_2 and MDA content. Among two ecotypes of reed, dune reed showed higher tolerance after ABA applications (Ding et al. 2010). HT acclimation and exogenous abscisic acid may lead to the enhancement of thermotolerance in pea plants. The roles of ABA in regulating enzyme and gene for lipid metabolism [phosphatidylinositol-4,5-bisphosphate (PIP2)-specific phospholipase C (PLC)] and thermotolerance development induced by HT acclimation (38 °C) were investigated. Severe injury of pea plant was brought about by reduced antioxidant enzyme activity. The most severe head injury was investigated which resulted in increased MDA content and degree of wilting because of inhibition of PIP2-PLC activity. However, PsPLC gene expression was activated by exogenous ABA treatments that enhanced activity of PIP2-PLC and thermotolerance. Free ABA-associated reinforcement of thermotolerance resulting from HT acclimation was also demonstrated in this study (Liu et al. 2006). *Brassica napus* L. seedlings were subjected to short-term HT stress (45 °C, 4 and 8 h). At a normal temperature of 20 °C the ABA concentration did not change. But, ABA concentration was significantly elevated by HT stress alone. Moreover, ABA levels were further increased twofold after brassinolide supplementation with HT stress, which also enhanced tolerance, which proves the beneficial roles of ABA under HT stress (Kurepin et al. 2008). The roles of endogenous ABA and exogenously applied ABA were studied to confer HT tolerance in leaves and cultured grape cells (*Vitis* spp., cv. Venus and Veeblanc). Plants and cultured cells were acclimated at 38 and 36 °C, respectively. The increase of free and bound ABA was recorded two to threefold higher during HT acclimation, compared to the nonacclimated control which enhanced HT tolerance of acclimated treatment. HT tolerance was increased significantly by exogenous ABA application (7.6 or 9.5 μM) (Abass and Rajashekar 1993). In lettuce, genes encoding ABA biosynthetic enzyme (*LsNCED4*) helped to enhance germination under HT stress (Argyris et al. 2011). High temperature stress resulted in pollen sterility in rice. Tolerant Shanyou63 and susceptible Teyou559 cultivars of rice exhibited a marked decrease in pollen activity, pollen germination, and floret fertility. But the susceptible cultivar showed more damage effects, compared to the tolerant one. Shanyou63 (tolerant) retained significantly higher levels of free Pro and GAs contents and a lower level of ABA, along with higher pollen vigor and pollen germination rate even after prolonged HT treatment, compared to the sensitive cultivar (Tang et al. 2008).

5.2.2 Indole Acetic Acid

Auxins are a class of plant hormones widely distributed in different plant parts. Auxin is involved in plant developmental pathways through signaling action. The auxin function is involved in root growth and elongation, apical dormancy, wound response, flowering, fruit growth and development, wound responses, ethylene biosynthesis, and so on (Nemhauser et al. 2000; McSteen et al. 2007; Sorefan et al. 2009). In plants, auxin can be presented in different forms and different forms of artificially prepared auxins are applied exogenously to regulate plant growth. Indole-3-acetic acid (IAA) is recognized as the key auxin in most plants (Woodward and Bartel 2005).

Indole-3-acetic acid (IAA) is considered as the most abundant type of auxin in plants. It is supposed to be involved in temperature-dependent growth of plant cells. Karcz et al. (2008) found that growth of maize coleoptile segments in the presence of IAA was the highest at 30–35 °C. The high temperature response of plants is linked to increased auxin production. High temperature alters the cellular homeostasis of auxin, then auxin participates in signaling and regulating plant growth. Under elevated temperatures, roots adopt an auxin homeostasis mechanism which increases the auxin level, thus regulating root growth and gravistimulation (Sun et al. 2012). Plant architectural changes in response to the external environment have been known for a long time. Plants in elevated temperatures show phenotypic adaptations. Elongated hypocotyls in seedlings and elevated and elongated leaves at later developmental stages are common adaptive responses under HT stress. In *Arabidopsis* temperature-induced growth and elongation of hypocotyls were induced by auxin biosynthesis and signaling from cotyledons to the hypocotyls (de Wit et al. 2014). High temperature stress (42 °C) at different durations differentially affected IAA levels of rice plant. HT of 1 h increased IAA content by 1.1-fold. After 6 h of HT stress it was increased to about 1.3-fold. But IAA level was reduced to the normal level after 12 h of HT stress. It was mentioned that HT stress up to a certain duration increased the IAA level, which changed the IAA induced signal that changed developmental progress. Thus, IAA helped survival and adaptive growth responses under HT stress (Du et al. 2013). Different concentrations of 4-chlorophenoxyacetic acid (4-CPA) were applied in tomato plant to observe its fruit set, yield, and economic benefit of tomato under HTs. The application of 4-CPA significantly increased fruit set and yields of tomato. With the increase of concentration of 4-CPA from 0 ppm (control), 15 ppm, 45 ppm, and 75 ppm, the fruit set and yield showed increased values (Baliyan et al. 2013). High temperature represses the expression of *YUCCA* auxin biosynthesis genes for which endogenous auxin levels reduced in the developing anthers of barley and *Arabidopsis*. High temperature also inhibited the DNA proliferation in mitochondria, chloroplasts, and nuclei of developing panicles of barley. Various anomalies, such as DNA proliferation suppression, mitochondrial swelling, and overdevelopment of chloroplasts were noticed. But the application of exogenous auxin promoted the expression of DNA replication-related genes which helped to alleviate the damage effects and resulted in vigorous anther development (Oshino et al. 2011).

5.2.3 Gibberellic Acid

Gibberellins (GAs) are plant hormones that are involved in diverse aspects of growth and development. Current studies have highlighted that GA biosynthesis is affected and correlated with developmental, hormonal, and environmental signals; GA contents are affected by other plant growth regulators. GA can modulate other phytohormones, and GA concentrations in plant tissues are regulated during development and in response to environmental stimuli which are related to plants' stress responses and tolerance (Yamaguchi 2008; Alonso-Ramírez et al. 2009a).

In *Arabidopsis thaliana*, suppression of seed germination at supraoptimal HT was associated with repressed GA synthesis and increased ABA synthesis, which was due to the modulation of their biosynthesis and metabolic genes under HT stress (Toh et al. 2008). Exogenous application of GA reversed the inhibitory effect of HT stress in *Arabidopsis thaliana*. Seeds were HT stressed for 3 h at 50 °C. Germination and seedling establishment of *Arabidopsis* were inhibited by HT. Exogenous GA improved the seedlings' growth, compared to seedlings without

GA treatment. Moreover, transgenic plants overexpressing the GA-responsive gene stimulated in the *Arabidopsis* (*GASA*) family (*FsGASA4*) also showed improved responses to HT during seed germination and seedling establishment (Alonso-Ramírez et al. 2009b). High temperature both delayed and inhibited the germination of barley and radish. For barley, 35 °C and for radish 38 °C were considered as HT. The GA (900 μM) effectively recovered seedlings of both species from those damage effects. The GA-treated plants showed better performance in terms of germination percentage, coleoptile length, radical length, and fresh weight of germinated seedling. Furthermore, the better performances were observed in terms of shoot elongation and shoot generation percentage (Cavusoglu and Kabar 2007). As a hormone GA is responsible for growth, stress tolerance, and regulation of many enzymes such as amylase. Amylase hydrolyzes starch into maltose which has vital roles in plant growth. This experiment was carried out to study the effect of GA3 on α-amylase activity under HT stress conditions of four genotypes of mung bean (NM 19-19, NM 20-21, NM 121-123, and NCM 89). Seeds were sown in Petri dishes and incubated at different temperatures with and without 100 μM GA3. At lethal temperature (50 °C) for 2 h α-amylase activity was reduced in four genotypes of mung bean (NM 19-19, NM 20-21, NM 121-123, and NCM 89) which increased under a mild temperature of 40 °C for 1 h. The applications of 100 μM GA3 can further alleviate the effect of HT by increasing α-amylase activity. Genotypic variations were also observed as well as activity of amylase. The HT tolerance index was highest in NM 19-19 and lowest in NM 20-21 (Mansoor and Naqvi 2012). The effect of temperature on germination responses and roles of gibberellic acid (GA3) treatments were studied in kiwifruit (*Actinidia deliciosa* Chev. cv. Hayward) seeds. The seeds were treated with four GA3 concentrations at different concentrations: 0, 2000, 4000, and 6000 ppm. Then the seeds were exposed to different temperatures of 20 °C, 25 °C, 30 °C, and 35 °C. All the treatments significantly affected the kiwifruit seed germination. The GA3-treated kiwifruit seeds showed a higher germination rate, compared to untreated seed (Çelik et al. 2006).

5.2.4 Jasmonic Acid

Jasmonic acid (JA) is a member of the jasmonate which is a class of plant hormones. Jasmonic acid has roles in plant growth and development processes. It can regulate growth inhibition, senescence, tendril coiling, flower development, leaf abscission, tuber and bulb formation, and so on. Jasmonic acid and its various metabolites also function during plant responses to abiotic and biotic stresses (Zavala et al. 2004; Delker et al. 2006; Dar et al. 2015).

There are few studies that demonstrate the roles of JA under HT stress. The roles of JA under HT stress are primarily related to signal transmission. Rice seedlings under the HT stress of 42 °C reduced JA content. After 1 h of HT no significant difference of JA level was noticed. In contrast, after HT for 6 or 12 h, the JA level was reduced to about 85 %, compared to the control. This reduction was correlated to the adaptive response of rice plant under HT (Du et al. 2013). In cpr5-1 *Arabidopsis* *thaliana* mutant activation of JA signaling pathways enhanced tolerance of HT stress (45 °C, 2 h). When cpr5-1 *Arabidopsis thaliana* was crossed with jar1-1 (a JA-amino acid synthetase) was compromised, basal thermotolerance was enhanced. Exposure of wild-type *Arabidopsis* to HT stress led to the accumulation of jasmonates: JA, 12-oxophytodienoic acid (OPDA), and a JA-isoleucine (JA-Ile) conjugate. The role of JA in developing thermotolerance was also conferred by exogenous application of JA (5 μM) in wild-type *Arabidopsis* (Clarke et al. 2009). *Arabidopsis* treated with HT (33 °C, 3 days) did not express the auxin receptor gene *TIR1* or *ARF6* which were involved in JA production and linked to anther development and flower maturation (Nagpal et al. 2005; Sakata et al. 2010).

5.2.5 Salicylic Acid

Salicylic acid (SA) is a plant growth regulator of phenolic nature and signaling molecule. It regulates physiological and metabolic processes of plants and thus influences growth and development (Syeed et al. 2011; Khan et al. 2012). Salicylic acid by modulating plant responses confers tolerance to various abiotic stresses including HT stress (Kaur et al. 2009; Hayat et al. 2010a, b; Kadioglu et al. 2011).

The impact of SA pretreatment on photosynthesis was examined in the leaves of young grapevines under HT (43 °C for 5 h). Pretreatment of SA alleviated the HT-induced decrease in photosynthesis. Salicylic acid helped to maintain a higher RuBisCO activation state and maintained better PSII function and photosynthesis compared to nonpretreated grapevines under the same stress conditions. Salicylic acid enhanced levels of heat shock protein HSP21 which might have roles in contributing to HT tolerance (Wang et al. 2010c). The effects of heat shock, HT acclimation, and SA in different genotypes of *Brassica* spp. were investigated. Preincubation at 35 °C 3 h, followed by exposure of *Brassica* seedlings to lethal temperature at 45 °C for 3 h proved to be effective in imparting thermotolerance to the seedlings. HT acclimation for 3 h at sublethal temperature and SA pretreatments at 10 and 20 μM for 2 h prior to heat shock were found to be effective in imparting thermoprotection at the seedling stage. These pretreatments recovered *Brassica* seedlings from HT by increasing seedling length, reducing electrolyte leakage, and conferring membrane protection. The increased total soluble sugars, fresh/dry weight, and also increases in enzymatic activities of invertase, CAT, and POD, also conferred thermotolerance in HT acclimated or SA-treated seedlings (Kaur et al. 2009). High temperature (38 °C) stress significantly affected the antioxidative enzyme activity and resulted in increased lipid peroxidation or MDA content and degree of wilting in pea plants. Biosynthesis of free SA and exogenous application of SA both enhanced thermotolerance of pea plant by PsPLC gene expression, and modulating PIP2-PLC activity (enzymes in lipid metabolism) (Liu et al. 2006). Effects of exogenous SA (0, 0.1, 0.25, 0.5, 1, and 1.5 mM) on HT tolerance were studied in Kentucky bluegrass (*Poa pratensis* L.) exposed to 46 °C for 72 h. Influences of SA on regulating ROS, $O_2^{\bullet -}$, and H_2O_2 production and activities of antioxidant enzymes SOD and CAT were studied. Exogenous SA reduced oxidative damage and enhanced antioxidant enzymes. The SA application also induced regrowth of plant and leaf water content under HT. Among different SA concentrations, 0.25 mM was most effective in enhancing HT tolerance in Kentucky blue grass (He et al. 2005). Salicylic acid plays a key role in imparting tolerance against HT stress. Foliar spray of SA conferred HT tolerance in mustard. Foliar spray of SA accompanied with hardening at 45 °C (1 h) enhanced thermotolerance by regulating the H_2O_2 level and reduced CAT activity (Dat et al. 1998). Supplementation of acetylsalicylic acid enhanced HT tolerance of potato plantlets (Lopez-Delgado et al. 1998). Pretreatment of SA in plants of *Agrostis stolonifera* protected plants from oxidative damage by enhancing APX activity; but SA could not improve CAT and POD activity (Larkindale and Huang 2004). High temperature stress induced membrane injury in *Cicer arietinum*. Application of SA (100 μM SA solution) enhanced the protein and Pro contents and induced enzymes such as POD and APX, which were recognized to enhance HT tolerance (Chakraborty and Tongden 2005).

5.2.6 Brassinosteroids

The brassinosteroids (BRs) occur ubiquitously in the plant kingdom and their occurrence has been demonstrated in almost every part of plants, such as pollen, flower buds, fruits, seeds, vascular cambium, leaves, shoots, and roots (Bajguz and Tretyn 2003). The BRs play vital roles in the growth and development of plants from germination to reproductive and postreproductive stages (Taiz and Zeiger 2006). The BRs also confer resistance to plants against various biotic and abiotic stresses including salt stress (Hayat et al. 2010a, b), drought (Fariduddin et al. 2009), extreme temperature stress (Fariduddin et al. 2011; Gomes 2011), and toxic metal stress (Yusuf et al. 2011, 2012).

The effects of 24-epibrassinolide on barley and radish seeds were studied during germination and early seedling growth under HT. The 24-epibrassinolide recovered those seedlings from damage effects of HT stress and improved germination percentage, coleoptiles and radical length, shoot elongation, and fresh weight of seedlings (Cavusoglu and Kabar 2007). *Arabidopsis thaliana* seedlings were exposed to 43 °C. The temperature was imposed in the presence or absence of epibrassinolide for 1, 2, 3, or 4 h and then recovered at 22 °C for 7 days. There was high temperature stress, and increased bleaching of seedlings with the increase of exposure of duration. On the other hand, epibrassinolide-treated seedlings showed bleaching only after 4 h of the HT stress (Kagale et al. 2007). High temperature (34 °C) increased stress symptoms, i.e., necrotic areas on the leaves of bananas. Plants treated with a trihydroxylated spirotane analogue of BR for the effects of thermal stress alleviated its adverse effects and reduced injury symptoms from banana leaves and plant growth was also improved (González-Olmedo et al. 2005). Treatment of tomato seedlings with 24-epibrassinolide enhanced basic thermotolerance. The 24-epibrassinolide induced heat-shock proteins (hsps) hsp100, hsp90, hsp70, and low-molecular-weight hspsd, compared to untreated seedlings. The 24-epiBL treatment restricts the loss components of the translational apparatus to some extent during prolonged HT stress. This helps to increase the level of expression of some of the components of the translational machinery during recovery. The results were BR-treated plants had better photosynthetic efficiency, in vitro pollen germination, enhanced pollen tube growth and low pollen bursting, and higher fruit yield (Singh and Shono 2005). Ogweno et al. (2008) reported that foliar application of brassinosteroid alleviated the detrimental effects of HTs on the growth of tomato. Pretreatment of tomato plants with epibrassinolide before exposure to HT protects RuBisCO and other enzymes involved in the Calvin cycle and RuBP regeneration under HT stress. Thus, it alleviated photosynthetic inhibition, increased carboxylation efficiency, and enhanced antioxidant enzyme systems in leaves. High temperature stress of 43 °C reduced the protein synthesis in wheat leaves to 2.5-fold. In BR-treated leaves protein synthesis was maintained similar to those at 23 °C (Kulaeva et al. 1991). Kagale et al. (2007) showed that BR can augment tolerance to HT stress. In BR-deficient *Arabidopsis* mutants (det2-1 and dwf4), BR deficiency, a form of cellular stress or a developmental state leads to activation of the hsp genes that was supposed to occur via other hormones and signaling components. In tomato plants, HT created oxidative stress. Tomato leaf discs were exposed to HT stress after treatment with epibrassinolide enhanced the activities of CAT, POX, and SOD which reduced oxidative stress (Mazorra et al. 2002).

5.3 Antioxidants

5.3.1 Ascorbic Acid

Ascorbic acid/AsA occurs in all plant tissues being higher in photosynthetic tissues and meristems tissues (Smirnoff 2000). It is considered the most abundant, powerful, and water-soluble antioxidant. It not only scavenges ROS but also maintains some other components such as α-tocopherol. Through the AsA-GSH cycle AsA helps to maintain the reduced status of antioxidant components (Smirnoff 2000, 2005; Athar et al. 2008). The activity of enzymes APX, monodehydroascorbate reductase (MDHAR), and dehydroascorbate reductase (DHAR) of the AsA-GSH cycle are involved in AsA metabolism and recycling. Research studies have proven that enhanced activities of these enzymes and enhanced level of AsA have roles in conferring HT stress tolerance. Increased AsA content was maintained by an enhanced AsA recycling system in *Arabidopsis* under HT stress. Overexpressing DHAR in different subcellular compartments occurred by 1.5- to 5.4-fold under HT imposed *Arabidopsis* which enhanced foliar ascorbic acid levels 2- to 4.25-fold and a ratio of AsA/DHA about 3- to 16-fold, compared to wild-type. Transgenic plants showed a larger AsA pool size, lower membrane damage, a higher level of chl compared to control that was largely contributed by higher AsA levels (Wang et al. 2010d). In their study Almeselmani et al. (2009) observed that the HT-tolerant wheat cultivars (C 306) showed higher activities of SOD, APX, CAT, GR, and POX under HT stress, compared to susceptible cultivar (PBW 343). The expression of

APX and APX-mRNA level was also significantly higher in C 306 at the vegetative and anthesis stages under HT stress and were also regarded as indicative of enhanced tolerance against HT stress. *Triticum aestivum* L. seedlings exposed to HT (38 °C) significantly decreased the chl content and increased the lipid peroxidation/MDA and H_2O_2 levels and GSSG content. Exogenous NO supplementation in HT-treated seedlings enhanced AsA and GSH contents, upregulated the activities of APX, MDHAR, DHAR, and GR which reduced the HT-induced MDA, H_2O_2 content, increased content of chl, and thus improved HT stress tolerance as well (Hasanuzzaman et al. 2012). Cucumber seedlings subjected to HT stress showed physiological disorders. The functions of antioxidant components resulted in oxidative damages. Foliar spraying melatonin effectively restored physiological adaptation, restrained the accumulation of H_2O_2 and MDA in seedling leaves, and increased AsA and GSH content. Melatonin application also upregulated the activities of AsA metabolizing enzymes: APX, MDHAR, DHAR, and GR. The upregulated antioxidant system enhanced the H_2O_2-scavenging ability, inhibited the production of active O_2, maintained the stability of cell membrane, and reduced the damage of HT to the plants (Xu et al. 2010).

5.3.2 Glutathione

Glutathione (γglu–cys–gly; GSH) is an abundantly occurring antioxidant plant that localizes in almost all the cell compartments including the cytosol, endoplasmic reticulum, vacuole, mitochondria, chloroplasts, peroxisomes, and apoplast and performs vital roles such as scavenging of ROS (Gill and Tuteja 2010), sulfate transport, conjugation of metabolites, detoxification of toxic metal and xenobiotics (Xiang et al. 2001), signal transduction, expression of stress-responsive genes (Jimenez et al. 1998; Mullineaux and Rausch 2005). So, the roles of GSH are very important for conferring abiotic stress tolerances including HT stress.

HT-induced changes of GSH content and its metabolic enzymes regulate HT stress tolerance in plants. Apple plant (*Malus domestica* Borkh.) exposed to HT of 40 °C (2, 4, 6, and 8 h) showed oxidative stress which was indicated by higher MDA and H_2O_2 concentrations. High temperature stress up to 2 h significantly increased the total AsA, reduced AsA, total GSH contents. The activities of DHAR and GR increased up to 4 h of HT stress. The enhancement of antioxidant components was correlated with shorter term HT stress tolerance of apple plant (Ma et al. 2008). High temperature stress enhanced GSH metabolism enzymes in wheat, which helped to accumulate GSH and increase the GSH/GSSG ratio (Kocsy et al. 2002). The expression of a number of redox-related proteins including heat shock proteins (HSPs) and other defensive proteins were related to the accumulation of GSH in *Arabidopsis*. Accumulation of these proteins in plant cells regulated HT tolerance or sensitivity at different growth stages of *Arabidopsis* (Vivancos et al. 2010). An increase of GSH level in the flag leaf of wheat genotypes under HT stress enhanced tolerance at stages of grain development (Chauhan 2005). Turf grass species acclimated to HT stress enhanced synthesis of GSH and AsA, prevented generation of ROS, and improved HT stress tolerance (Xu et al. 2006). Heat shock treatment (40 °C) of maize roots decreased cysteine levels and increased GSH levels (Nieto-Sotelo and Tuan-Hua 1986). Pea showing higher GR activity under HT stress did not express the GR gene and the reason for the increased GR activity was supposedly due to the existence of translational or posttranslational regulation (Kurganova et al. 1999; Escaler et al. 2000). Tomato seedlings also accumulated GSH under HT to cope with that environment (Rivero et al. 2004). In our recent study, it was investigated that exogenous GSH has roles in conferring HT stress (HT, 42 °C) tolerance in mung bean (*Vigna radiata* L. cv. Binamoog-1) seedlings by modulating the antioxidant defense and methylglyoxal (MG) detoxification systems. Six-day-old seedlings were exposed to HT stress with or without exogenous GSH (0.5 mM for 24 h as pretreatment) for 24 and 48 h. HT stress at any duration significantly increased lipid peroxidation, H_2O_2, MG, and Pro content, the generation rate of $O_2^{\bullet-}$ and lipoxygenase (LOX) activity; decreased leaf chl and leaf relative water content (RWC), and the level of AsA; increased endogenous GSH and GSSG (glutathione disulfide); and decreased the GSH/GSSG ratio. For both treatment durations, activities of APX, GR, glutathione-*S*-transferase (GST) increased; the activities of MDHAR, DHAR, and glyoxalase I (Gly I) decreased; the activity of glyoxalase II (Gly II) increased at 48 h. Mung bean seedlings pretreated with exogenous GSH under HT improved chl and leaf RWC; increased APX (only after 24 h), MDHAR, DHAR, GR, glutathione peroxidase (GPX), GST (increased only after 24 h), CAT, Gly I, and Gly II activities; improved endogenous GSH content, and the GSH/GSSG ratio; and lowered GSSG content. Glutathione supplementation with HT stress significantly decreased MDA, H_2O_2, and MG content, $O_2^{\bullet-}$ generation rate, and LOX activity. Pretreatment with GSH resulted in better physiological performance, improved antioxidant and glyoxalase systems, and reduced MG and oxidative stress under 24 h of HT stress, compared with that of 48 h (Nahar et al. 2015).

5.3.3 Tocopherol

Alpha tocopherol (α-Toc or vitamin E) is a lipophilic antioxidant widely distributed and synthesized in all plants. The most important roles of α-Toc is the scavenging of ROS, preventing peroxidation of lipids and stabilization of membranes (Cvetkovska et al. 2005). The level of α-Toc in response to environmental stresses varies within the plant and magnitude of which, depending upon the stress and the plant species. Enhanced α-Toc levels contribute to plant stress tolerance (Munné-Bosch 2005). Beneficial roles of tocopherol have been documented in few research studies during HT stress. Seasonal changes induced HT stress tolerance and stress-related metabolite changes were observed in leaves and stems of sea buckthorn, apple, and pear. The high temperature stress of 51 °C significantly increased electrolyte leakage in all plant species. However, the sea buckthorn plant showed lower electrolyte leakage compared to other two plants species: apple and pear. The metabolic profile of these plants showed that sea buckthorn contained higher tocopherol content than other plant species which due to antioxidant properties reduced electrolyte leakage (Kanayama et al. 2013). The effect of tocopherol in embryo development and in oil quality of sunflower (*Helianthus annuus* L.) was investigated under HT stress (35, 37, and 40 °C). Total tocopherol content increased gradually from 12 to 33 days after anthesis. The content of γ-tocopherol content reached a maximum on 33 days after anthesis and then decreased. The embryos exposed to a temperature of 35 °C from 12 to 19 days after anthesis significantly increased the tocopherol yield per embryo. The increase of tocopherol levels at various developmental stages of sunflower embryo helped to prevent embryo and this also helped to maintain the high quality of the oil (Dong et al. 2007). Performances of *Triticum aestivum* seedlings were studied in the absence or presence of α-Toc (5 μM) under 25, 30, and 35 °C temperature for 7 days. High temperature stress resulted in severe damage effects of seedlings in terms of growth and physiology. The endogenous α-Toc level increased with increased temperature (except for the highest temperature). Again, when elevated exogenous α-Toc was applied, its endogenous levels increased further. The higher level of tocopherol contributed improved growth, chl content, and photochemical efficiency and reduced membrane damage under HT stress. Higher tocopherol was also correlated to the high antioxidant components (both enzymatic and nonenzymatic) of wheat seedlings (Kumar et al. 2013).

5.4 Signaling Molecules

Nitric oxide (NO) is a highly reactive and membrane-permeable free radical. Although previously NO was considered a highly toxic compound (Gordge 1998), the discovery of its signaling role in the cardiovascular system drew attention of the scientific world apart from its cytotoxicity (Korhonen et al. 2005). Depending upon the concentration, NO approaches both beneficial and harmful effects in plant cells; NO can affect ROS and directly interact with other molecules and signals (Arasimowicz and Floryszak-Wieczorek 2007). Plant development and physiological processes such as germination (Šírová et al. 2011), root development (Yemets et al. 2011), stomatal movement (He et al. 2011; Hancock et al. 2011), pollen tube growth (Šírová et al. 2011), flowering (Khurana et al. 2011), and leaf senescence (Procházková and Wilhelmová 2011) are regulated by NO. Nitric oxide has antioxidant properties and it acts as a signal to activate the antioxidant system which scavenges ROS under various abiotic stresses (Hao and Zhang 2010; Mazid et al. 2011). The similar roles of NO contribute extreme temperature tolerance in plants (Neill et al. 2002). The protective effects of NO were observed in *Vicia faba* where NO was involved in signal transduction in relation to JA-induced stomatal closure (Xin et al. 2005). Hasanuzzaman et al. (2012) investigated the role of exogenous NO in alleviating HT (38 °C) induced adverse effects on wheat (*Triticum aestivum* L. cv. Pradip) seedlings. Exogenous NO concomitantly enhanced the antioxidant system and glyoxalase system. The antioxidant components such as AsA and GSH as well as the GSH/GSSG ratio, and activities of APX, MDHAR, DHAR, GR, GST, and

CAT significantly reduced oxidative stress as indicated by the reduction of temperature-induced lipid peroxidation and H_2O_2 content. The glyoxalase system components, GSH and the activity of enzyme Gly I, detoxify the cytotoxic methylglyoxal and were also improved by exogenous NO application under HT stress. Exogenous NO prevented the loss of chl and improved chl *a*, chl *b*, and total chl content under HT stress (Hasanuzzaman et al. 2012). Increased NO production was observed in response to HT stress in tobacco, rice, and alfalfa (Qiao and Fan 2008). The high temperature stress created oxidative stress in wheat cultivars (C 306, HT tolerant and PBW 550, comparatively HT susceptible) which decreased membrane thermostability, increased lipid peroxidation, and decreased cell viability. The tolerant cultivar C 306 showed less damage under HT stress. Activities of antioxidant enzymes viz, SOD, CAT, APX, guaicol peroxidase, and GR increased with HT in both the cultivars. Treatment with sodium nitroprusside (SNP), a donor of nitric oxide (NO), increased activities of SOD, CAT, APX, guaicol peroxidase, and GR which alleviated HT-induced damages. The tolerant wheat cultivar C 306 showed better performance after SNP application with HT (Bavita et al. 2012). *Arabidopsis* mutants bearing *GSNOR1* gene encoding enzymes of the NO metabolizing pathway showed enhanced thermotolerance (Lee et al. 2008). Song et al. (2006) showed an enhanced antioxidant system and thermotolerance (45 °C, 2 h) by pretreating callus of *Phragmites communis* (reed) with NO donors viz. SNP and *S*-nitroso-*N*-acetyl penicillamine (SNAP).

Hydrogen peroxide/H_2O_2 is a reactive oxygen species produced within the plant stress under different stress conditions including HT. It has dual physiological functions within plants. Low concentrations of H_2O_2 act as a signal molecule which renders acclamatory signaling triggering tolerance to various stresses. A high concentration of H_2O_2 leads to programmed cell death (Quan et al. 2008). An increase of H_2O_2 under various abiotic stresses enhances gene expression of ROS scavenging enzymes and other enzymes of physiological functions (Uchida et al. 2002). There are some examples of H_2O_2 -induced HT tolerance in different plants. Pretreating rice seedlings with low levels (less than 10 mM) of H_2O_2 rendered the survival of more green leaf tissue, and of higher quantum yield for photosystem II, under HT stresses, compared to the untreated seedlings. Pretreatment with H_2O_2 induces ROS enzyme activities. It also induced the expression of transcripts for stress-related genes encoding sucrose–phosphate synthase, Δ-pyrroline-5-carboxylate synthase, and small heat shock protein 26 which proved the signaling roles of H_2O_2 enhance HT tolerance in rice seedlings (Uchida et al. 2002). The effects of H_2O_2 pretreatment on the germination and early seedling growth of barley was observed under various temperatures (20, 25, 30 and 35 °C). Hydrogen peroxide reduced delayed germination induced by HT. Beneficial roles of H_2O_2 under HT were also observed in terms of enhanced percentages of coleoptile emergence, elongated radicle and coleoptiles, and increased seedling fresh weights (Çavusoglu and Kabar 2010). Application of 1.5 mM H_2O_2 as a pretreatment protected cucumber (*Cucumis sativus* cv. Lvfeng no. 6) seedlings from HT stress. Cucumber seedlings were subjected to HT stress of 42/38, the performance of which was compared with plants subjected to 25/18 °C (normal temperature). High temperature stress disintegrated the membranes of 71.4 % of chloroplasts of leaf cells and increased MDA content resulted from membrane lipid peroxidation and increased endogenous H_2O_2. Pretreatment of H_2O_2 decreased chloroplast membrane damage to 33.3 %; it also decreased MDA and endogenous H_2O_2. The protection resulted from enhanced antioxidant system components such as activities of enzymes, including SOD, APX, MDHAR, DHAR, GPX, and GR. Thus exogenous H_2O_2 protected cucumber seedlings from HT stress by improving the antioxidant system (Gao et al. 2010).

Calcium (Ca^{2+}) is an essential macronutrient and has a major physiological role in plants, such as cell wall stabilization and membrane stabilization. Calcium is also recognized for transduction of signals under stress conditions of environment. Exogenous calcium chloride ($CaCl_2$; 20 mM) enhanced HT tolerance (43 °C, 2 h) in tobacco plants by improving photosynthetic gas exchange, photosystem II photochemistry, and the activities of antioxidant enzymes, and decreasing H_2O_2 and superoxide content (Tan et al. 2011). Lu et al. (2011) reported that HT stress caused oxidative damage to tobacco plants and reduced chl content and growth of plants. The effects of exogenously applied $CaCl_2$ (10 mmol L^{-1}) on HT affected tobacco plants were investigated. Exogenous $CaCl_2$ improved SOD and POD activities which helped to reduce MDA contents and membrane permeability. Calcium chloride also reduced the HT induced high Pro contents. Calcium chloride also improved leaf chl and recovered plant growth and biomass production (Lu et al. 2011). The high temperature signal is translated into an effective heat shock response by way of a specific membrane-regulated Ca^{2+} influx which develops thermotolerance in *Physcomitrella patens* (Saidi et al. 2009). *Arabidopsis*, maize, and wheat Ca^{2+} and calmodulin proteins were also involved in heat shock response (Li et al. 2004a, b; Liu et al. 2005; Zhang et al. 2009).

5.5 *Polyamines*

Polyamines (PAs) are low molecular mass aliphatic amines and organic polycations. Polyamines are widely distributed compounds in plants (Alcázar et al. 2006). The major PAs presenting in the plants are diamine putrescine (Put), triamine spermidine (Spd), and tetraamine spermine (Spm). Polyamines are involved in a vast number of plant developmental processes such as seed germination, growth, morphogenesis, differentiation, reproductive development, signaling growth and abiotic stress, and programmed cell death (Kusano et al. 2007, 2008; Gill and Tuteja 2010; Hussain et al. 2011; Ahmad et al. 2012). Thus PAs can act as a potent abiotic stress protectant. Polyamines enhance HT stress tolerance in diversified ways. High temperature stress differentially regulates the PAs level within the plants. Exposure to HT increased Spd and Spm levels and decreased Put levels in wheat (Goyal and Asthir 2010). High temperature delayed and inhibited the germination of barley and radish seedlings. Applications of different polyamines such as cadaverine, Put, Spd, and Spm alleviated the adverse effects of HT (Cavusoglu and Kabar 2007). High temperature stress in wheat plant reduced growth, disturbed the life processes, adversely affected reproductive development which resulted in a decreased number of spikes per plant, weight of grains per plant, weight of 1000 grains, and reduced crop yield and straw yield, harvest index. In contrast, foliar application of arginine or Put (1.25 and 2.5 mM) alleviated adverse effects of HT stress and improved the yield of wheat (Mostafa et al. 2010). Polyamines have roles in regulating the structure and function of the photosynthetic apparatus and the photosynthesis process also. Polyamine helps to contribute thermostability of thylakoid membranes under HT and thus increase photosynthetic efficiency (Kusano et al. 2007; Cheng et al. 2009). The PAs biosynthesis enzymes can be involved in the carotene biosynthesis process and accumulation in xanthophyll cycles and thus play vital roles in the photosynthesis process (Mehta et al. 2002). Polyamines directly scavenge the ROS like $O_2^{\bullet-}$ or act as positive modulators of antioxidant genes (Liu and Moriguchi 2007; Cheng et al. 2009). High temperature stress (35 ± 2 °C), 4 or 8 h) significantly increased the MDA contents in wheat seedlings. Exogenous application of arginine or Put (0.0, 1.25, and 2.5 mM) reduced the MDA contents by increasing SOD and CAT activities, compared to HT stress affected seedlings alone. Application of arginine and Put improved nucleic acid contents and protein electrophoretic pattern. Arginine or Put application increased both DNA and RNA content (Khalil et al. 2009). Polyamine influences synthesis of heat-shock proteins which have roles in developing HT stress tolerance (Königshofer and Lechner 2002).

5.6 Trace Elements

Trace elements at low concentration showed beneficial effect in HT stressed plants reported in several plant studies. *Euphorbia pulcherrima* "Ichiban," showed better tolerance to HT (35 ± 1 °C) after Si-treatment (50 mg L^{-1} Si as K_2SiO_3, Na_2SiO_3, and $CaSiO_3$) compared to control plants (Son et al. 2011). Application of 100 ppm SiO_2 in rice resulted in 2.5-fold reduction in HT stress-induced electrolyte leakage, thermal stability of lipids in cell membranes, structural and functional integrity of cell membranes, and increased the levels of polysaccharide in the cell walls (Agarie et al. 1998). Silicon supplementation increased the number and diameter of pollen grains of rice under HT stress (39 °C). Silicon application increased partial dehiscence (by 135 %) of the anthers of rice flowers, and gradually increased fully dehiscent anthers, which was 111 % higher in plants in the Si-fertilized treatment, compared to plants exposed to HT stress alone. Si also increased anther cracking rate (by 130 %) and the stigma pollination probability (by 66 %) which enhanced fertilization (Liu et al. 2005).

Few reports are available regarding the role of selenium (Se) under extreme temperature. Foliar spray of Se (75 mg L^{-1}) improved the performance of sorghum (*Sorghum bicolor*) plants grown under HT stress (40/30 °C). Selenium application improved the photosynthetic rate, stomatal conductance, and transpiration rate by 13.2 %, 12.4 %, and 8.11 %, respectively, compared with the unsprayed control. Selenium significantly increased CAT and POX activity which reduced oxidative stress as shown from reduced $O_2^{\bullet-}$ content, H_2O_2 content, MDA level, and membrane injury by 11.5 %, 35.4 %, 28.4 %, and 17.6 %, respectively, compared with unsprayed plants under HT stress. Ultimately, Se increased seed size, weight, and yield of sorghum under HT stress, compared to unsprayed seedlings (Djanaguiraman et al. 2010). In a recent report, Hasanuzzaman et al. (2014) investigated the protective role of Se in minimizing HT-induced damages to rapeseed (*Brassica napus* L. cv. BINA Sarisha 3) seedlings. Ten-day-old seedlings that had been supplemented with Se (25 μM Na_2SeO_4) or not were grown separately under control temperature (25 °C) or HT (38 °C) for a period of 24 h or 48 h in nutrient solution. HT stress caused a decrease in the chl and leaf RWC and increased MDA, H_2O_2, Pro, and MG contents. AsA content decreased at any duration of HT treatment. The content of reduced GSH increased only at 24 h of stress, whereas GSSG markedly increased at both duration of HT exposure with an associated decrease in GSH/GSSG ratio. Upon HT treatment the activities of APX, GST, and Gly I were increased, and the activities of MDHAR, DHAR, and CAT were decreased. The activities of GR and GPX remained unchanged under HT stress. However, the HT-treated seedlings supplemented with Se significantly decreased the lipid peroxidation, H_2O_2, and MG content and enhanced the content of chl, Pro, RWC, AsA, and GSH as well as the GSH/GSSG ratio. Selenium supplemented HT treated seedlings also showed enhanced activities of MDHAR, DHAR, GR, GPX, CAT, Gly I, and Gly II as compared to HT treated seedlings without Se supplementation. This study concludes that exogenous Se application confers HT stress tolerance in rapeseed seedlings by upregulating the antioxidant defense mechanism and methylglyoxal detoxification system.

6 Conclusions

Interest in the effect of temperature on the development of crops has been a prominent concern of plant scientists for at least 250 years. Many years ago a summation index for expressing the combined influence of time and temperature on the development of plants was developed. By totaling the mean daily temperature for each day of the months in late spring, and comparing this to the date that plants reached a certain stage of development, reveals that each species requires a certain amount of heat (degree-days) to reach a certain stage of development. It was the first quantitative effort to relate year-to-year variation in climate and the plant development and is used even now, with some modifications to estimate the time required for seed germination or maturation of crops under cool temperatures. However, the problem has been that growth is most rapid at an optimum temperature and declines at temperatures above and below this optimum until high and low temperature thresholds for growth are reached. A physiological summation index has also been developed based upon empirical measurements of the temperature dependence for growth considering the limitations to growth at both low and high temperatures (Kappen 1981; Berry and Raison 1981; Steponkus 1981; Ozturk and Secmen 1999). Differences among species in their response to temperature have been highlighted in many studies on the growth and survival of plants native to contrasting thermal regimes. In general the plants showing rapid growth are unable to live. The adaptations permitting better performance at one temperature can be detrimental at another temperature. These responses can be related to the thermal regimes of the plant taxa in their native habitats. Under controlled environmental conditions with high atmospheric humidity, abundant water, and nutrients the growth responses are conditioned by temperature. A quantitative analysis of growth over a range of temperatures has shown marked differences between the species in their responses to temperature, corresponding to the differences in the response of photosynthesis of normal healthy leaves of these species to temperature. However, the photosynthetic response to temperature may change after prolonged exposure to a given thermal regime. Therefore, there is a stronger inhibition of growth of cool climate species at high temperature as compared to short-term photosynthetic responses to temperature.

The differences between species in the amount of new growth directed to leaves, stems, roots, and flowers accounts for some differences in growth rate; however, the overall pattern of the response to temperature is dominated by the response of photosynthesis to temperature. Large genetically determined differences in the constitution of the basic growth-related physiological processes apparently underlie the different growth responses of different species in nature. The physiological acclimations permit a plant to grow over a range of thermal regimes such as may occur in a single site within a year. The importance of seasonal patterns of physiological activity in environments is also important in this connection. The ability to acclimate is most likely again genetically determined. The phenomenon of separate or partially separate growing seasons is common in many areas. Appropriate seed germination control is important for such seasonal displacement of activity. In temperate climates seasonal displacement of growth may result in differences in temperature that correspond to rather large geographical separations in the same season (Kappen 1981; Berry and Raison 1981; Steponkus 1981).

Temperature changes are an important factor in the metabolic functions, because the overall metabolism rate is affected, together with the balance between individual steps in metabolic pathways. The latter must be well buffered against the impact of changes in temperature so as to cope with the temperature variations the plants face in their native habitats. Plants from differing natural environments appear to have metabolic characteristics that compensate in part for the differences in tissue temperature: there may be qualitative changes in the properties of key constituents of the metabolic apparatus, such as new enzymes or different lipid mixtures, that have different temperature response characteristics; there may be quantitative changes in the amount of specific constituents which compensate for the effects of temperature on the rate of the corresponding reaction or there may be immediate responses of the existing metabolic systems that control or minimize the perturbation caused by a change of temperature. These strategies are not mutually exclusive (Kappen 1981; Berry and Raison 1981; Steponkus 1981).

High temperatures arising from global warming are predicted to be one of the factors producing negative effects on global plant life. The plants are continuously suffering from HT stress and their growth and development is altered leading to catastrophic losses in crop productivity and ending up with massive food insecurity (Ashraf et al. 2012; Hakeem et al. 2013). Although some plants are able to tolerate HT under natural conditions, temperatures exceeding the limit of adaptation cause HT stress, which has a substantial influence on the metabolism, plant viability, physiology, and yield. The unfavorable effects of HT stress can be mitigated by developing crop plants with improved thermotolerance using an assortment of genetic approaches. For this reason, a thorough understanding of physiological responses of plants to HT, mechanisms of HT tolerance, and possible strategies for improving crop thermotolerance is crucial. Exploring suitable crop improvements or ways to mitigate stress is one of the tasks of plant biologists. During the last few decades, application of exogenous phytoprotectants such as osmoprotectants, plant hormones, antioxidants, signaling molecules, polyamines, and trace elements have provided significant protection against HT-induced damage in plants. However, the precise mechanisms of protection and signal transduction pathways are still unclear. The appropriate dose and duration of treatment of the exogenous protectants and the proper methods of application need to be studied more precisely. In addition, further investigations considering molecular approaches are needed to reveal the underlying mechanisms of the protection under stressful conditions upon application of the protectants. Engineering plants to synthesize such compatible compounds may be an alternative way of developing thermotolerance in important crop plants that undoubtedly and fascinatingly represent a potentially important area of research. It is notable that thus far HT stress experiments are mostly confined to laboratory conditions and/or short-term studies. Therefore, one of our major future tasks should be to extend such studies to the field scale, with help from physiological, biochemical, and molecular approaches coupled with agronomic management practices for elucidation of authentic HT stress responses and subsequent effects on crop productivity (Kappen 1981; Berry and Raison 1981; Steponkus 1981).

The mechanisms adapting plants to different thermal regimes may be viewed as compensating mechanisms that permit plants to buffer the effects of these different thermal regimes on their metabolic systems. A major concern is the maintenance of appropriate rates of reaction and appropriate balance between reactions as temperature changes. Much remains to be learned concerning the biochemical details of these mechanisms.

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Agricultural Adaptation and Climate Change Policy for Crop Production in Africa

Moin Ahmad Khan and Mohd Sayeed Akhtar

Abstract Africa is considered among the most highly vulnerable regions to climate change because of extremes of drought, flooding, inappropriate land tenure systems, overdependence on rainfed agriculture, and widespread poverty. The impact of climate change is moderated by several factors such as access to land, inputs, credit, and markets. Thus, there is a critical need for decision makers at different levels in Africa to develop matching response strategies and policies to reduce vulnerability and foster resilient livelihood systems on a sustainable basis. The smallholder farming communities are inherently the most vulnerable to the negative impacts of climate change, and are always away from the advantage of any emerging opportunities due to resource constraints. About 65 % of national agricultural earnings in this continent is derived from the crop production of staple cereals, particularly maize. Due to shrinkage in cultivated area, production is also about 5–25 %, and the region's need is more chronic for food and feed. The climate change challenge is aggravated by diminishing soil productivity and the decline in natural resources has affected the livelihood of rural and peri-urban communities. The communities have drawn on their indigenous knowledge systems with the support of local institutions and traditional social safety nets to adopt the various multiple stress factors related to climate change and variability. However, there is still limited empirical evidence on the robustness of these systems in support of social collaborations and resolving conflicts arising from the resource scarcity in the wake of climate change. Comprehensive policy frameworks are therefore required to expand the climate change adaptation horizons beyond the boundaries of current farming systems. For instance, the risk of crop-based enterprises has increased by deteriorating climatic conditions. There is much evidence of multiple stresses characterising the existing poverty traps for the predominantly rural communities, and challenges of chronic food insecurity, but no evidence on how current agriculture and climate change policy frameworks are able to address these multiple stress factors against

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the increasing risk and uncertainty of agriculture as a source of climate change adaptation. Currently, the majority of the farmers lives beyond the reach of markets, yet agricultural development policies are hinged on the principles of market participation. Transformation of these subsistence farms into commercially oriented and market-driven production systems will effectively call for structural and process changes in knowledge systems, technology development and delivery, institutions, and policies.

The empirical research shows evidence of current and future impacts of climate change and variability on agricultural production systems, and their implications on the resilience of smallholder farming systems currently supporting the poorer and more vulnerable communities. Over the past decade, there has been a remarkable increase in awareness about climate change issues with diverse stakeholders, including policy makers. The lack of knowledge on the nature, magnitude, and direction of impacts at the indigenous community and national scales will likely continue to haunt decision-making processes regarding the development of robust strategies and policies to support adaptation. However, the regional agricultural sector has to undergo major transformation processes in order to meet emerging demands for adaptation. This may entail changes in the types and forms of information, knowledge, technologies, resource regimes, and institutions driving current production systems. There are still major knowledge gaps across disciplines on how local-level changes in climatic factors influence the socioecological processes that underpin agricultural production systems across spatial and temporal scales. Thus, it has been concluded that the policy making on climate change in Africa is not necessarily constrained by the lack of empirical evidence, but instead by the failure of policy makers to use available empirical evidence. The current failures in linking research to policy could be a major barrier to further research and development innovations for climate change adaptation. Evidence from limited climate change adaptation studies conducted with communities in the region revealed the importance of policy dialogue platforms as an integral part of research and development initiatives.

Keywords Climate change adaptation • Crop production • Environmental risks • Policy makers • Smallholders

Acronyms and Abbreviations

ACMAD	African Centre of Meteorological Application for Development
ACT	African Conservation Tillage Network
AGRHYMET	Agro-Hydro-Meteorology
APRM	African Peer Review Mechanism
APSIM	Agricultural Production System Simulator
ASARECA	Association for Strengthening Agricultural Research in Eastern and Central Africa

ASWAp	Agriculture Sector Wide Approach of the Government of Malawi
CA	Conservation Agriculture
CAADP	Comprehensive African Development Programme
CCAA	Climate Change Adaptation for Africa
CILSS	Comité permanent Inter-État de Lutte contre la Sécheresse au Sahel
COMESA	Common Market for Eastern and Southern Africa
CORAF/WECARD	Council for Agriculture Research and Development in West and Central Africa
DFID	Department For International Development (UK)
EAC	East African Community
EACCCP	East African Community Climate Change Policy
ECOWAS	Economic Community of West African States
ENDA-TM	Environnement et Développement du Tiers-Monde
FANRPAN	Food, Agriculture and Natural Resources Policy Analysis Network
FAO	Food and Agriculture Organization of United Nations
FARA	Forum for Agricultural Research in Africa
GCOS	Global Climate Observation System
GDP	Gross Domestic Product
GEF	Global Environment Facility
GHG	Green House Gas
GIS	Geographic Information System
ICRAF	World Agroforestry Centre
IDRC	International Development Research Centre
IFAD	International Fund for Agricultural Development
IITA	International Institute of Tropical Agriculture
IPCC	Intergovernmental Panel on Climate Change
IRAD	Institut de Recherche Agricole pour le Developpment (Cameroon)
ISFM	Integrated Soil Fertility Management
IUCN	International Union for the Conservation of Nature
IWMI	International Water Management Institute
LGP	Length of Growth Period
MDG	Millennium Development Goal
NAPA	National Adaptation Programme of Action
NARES	National Agricultural Research and Extension System
NEPAD	New Partnership for Africa's Development
NGO	Nongovernmental Organisation
OECD	Organization for Economic Co-operation and Development
PAR	Participatory Action Research
SADC	South African Development Community
SOFECSA	Soil Fertility Consortium for Southern Africa
UNDP	United Nations Development Programme

UNEP	United Nations Environment Programme
UNFCCC	United Nations Framework Convention on Climate Change
WAEMU	West African Economic and Monetary Union
WWF	World Wildlife Fund for Nature

1 Introduction

There is much undisputed evidence that shows the climate is changing and there is a lot of uncertainty regarding the pace and extent of the change, and the different impacts on the regions, sectors, nations, and communities. Climate has been a source of threat to agriculture for decades in Africa. With climate change, the continent's vulnerability is increasing, making Africa one of the most exposed regions in the world to climate change (IPCC 2007a). This uncertainty renders policy decision making more complex and magnifies the need for Africa to build its knowledge and analytical base and to strengthen the capacity of country and regional institutions in developing the evidence base needed to address climate change adaptation issues. At present, virtually all countries on the continent have performed some stocktaking of the variability and change in the climate and of the impact of those changes on livelihoods. The least developed countries in Africa have been supported by the United Nations Framework Convention on Climate Change (UNFCCC) to undertake National Adaptation Programmes of Action (NAPAs), and all remaining countries have, to varying degrees, pursued climate change adaptation measures on their own.

This chapter aims to help by identifying gaps in research and policy making for climate change adaptation in the agricultural sector. It further provides information and insights that can be used to bring researchers and policy makers together to improve evidence-based policy making that can enhance food security and protect different categories of populations vulnerable to climate change with respect to the following key questions.

1. What is the role of climate change challenges in the context of the multiple challenges and opportunities facing the agriculture sector in the African region?
2. What is the current state of knowledge on adaptation to climate change in the agricultural sector in the African region?
3. What is the current state of knowledge on whether and how research findings are integrated in agriculture sector policies in the African region?
4. What are the major gaps in research on adaptation to climate change in the agricultural sector?
5. What is needed to ensure that research findings are better integrated into agriculture sector policies?

In the past few decades, there has been growing research interest in and support for adaptation of agriculture to climate change in Africa. The research is called upon to ensure that the findings emerging from relevant field investigations in this domain are actually applied and used to inform policy makers about the necessity of harnessing efforts to make the necessary adaptation to climate change. Therefore, it is highly desirable to make a stocktaking synthesis and to review research results from relevant sources and the way these feed into and influence policies for climate change adaptation in key sectors, particularly the agricultural sector that employs the bulk of the population. It is critical that the concerned ministries in the African countries make policies informed by the existing body of knowledge on climate change, climate variability, and climate change impacts. Results generated by scientific research should, it is hoped, enable the respective sectors to build resilience against climate change and climate variability through adequate adaptation strategies and contribute to mitigation of climate change impacts through the use of improved and innovative technologies and management practices.

2 East Africa

With the change in the climate, the continent's vulnerability is deepening, which has made East Africa the most exposed region in the world regarding the effects of climate change (World Bank 2008). As a result, food and water security, livelihoods, shelter, and health are all at risk. Thus, there is growing research interest in and support for adaptation to climate change in Africa. It is thus imperative that the findings emerging from relevant research are applied and used to inform policy making with regard to climate change adaptation. It is critical that the sector policies are appropriately informed by the existing body of knowledge on climate change and climate variability generated from scientific research. These policies should enable the respective sectors to build resilience against climate change and climate variability through adequate adaptation strategies and contribute to mitigation of climate change through the use of improved and innovative technologies and management practices.

2.1 Overview of Agriculture in the East African Region

2.1.1 State of Knowledge on Climate Change and Impacts on the Agricultural Sector

The African continent is experiencing a general warming trend, with certain regions warming more than others (IPCC 2007a). The warming has been approximately 0.5 °C per century since 1900 (Hulme et al. 2001). Accordingly, temperature projections for East Africa indicate that the median near-surface temperature in the 2080–2099 period will increase by 3–4 °C compared to the 1980–1999 period. It has to be noted that this increase is about 1.5 times the projected global mean response.

Averages of precipitation projections for East Africa, however, quite clearly indicate an increase in rainfall in East Africa for the 2080–2090 period. The changes in precipitation are likely not to be uniform throughout the year, but will occur in sporadic and unpredictable events. It is estimated that the number of extreme wet seasons in East Africa in the 2080–2099 period will increase from about 5 to 20 % (Seitz and Nyangena 2009). It should, however, be noted that precipitation is also highly variable across the continent, although much of the continent has experienced decreases in annual precipitation. An increase in interannual variability has been noted with the indication that extreme precipitation events (floods and droughts) are on the rise (IPCC 2007a). Notwithstanding the inconsistency of predictions about climate change, the effects of the phenomenon are being experienced throughout sub-Saharan Africa, especially in areas typified by variable rainfall shifting growing seasons (IPCC 2001). Most African farmers, particularly those working in rainfed agriculture, have been affected in one way or another.

According to an analysis of countries by NAPA reports, the climate change is expected to increase the frequency and intensity of extreme weather events such as droughts, floods, landslides, and heat waves in the East African region. Despite rigorous and detailed vulnerability and adaptation options not being done in Uganda, the literature review and analysis of empirical information shows that in Uganda the frequency (seven times) of drought has increased between 1991 and 2000 (Government of Uganda 2007).

Climatic projections undertaken for Burundi and Rwanda (Baramburiye et al. 2013; Tenge et al. 2013) suggest that the countries' climate will become warmer (by 1.0–2.5 °C). Furthermore, the CSIRO model projects that temperature increases for the entire country will be in the 1.0–1.5 °C range. Given Burundi's tropical humid climate, this would imply high evaporation–transpiration rates, reducing the water available for plant growth and other uses. Likewise, in Kenya, recent studies that have considered projections of future climate change indicate future increases in mean annual temperature (average monthly temperatures) of broadly 1–3.5 °C over the range of models by the 2050s (2046–2065) (SEI 2009).

Projections of climate change in Tanzania expect a temperature rise of 2.2 °C by 2100, with a high increase (2.6 °C) in June, July, and August. According to meteorological data, monthly temperatures over the past 30 years have shown an upward trend (Government of Tanzania 2007). Although the literature states that rainfall is expected to continue to decrease in inner and dry land regions, coastal areas of Tanzania such as Dar-Es-Salaam are predicted to receive increased rainfall during the rainy season. A detailed account of climate change trends and effects in different sectors including agriculture in Tanzania is presented in its NAPA (Government of Tanzania 2007). Predictions show that the mean daily temperature will rise by 3–5 %. Some areas of northern Tanzania will likely get wetter (by 5–45 %), and others, especially in the south, will likely experience severe reductions in rainfall (up to 10 %). Rainfall is predicted to decrease by up to 20 % in the inner parts of the region and the country, with dry seasons becoming longer and having less rainfall, however, rainfall is predicted to increase by 30–50 % in the coastal areas.

Thus far, all the climate models for the East African region show that rainfall regimes will change, but these changes will vary with season and region. Most models project rainfall will increase on average, although some models project rainfall reductions in some months in some areas. Future predictions on extreme events (floods and droughts) vary much more widely. Many models indicate an intensification of heavy rainfall in the wet seasons, particularly in some regions, and thus greater flood risks. Droughts are likely to continue, but here too the projections are varied: some models project an intensification of these events, particularly in some regions, whereas other models indicate reductions in severity.

The range of models and results highlights a considerable uncertainty in predicting future effects, especially in relation to scenarios of future rainfall, floods, and droughts, although also due to future socioeconomic conditions and environmental services. Nevertheless, the analysis here does reveal potential areas of concern and helps focus priorities. Furthermore, it is essential to recognise this uncertainty, not to ignore it. There is a need to plan robust strategies to prepare for uncertain futures, rather than using uncertainty as a reason for inaction.

2.1.2 Challenges and Opportunities within the Agricultural Sector in the Context of Climate Change

The East African region exhibits considerable climatic and topographic variability. Much spatial and temporal variation in the response of different crops to climate change can thus be anticipated (Thornton et al. 2010). According to Moore et al. (2011), high spatial variability in yield is indicated in several key agricultural subregions of East Africa. It was further established that the broad range of projected crop yields reflects enormous variability in key parameters that underlie regional food security; hence, donor institutions' strategies and investments might benefit from considering the spatial distribution around mean impacts for a given region. Ultimately, global assessments of food security risk would benefit from including regional and local assessments of climate impacts on food production.

In East Africa, climate variability may have devastating impacts on economies. Major droughts typically result in sharp declines in agricultural output along with related productive activity and employment. In turn, this will lead to lower agricultural export earnings and other losses associated with a decline in rural income, and reduced consumption, investment, and destocking (World Bank 1994). Significant droughts also have additional multiplier effects on the monetary economy, the rate of inflation, interest rates, credit availability, levels of savings, government budget deficits, and external debt stocks. Of the top ten disasters in East Africa between 1970 and 2003, nine were caused by droughts (in 1969, 1979, 1980, 1984, 1989, 1990, 1992, 1999, and 2000). The greatest number of people affected by drought was in 1999–2000, totaling 4.4 million people in Kenya alone and about 14.2 million in other EAC countries (World Bank 2007). Many drought periods (1966–1970, 1979–1984, 1990–1992, and 1999–2000) in East Africa have been

Table 1 Major drought years and changes in GDP in the EAC countries

Drought years	Rainfall deficiency (%)	Agricultural GDP loss (%)	Gross GDP loss (%)	Loss in export earnings (%)
1970/1971	15.2	0.50	0.07	17.00
1978/1979	22.0	1.58	1.13	7.98
1980–1983	29.0	27.00	10.00	20.00
1990/1991	10.2	(0.22)	0.43	17.50
1992–1994	11.9	3.64	(1.60)	(9.00)
1999/2000	7.0	11.18	1.44	(8.48)

Adapted from Seitz and Nyangena (2009); figures in brackets are computed from rainfall data and country accounts bulletins

associated with the El Niño Southern Oscillation. Table 1 presents the implications of major droughts on GDP for the countries of the EAC.

Although the potential to invest in irrigation in much of East Africa is high, poor performance of large-scale irrigation schemes in the region and competition for diminishing water resources suggest that smallholder irrigation is preferable. When population grows rapidly, this leads to conflict over natural resources, especially water, which is a limited resource in the first place, given the erratic rainfall, droughts, seasonal shifts, shorter seasons, and dry spells (Liwenga et al. 2012). Climate change and increasing population contribute to water scarcity and limit its availability for irrigation and other productive uses (Turner 2006).

Climate change and variability can impose additional pressures on water availability, water accessibility, and water demand in the East African region. A regional analysis of climate change within the East African region shows that the supply and quality of water will both be affected (Seitz and Nyangena 2009). Changes in the physical and chemical aspects of lakes and rivers, such as higher water temperatures, shorter periods of ice cover, and decreases in river and lake ice thickness have been documented in recent decades. In East African lakes (Edward, Albert, Kivu, Victoria, Tanganyika, and Malawi), deep-water temperatures, which reflect long-term trends, have risen by 0.2–0.7 °C since the early 1900s (IPCC 2007a). Interannual lake-level fluctuations and lake-level volatility have been observed in lakes, including Tanganyika, Victoria, and Turkana since the 1960s. This is probably due to periods of intense drought followed by increases in rainfall and extreme rainfall events in late 1997 (IPCC 2007a).

Despite the fact that the key livelihood activity is agriculture, a recent study examining rainfall, food security, and human mobility in Tanzania indicated that amid an increase in uncertainty in agriculture and high land pressure, nonfarm activities will be the key elements of livelihood strategies for many youths in the future (Liwenga et al. 2012). The findings further established that climate variability causes short- and long-term changes that result in water deficits affecting crop production, and thus influencing decisions to migrate. Accordingly, the preference of the youths has been for migrating to other areas, both rural and urban. Future destinations of migration included cities such as Dar-Es-Salaam, Mwanza, and Arusha.

The migration pattern could be temporal or seasonal depending on the effects of climate-related events such as droughts.

Furthermore, research findings have established that agricultural biodiversity is central to human existence and in particular to climate change adaptation. Farmers, rural communities, and indigenous people around the world maintain the diversity of crops, forage, and tree species, as well as the many other plant, animal, and microbial species found in and around their production areas and depended on to provide food, fuel, medicine, and other products. Climate change, in combination with other drivers, is expected to alter agricultural biodiversity substantially (Chakeredza et al. 2009).

2.2 Climate Adaptation Research in the Agricultural Sector

The adverse impacts of climate change and variability being aggravated by increasing average global temperatures are a threat to the livelihoods of people in almost all sectors of the economy in East Africa. Severe droughts, floods, and extreme weather events, associated with the climatic variability phenomenon of the El Niño Southern Oscillation, are occurring with greater frequency and intensity in the region. This is worsening the state of food security and threatening all the other drivers of economic development. The following section highlights some of the findings based on climate change adaptation research in the agricultural sector in the sub-Saharan region with a specific focus on the East African region.

2.2.1 Vulnerability and Adaptation of Crop-Farming Systems in the Region

Changes in rainfall amounts and seasonal patterns are already being experienced in many parts of the world, including the East African region, creating problems for vulnerable farmers and other land users in securing their livelihoods, and increasing the risks they face. The frequency and intensity of extreme climatic events such as heat waves and erratic heavy rainfall, as well as the long-term chronic effects of higher temperatures, are set to increase (IPCC 2012).

In East Africa, the link between climate and agriculture as the main livelihood activity is very strong. As East Africa depends heavily on rainfed agriculture, rural livelihoods are highly vulnerable to climate variability such as shifts in growing season conditions. Furthermore, agriculture contributes 40 % of the region's GDP and provides a living for 80 % of East Africans (Seitz and Nyangena 2009). In 2003–2004, all East African countries suffered from weather-related food emergencies, and can therefore be considered vulnerable to the impacts of climate change on their agriculture.

The various studies conducted in the East African region indicate that smallholder farmers have observed changes in the amount and distribution of precipitation, associated with increases in temperature (Komba and Muchapondwa 2012). Farmers' responses have generally been using short season and drought-resistant crops, employing irrigation, adjusting planting dates, and planting trees to adapt to the potential negative impacts of climate change on their agricultural yields (Ibid).

Some specific studies and analyses of potential impacts of climate change on crops in East Africa are available. It is reported in Tanzania that in the same farming system, positive and negative impacts may occur on different crops. It is suggested that impacts on maize, the main food crop, will be strongly negative for the Tanzanian smallholder, whereas impacts on coffee and cotton, significant cash crops, may be positive (Agrawala et al. 2003). In Kenya, a 1-m sea-level rise would cause losses of almost US$500 million for three crops (mango, cashew nut, and coconut) (Government of Kenya 2002). In the tea-producing regions of Kenya, a small temperature increase of 1.2 °C and the resulting changes in precipitation, soil moisture, and water irrigation could cause large areas of land that now support tea cultivation to be largely unusable. As Kenya is the world's second largest exporter of tea, and as tea exports account for roughly 25 % of Kenya's export earnings and employ about three million Kenyans (10 % of its population), the economic impact could be tremendous (Simms 2005; WWF 2006). The Ugandan NAPA demonstrates the dramatic impact that a 2 °C temperature rise might have on coffee-growing areas in Uganda. The analysis indicates that most areas could become unsuitable for coffee growing (Government of Uganda 2007).

According to a study on the economics of climate change in East Africa, major rainfall deficient years and the major macro variables show a significant relationship between rainfall amount and GDP (Seitz and Nyangena 2009). Focusing on major drought years, a negative rainfall anomaly, especially one of more than 10 %, brings a loss in agricultural GDP. When the 1999–2000 drought affected an estimated 13.2 m people, destroyed crops, caused deaths of animals, and affected millions of people, the rainfall anomaly was about 29 % based on the annual average figures, although the rainfall distribution was not uniform. The crop production loss was recorded at 16.8 %. In the two consecutive years of 1999 and 2000, agricultural GDP in the EAC declined by 11 and 14 %, leading to a GDP growth rate of −5 and −5.8 %. An increase in temperature significantly lowers the value of output for Kenya, Uganda, and Rwanda.

Based on the study of economics of climate change in Kenya, it is reported that adaptation can reduce the economic costs of climate change but it too has a cost (SEI 2009). The costs of adaptation are still emerging. A number of categories of adaptation have been identified that relate to the balance between development and climate change. An initial estimate of immediate needs for addressing current climate impacts as well as preparing for future climate change in Kenya is US$500 million per year. The cost of adaptation by 2030 will increase: an upper estimate of the cost is likely to be in the range of $1–2 billion per year. The study has also prioritised early adaptation across the sectors. These studies demonstrate that adaptation has potentially very large benefits in reducing present and future damages. However, although adaptation reduces damages, it does not remove them entirely.

Research on adaptation to climate change in the agricultural sector indicates that the choices for adaptation depend on the available options in specific agroecological zones. Furthermore, the government can play a significant role by promoting adaptation methods appropriate for particular circumstances, crops, and agroecological zones. According to the United Nations Food and Agriculture Organization FAO (2011a), conservation agriculture (CA) provides many benefits, including to the environment, such as addressing land degradation. CA helps foster agrobiodiversity and other essential environmental services, which improve agroecosystem resilience, helping farmers to better face risks and uncertainties. The productivity and diversity of crops also increase incomes and improve rural livelihoods. CA practices such as using leguminous crops, crop residues, cover crops, and agroforestry enhance soil fertility and lead to the stabilisation of soil organic matter and in many cases to a heightened sequestration of carbon in the soils.

CA assists farmers in adapting to climate change by establishing conditions that increase agroecosystem resilience to stress. Increasing an agroecosystem adaptive capacity allows it to withstand climate variability better, including erratic rainfall and temperature variations and other unexpected events. Drawing on strong local community and farmers' knowledge and agrobiodiversity, ecological agriculture improves soil quality by enhancing soil structure and its organic matter contents, which in turn promotes efficient water use and retains soil moisture. Such conditions simultaneously enhance soil conservation and soil fertility, leading to increased crop yields (FAO 2011a). CA is claimed to be a panacea for the problems of poor agricultural productivity and soil degradation in sub-Saharan Africa, reported to increase yield, reduce labour requirements, improve soil fertility, and reduce soil erosion. It is thus being actively promoted by international research and development organisations. Some studies, however, raise concerns regarding the practicality of CA, which contributes to its low uptake in most sub-Saharan African countries (Giller et al. 2009). The concerns include decreased yield, increased labour requirement, and an important shift of the labour burden to women. This calls for critical assessment regarding under which ecological and socioeconomic conditions CA is best suited for smallholder farmers in the region.

According to Chakeredza et al. (2009), a number of organisations worldwide, for example, the FAO, are promoting the use of indigenous and locally adapted plants and animals as well as the selection and multiplication of crop varieties adapted or resistant to adverse conditions. The selection of crops and cultivars with tolerance to abiotic stresses (e.g., high temperatures, drought, floods, and high salt content in soil) allow harnessing genetic variability in new crop varieties. National programmes should have capacity built and long-term support to use these options. The study concludes that agroforestry can enhance adaptation to climate change through provision of diversified tree products and services.

The predicted effects of climate change must be introduced into development planning, including land-use planning, natural resources management, infrastructure design, and measures to reduce vulnerability in disaster reduction strategies. The array of adaptation options is very large, ranging from purely technological measures to managerial adaptation and policy reform. For developing countries, availability of resources and adaptive capacity building are particularly important. Based on anticipated climate change and impacts on water resources in Africa, the Intergovernmental Panel on Climate Change (IPCC 2001) identified four necessary adaptive strategies.

(a) *Adaptive measures*. Measures should be adopted that would enhance flexibility, resulting in net benefits in water resources (irrigation and water reuse, aquifer and groundwater management, desalinisation), agriculture (crop changes, technology, irrigation, husbandry), and forestry (regeneration of local species, energy-efficient cookstoves, sustainable community management).
(b) *Risk sharing*. A risk-sharing approach between countries will strengthen adaptation strategies, including disaster management, risk communication, emergency evacuation, and cooperative water resources management.
(c) *Enhancement of adaptive capacity*. Local empowerment is essential in decision making in order to incorporate climate adaptation within broader sustainable development strategies. Most countries in Africa are particularly vulnerable to climate change because of limited adaptive capacity as a result of widespread poverty, recurrent droughts, inequitable land distribution, and dependence on rainfed agriculture.
(d) *Diversification*. To minimise sensitivity to climate change, African economies should be more diversified, and agricultural technology should optimise water usage through efficient irrigation and crop development.

All of the above adaptive strategies need to have strong gender perspectives. These strategies must consider the physical, gender, and socioeconomic factors that create vulnerability. The reality of climate stresses combined with diverse socioeconomic and gender roles and uneven ownership of resources such as land make it necessary to re-examine the adoptive conditions based on realities on the ground. The diverse roles and responsibilities become very significant in adoption of climate change strategies for different categories of people. Gender inequalities in access to resources, such as land and other productive assets, including credit, extension services, information, and technology, must be taken into account with the root causes of gender inequality in developing mitigation activities and adaptation efforts.

As explained above, despite the usefulness of climate-smart initiatives in the East African countries, only very few initiatives are being realised. In Kenya, for instance, there are several ongoing initiatives through the World Agroforestry Centre (ICRAF), and a number of initiatives are being developed. By yielding a broad range of products, including fruits, fuel wood, timber, and resins, agroforestry helps farmers to diversify their incomes, providing them with greater protection against market failures and climate fluctuations. The use of nitrogen-fixing trees and shrubs increases soil fertility and crop yields. Trees also help farmers adapt to climate change, as perennial crops are better able to cope with droughts and floods than annual crops. Trees sequester much greater quantities of carbon than annual crops, and in some instances provide farmers with access to the carbon market. Agricultural carbon finance presents an opportunity for climate justice for smallholder farmers who are most vulnerable to climate change, while addressing the mitigation challenge. The triple win of higher yields, climate-resilient farming, and carbon sequestration is theoretically possible. However, these wins are subject to complex socioeconomic, political, and cultural conditions that have strong bearing on their achievements, as the KACP case of Kenya highlights. In any case, farmers have a right to informed engagement in such mitigation and adaptation programmes. Exclusion, marginalisation, and dependency may result from uninformed engagement and create new vulnerabilities. Capacity building about agricultural carbon finance for national policy makers and farmers is critical.

Regarding the whole aspect of carbon trading in Africa, the argument that carbon trading offers real benefits to the poor in Africa is simply not credible (Reddy 2011). It is found that if anything, offset schemes allow industrialised countries to maintain their affluent lifestyles by exporting the burden of reducing greenhouse gas emissions to countries in the South. It further argues that fundamentally, inequality is behind the climate problem, and the search for solutions must involve industrialised societies making fundamental structural changes to their lifestyles, energy practices, and their production and consumption systems.

2.3 Agricultural Policies for Climate Change Adaptation

Although the East African countries have developed policies and established institutions or structures for environmental management and climate change issues, there are still a number of gaps pertaining to mainstream climate change matters in sectoral plans and programs. Some key gaps were identified in the reviewed policies, macro strategies, and sectoral strategies and plans.

Most African countries gained independence in the 1960s, a time when central planning was widely seen as a promising strategy for economic development (Anderson and Masters 2008). In this environment, elected governments across Africa typically kept the marketing boards and other instruments for intervention that had been developed by previous administrations, expanding their mandate and increasing public employment, in many cases as a means for electoral politics. In the 1970s, growing fiscal deficits, current account imbalances, and overvalued exchange rates were supported by project aid and loans at a time of zero or negative real interest rates, as governments chose to ration credit and foreign exchange rather than expand the money supply. The result of growing government intervention was political instability and weak market institutions. It can be seen that during the first two to three decades, climate change issues were not key issues in the development agenda.

Most of the policies and strategies in the East African region, especially those produced prior to 2000 and before the production of NAPA, do not directly link to climate change matters. Even though they articulate matters that may contribute to climate change adaptation and mitigation, they have to be reviewed or implemented in the context of the changing climate, which has significant implications for sustainable natural resources management, sustainable development, and community livelihoods. This is largely attributed to the fact that climate change is an evolving and cross-sectoral concern, which requires proactive, collective, and gender response adaptation measures among interrelated sectors.

All the NAPA documents in the EAC have recognised the negative impacts of climate change on the main ecosystems in various ways depending on the disaster. Accordingly, drought is the single most important and widespread disaster in Uganda, Tanzania, Burundi, and Rwanda. According to the Government of Uganda (2007), the drought is increasing in frequency and severity, particularly in the semi-arid Cattle Corridor. It affects a wide range of ecosystems, sectors, and key social and economic programmes. Furthermore, storms, heavy rains, and floods are the second most important cluster of disasters. This cluster of disasters has negative impacts on key sectors such as water resources, health, soils, wildlife, and infrastructure. Loss of lives and physical injuries are associated with this cluster of disasters. The effects of this cluster of disasters are most pronounced in the highland ecosystems.

Recently, Burundi worked out a Biological Biodiversity National Strategy and Plan of Action (SNPA-DB). Burundi also submitted its first National Communication to the UNFCCC. Regarding the Convention to Combat Desertification, Burundi further developed a National Plan of Action to Combat Desertification (PAN-LCD) (Government of Burundi 2007). In Rwanda, with a present weak adaptative capacity to the climate change due to a high level of poverty, drought, recurrent floods, strong dependence on rainfed agriculture, and a serious energy crisis hindering human development, building adaptative capacity necessitates the integration of adaptation measures to climate change in the global strategies of sustainable development (Government of Rwanda 2006). This principle is strongly applied in the choice of immediate and urgent adaptation measures identified in the framework of Rwanda's NAPA by the analysis of coherence and synergies with the sectoral policies and strategies of the country.

Apparently, climate change has not thus far been adequately mainstreamed or integrated in sector-specific plans and strategies. Where efforts have been initiated, as in the water and agriculture sectors, there are still remaining implementation gaps. As such there is a need to develop climate change policy and legislation in the East African countries which will promote establishment of an institutional framework for mainstreaming climate change matters in sectoral plans and programmes. Shayo (2006) notes that the completed Tanzanian NAPA was prepared in order to look at the country's climate change-related vulnerabilities in various sectors which are important for the economy. The completion of the NAPA in Tanzania will certainly enable the country to further integrate adaptation issues in the development process.

For most of the countries in the East African region, agriculture is the key to achieving broad-based, pro-poor economic growth and attaining the MDGs. Throughout history, increases in agricultural sector productivity have contributed greatly to economic growth and the reduction of poverty (OECD/FAO 2006). However, in the last decades, both governments and the donor community for various reasons have neglected the agricultural sector in Africa. From the 1980s onward, agriculture became increasingly ignored in many developing countries. This happened both in development cooperation policies – where the share of agriculture dropped from 18 % in 1980 to 4 % in 2007 – and in national budgets. The share of official development assistance (ODA) to agriculture dropped significantly, falling from a peak of 17 % in 1979, the height of the Green Revolution, to a low of 3.5 % of total investment in 2004. It also declined in absolute terms: from US$8 billion in 1984 to US$3.5 billion in 2005 (World Bank 2008). Public investment in agriculture, particularly in smallholder agriculture and food security, from international donors and national governments declined sharply during the 1980s and 1990s, however, this period also witnessed strong growth in private sector agribusiness and the food industry, with structural shifts in research to private crop breeding and agrichemical development (de Janvry and Sadoulet 2010).

In assessing how much policy reform had taken place in Africa by the mid-1990s, how successful it had been, and how much more remained to be done, the World Bank (1994) concluded that progress had been made but reforms remained incomplete. The report also stressed that poor macroeconomic and sectoral policies were the main factors behind the poor performance of sub-Saharan Africa's economy between the mid-1960s and the 1980s. Food markets were controlled by state enterprises, which also monopolized the import and distribution of fertilisers and other inputs that were often supplied to farmers at subsidised prices and on credit. The prices farmers received were generally low because of taxation or high costs incurred by state enterprises. The negative impact of such policies on agricultural prices was particularly significant in the case of export crops. During this period, African governments followed a development strategy that prioritised industrialisation, with a clear bias against agriculture (Kherallah et al. 2000). Since the implementation of structural adjustment programmes promoted by international financial institutions in the 1980s and 1990s, policymakers and academics have argued about the causes of and solutions to the African crisis, as well as the impact of the structural adjustments (Mkandawire 2005).

Encouragingly, the New Partnership for Africa's Development (NEPAD), the economic programme of the African Union (AU), has recognised the importance of agriculture and wants to boost Africa's growth through agriculture-led development. This has led to establishment of two major initiatives, namely the Comprehensive Africa Agriculture Development Programme (CAADP) and African Peer Review Mechanism (APRM), NEPAD activities concerned with agricultural policies and institutions in sub-Saharan Africa.

- CAADP is directed at agricultural sector policies including:
    (a) Improving national agricultural policy frameworks
    (b) Strengthening institutions and governance
    (c) Enhancing agricultural productivity
    (d) Fostering trade, investment, economic growth, and sustainable development
    (e) Promoting regional integration
- APRM aims at improving national governance and institutional settings in general. Given the prominence of agriculture in the economies of Africa, APRM may be expected to influence the agricultural sector as well.

It is important to highlight some common weaknesses of both APRM and CAADP, which strongly hamper their effectiveness in influencing national agricultural policy processes and the policies themselves. According to Zimmermann et al. (2009), the key weaknesses are:

- Both initiatives, when implemented at the national level, were not well linked to ongoing, national policy processes but instead are stand-alone initiatives. Not enough care has been devoted to the docking of the processes onto and the channeling of the results into national processes. The implementation of the initiatives at the country level is planned without taking into account the existing policy cycles and windows of opportunities such as five-year plans, revisions of Poverty Reduction Strategy Paper (PRSP), or agricultural sector planning cycles. This, however, is crucially important because there can and should be only one relevant policy document per sub-sector. The incentives to adopt the results of the national exercises are not as high in cases such as immediate additional donor support or government spending. Therefore, it is difficult to create new windows of opportunities. In most cases, this is not even desirable inasmuch as reforms should not be bought but owned by convincing insiders. The initiatives do not sufficiently take into consideration the lengthy processes of agricultural policymaking, including parliamentary procedures that most democratic countries are committed to, particularly at the level of specific law formulation.
- Both APRM and CAADP tend to invite participation in an ad hoc manner. They both, and particularly CAADP, overestimate the capacity, especially of disadvantaged groups, to get involved in national policy processes. They do little to improve long-term and quality of participation in terms of participation capacity, networking, stabilisation of participatory structures, mandates of participants, and so on. Rural populations are easily left out in a self-organised process and disadvantaged in terms of representation by civil society organisations due to the low media presence and population literacy, leading to an urban bias.
- Similarly, APRM and CAADP overestimate the flexibility and the mechanisms of donor support and probably also the lack of willingness to align. Despite the lip service paid to agricultural development, the agricultural sector is nominally funded in aid allocations, although the food price crisis may have changed that recently. However, for governance issues in general, lack of interest is certainly not the case. Governance is rated very high on donor agendas. The fact that even the political governance findings of APRM are not acknowledged and supported quickly and massively by donors indicates that the lack of embeddedness into national policies (see above) and the lack of flexibility of donors may be important handicaps for such initiatives. Realignments are very slow, following the revision of key policies, and most often require lengthy adjustment processes such as bilateral negotiations and agreements. Donor representatives at the national level often do not have the mandate to react quickly.
- National and regional policy arenas are not yet well linked. The connections of agriculture, food security, and trade policies are not yet fully taken into account in setting the agenda for CAADP at the regional and national level. Although

> much focus in the African regions is put on regional integration in general, the specific implications and regulatory consequences for agriculture are not yet fully recognised. The link is almost absent in APRM and theoretically strongly developed but in practice limited in CAADP. However, regional aspects of agricultural policy making are predicted to increase in importance, if not due to CAADP and agricultural policy mandates for Regional Economic Communities (RECs), then due to regional trade policies, which heavily affect agricultural sectors of member countries. For the time being, however, regional links in African agricultural policies are not yet very strong.

The process to develop the East African Community Climate Change Policy (EACCCP) was initiated in response to a directive by the EAC heads of state made during the 11th Summit of the Heads of State held in Arusha, Tanzania in 2009, to develop a regional climate change policy and strategies to respond urgently to the adverse impact of climate change, including addressing the challenge of food insecurity as a result of the extreme climatic conditions associated with climate change.

The aim of the policy is to address the adverse impacts of climate change in the region, in response to the growing concern about the increasing threats of the negative impacts of climate change to national and regional development targets and goals. In addition, the development of the policy is in fulfillment of the objectives of the EAC: to develop policies and programmes aimed at widening and deepening cooperation among partner states in accordance with the Treaty for the Establishment of the EAC. The policy is consistent with the fundamental principles of the treaty establishing the EAC and principles of international environmental law, according to the EAC Protocol on Environment and Natural Resources, the Protocol on Sustainable Development of Lake Victoria Basin, and the UNFCCC. The preparation of the policy was also guided by emerging issues and challenges faced by the region and potential benefits and opportunities in light of the increasing climate change.

The policy was prepared in a consultative and participatory approach by experts drawn from the five EAC partner states (Burundi, Kenya, Rwanda, Tanzania, and Uganda) and facilitated by the EAC Secretariat and the Lake Victoria Basin Commission Secretariat. The effective implementation of the prioritised climate change adaptation and mitigation measures identified by the policy will depend on collaborative efforts by all relevant actors towards minimising the overall affects of climate change and consequently lead to regional social and sustainable economic development.

2.4 Gaps in Climate Change Adaptation Research and Policy in the Agricultural Sector

Agriculture is one of the most widely studied sectors with respect to the effects of climate change, as it is considered one of the most vulnerable sectors. Climate change and variability present new development challenges, particularly in sub-Saharan African countries where the majority of the population depends on climate-sensitive activities, in particular agricultural production (FAO 2010a; IFPRI 2010; Thompson et al. 2010).

It is further important to look through a gender lens and analyse the diverse situations of men and women across socioeconomic backgrounds when planning strategies. Each community has its own unique and dynamic situation. Gender roles and privileges vary from one location to another. Informed adaptation planning necessitates detailed gender analysis of each community. Sex-disaggregated data should be collected where possible to understand how men and women are being affected differently and how adaptation strategies may have different impacts on them. Analyses should include effective participatory processes that are gender responsive.

During the past 20 years in Africa, a great deal of emphasis has been placed on the development of national agricultural research strategies and priorities, which have often occurred within the context of World Bank loans (IAC 2004). In addressing research issues that address climate change adaptation the following four African farming systems have been reported to offer the greatest potential for reducing malnutrition and improving agricultural productivity:

- The maize-mixed system, based primarily on maize, cotton, cattle, goats, poultry, and off-farm work
- The cereal/root crop-mixed system, based primarily on maize, sorghum, millet, cassava, yams, legumes, and cattle
- The irrigated system, based primarily on rice, cotton, vegetables, rainfed crops, cattle, and poultry
- The tree crop-based system, based primarily on cocoa, coffee, oil palm, rubber, yams, maize, and off-farm work

The literature review indicates that there is a lack of detailed and systematic analysis of how climate change and variability affect the various agroecological zones of the East African Region. This implies that more research is needed to examine the existing farming systems to ascertain the effect of climate change in each of the respective agroecological zones. The literature review further shows that more research has been conducted in analysing the effects of climate change and variability on crop production. Apparently, little has been documented regarding the effect of climate change on the agricultural production systems in the East African region. The analysis of the gender implications of climatic changes on the agricultural sector also does not feature much in most of the articles reviewed. In considering how the impacts of climate change influence coping mechanisms, it is important to consider how both proactive and reactive adaptation mechanisms affect men and women differently. Without a gender-sensitive approach to adaptation planning, it is impossible to develop strategies that will meet the needs of both men and women and be effective in the long term.

CA appears to have potential in strengthening adaptation and resilience. However, empirical studies are needed in different agroecological zones to test its contribution to adaptation planning, including mainstreaming climate change issues in the agricultural sector. CA is claimed to be a panacea for the problems of poor agricultural productivity and soil degradation in sub-Sahara Africa. Yet, according to some studies there are concerns regarding the practicality of CA, which contributes to its low uptake in most sub-Saharan African countries. A great deal of the literature reviewed does not discuss much on the challenges associated with the employment of such practices. This calls for rigourous research on the applicability of CA in enhancing resilience in the various agroecological zones of the EAC in the context of climate change.

3 West Africa

There is evidence globally of changing climate, but there is uncertainty regarding the pace, extent, and effects on subregions, nations, communities, and sectors as well as adaptation to climate change. This uncertainty renders policy making difficult and underscores the need for Africa to build its knowledge base to strengthen the capacity of regional and national institutions in developing the evidence base for addressing climate change adaptation issues. The overall objective is to enhance the knowledge base and to support research-based policy formulation for climate change adaptation in the agricultural sector in West Africa. The expected outputs are:

1. A synthesis of research related to climate change in the agricultural sector accomplished
2. Research and policy gaps related to climate change adaptation in the agricultural sector identified
3. Key stakeholders and opportunities in climate change adaptation in the agricultural sector identified

3.1 Overview of Agriculture in West Africa

3.1.1 Climate Change Challenges

Key Characteristics of the Climate

Jalloh et al. (2011a, b, 2013) have summarised the key characteristics of climate in West Africa: average annual rainfall of 250–550 mm; length of growing period (LGP) of 60–90 days in the semi-arid zone (Sahel); 550–900 mm, LGP of 90–165 days in the Sudan savannah (dry subhumid); 900–1500 mm, LGP of 165–270 days in the Guinea savannah (subhumid); and 1500–4000 mm, LGP of 270–365 days in the coastal zone (humid). Rainfall is subject to a high degree of spatial and seasonal variability because of the modulation of the seasonal cycle linked to the position of and intensity of the intertropical convergence zone (ITCZ) plus the magnitude of rainfall due to squall lines. As a result, seasonal characteristics of monsoon rainfall (onset, length, and cessation of the rainy season), seasonal rainfall amount, and the intraseasonal distribution show high interannual variability. Sunshine is uniformly high, especially in the semi-arid and arid zones (2500–3000 h per annum). Temperatures are high across the region, with a mean annual temperature above 18 °C; within 10 °C north and south of the equator mean annual temperature is about 26 °C with a range of 1.7–2.8 °C, the diurnal range being 5.5–8.5 °C. Between latitude 10°N and the southern parts of the Sahara, the mean monthly temperature can rise up to 30 °C. Maximum temperatures range from 30 to 33 °C in countries along the coast to 36–39 °C in the Sahel.

Climate Change Projections for West Africa

Climate change scenarios are uncertain for West Africa, especially when it comes to rainfall. Namara et al. (2011) reported that global circulation models (GCMs) predict the start of the rainy season 1–2 months earlier than what is observed and that the observed Sahelian climate between 1961 and 1970 is at variance with the climates simulated by six GCMs of the Intergovernmental Panel on Climate Change (IPCC). The models show a marked rainy season almost throughout the year, along with a considerable bias (140–215 mm/year) in annual aggregate rainfall estimates as compared to the observed data. There are also discrepancies between models; in the coastal zone, for example, Sierra Leone, ECHAM4, and HADCM2 give rainfall values similar to observed values whereas CSIRO-TR and UKTR give lower values than observed (Jalloh et al. 2011b). The average rise in temperature between 1980–1999 and 2080–2099 is predicted to be +3 °C in the coastal zone of West Africa, rising to +4 °C in the western Saharan region (IPCC 2007a), that is, 1.5 times the global average (according to the most recent IPCC assessment, global mean surface change for 2016–2035 relative to 1986–2005 will likely be in the range of +0.3 to +0.7 °C. For the period 2000–2050, Nelson et al. (2010) reported lower temperature increases for West Africa (Table 2). Increase in intensity of rainfall per rainfall event is predicted across Niger, Mali, and Burkina Faso, whereas Senegal and Southern Nigeria may see decreases in rainfall per rainy day (Ericksen et al. 2011).

Table 2 Temperature and precipitation scenarios for West Africa from general circulation models (GCM)

GCM	Change in precipitation (%)	Change in precipitation (%)	Change in average minimum temperature (%)	Change in average maximum temperature (%)
CNRM-CM3	8.2	51.3	2.75	2.03
CSIRO MK30	1.9	11.7	2.05	1.73
ECHAM 5	1.3	7.9	2.21	1.98
MIROC 3.2	−1.7	−10.9	2.26	1.57

Adapted from Nelson et al. (2010)

Overview of the Range of Possible Impacts of Climate Change in the Agricultural Sector

There are several likely impacts of climate change on agriculture in the region. Land suitable for cropping and length of growing period could change, with the Sahelian zone potentially the hardest hit. The effects of the rise in temperature and extreme rainfall events on crop yields will generally be negative and crops least tolerant to drought will suffer most. Farming calendars will change. Climate change may entrain deforestation as more lands are brought under cultivation. Mangrove forest in coastal areas, some used for rice cultivation, may be damaged. Flows of major rivers would fall, in a situation of increasing demand for irrigation water and population growth. Rise in sea level will lead to entry of salty water into agricultural lands and cause degradation. By 2100, farm sector losses due to climate change and variability could reduce regional GDP by 2–4 % (Namara et al. 2011). These effects would be moderated by local conditions and factors such as availability and accessibility of adaptation options, markets, settlement patterns, institutions, and policies.

Overview of Key Causes of Vulnerability in the Agricultural Sector

Three major components or causes (social, economic, and environmental) of vulnerability of agriculture in relation to climate change have been identified (Brooks et al. 2005; Adebo and Ayelari 2011). Factors contributing to social vulnerability include rapid population growth, poverty, hunger, poor health, low levels of education, gender inequity, fragile and hazardous locations, frequent natural disasters, conflicts, poor national and local governance (including the marginalisation of certain groups in decision making), and lack of access to resources and services including knowledge and technology. Economic vulnerability refers to the importance of agriculture in the national economy, trade and foreign exchange, aid and investments, international prices of agricultural commodities and inputs, and production and consumption patterns. Regarding environmental vulnerability the concerns are for management of natural resources, such as land degradation, water scarcity, deforestation, and the threat to biodiversity.

3.1.2 Implications of Climate Change for Other Key Challenges (and Opportunities) for the Agricultural Sector

Water Resource Supply, Demand, and Governance Challenges

Detailed, up-to-date information on surface and underground water resources in sub-Saharan Africa (SSA) is scarce, but it is known that between 1971 and 1989 there was about a 30 % reduction in the flow of the River Niger and a 60 % reduction in that of the River Senegal and River Gambia (IUCN 2004; Namara et al. 2011). Water resources are much greater in the coastal compared to the Sahelian

Table 3 Major international water basins and irrigation potentials in West Africa

Basin	Countries	Area (km^2)	Irrigation potential (ha)
Lake Chad	Cameroon, Chad, Niger, Nigeria	2,381,635	1,163,200
Niger	Benin, Burkina Faso, Cameroon, Chad, Cote d'Ivoire, Guinea, Mali, Niger, Nigeria	2,273,946	2,816,510
Senegal	Mali, Senegal, Guinea, Mauritania	483,181	420,000
Volta	Benin, Burkina Faso, Cote d'Ivoire, Ghana, Mali, Togo	394,196	1,487,000

Adapted from FAO (2005)

zone, but the former can still have problems of scarcity. Molden et al. (2007) distinguished between physical scarcity of water and economic scarcity and classified countries in the coastal zone as experiencing economic scarcity, that is, investments needed to keep up with growing water demand are constrained by financial, human, or institutional capacity, although water is physically available.

Rainfed production (highly susceptible to climate change) accounts for about 75 % or more of agricultural production across West Africa (Molden et al. 2007). However, only 15–30 % of the rainfall is used as productive 'green water', that is, water stored in the soil; in arid areas it may even be below 10 % (Shah et al. 2007). The substantial irrigation potentials of four major international water basins in West Africa, each providing water to four or more countries, are shown in Table 3.

Conflicting needs (dams for irrigation and energy) have contributed to the decline of the water resources of Lake Chad, illustrating that governance of the international river basins cannot be done unilaterally and requires cooperation of the countries sharing the waters.

West African countries have varied challenges and opportunities in managing the impacts of climate change on water resources. In general, there are negative implications for the following: water quality (salinity in coastal areas), surface and groundwater systems (drop in level of lakes such as Lake Chad), precipitation, sea level rise, and the dynamics of oceans (Urama and Ozor 2010). A good example is Nigeria, which has an 800 km low-lying coastal belt running from Lagos to Calabar. Lagos, Africa's most populous city, is seriously affected by sea level rise. Flooding has resulted in the removal of beach fronts and sometimes adjacent roads, leading to acute traffic disruption and destruction of property, social conflicts, and migration. In the semi-arid areas such as Niger, pastoralists migrate in search of water and seasonal grazing, leading sometimes to conflicts with settled agrarian communities.

Land Resources

Climate change can result in increased temperatures, reduced rainfall, or excessive rainfall events leading to a reduction in soil vegetative cover and serious water and wind erosion, and therefore soil crusting and land degradation. Lands in coastal areas are being degraded from the intrusion of salt water resulting from a rise in sea levels. A reduction in agricultural production is the overall consequence.

Studies of the Niger Basin showed that threats to livelihoods and ecosystems through deterioration in the natural resource base have been posed by a combination of population growth, unsustainable resource use, and deteriorating climatic conditions (Namara et al. 2011). However, it is difficult to separate the effects of climate change from other stresses on land resources. Le et al. (2012) used response of green biomass to rainfall to separate areas of 'human induced decline biomass' from 'climate driven dynamics' in the Volta Basin. Their study, based on datasets covering 1982–2003, showed that land degradation occurred in 8 % of the Volta Basin (83 % of which is Ghana and Burkina Faso), but that when atmospheric fertilisation (caused by CO_2 and NO_x in the atmosphere) is considered, up to 65 % of the land is degrading in terms of soil quality and vegetation productivity. The degradation was most severe in woodland (12,200 km^2), agricultural land (8300 km^2), shrub land (7300 km^2), and dense woodland (1600 km^2).

Soil nutrient depletion (soil mining) contributes to poor soil quality. Crasswell et al. (2004) reported moderate to high nutrient ($N + P_2O_5 + K_2O$) losses in several countries in West Africa for the period 1996–1999 as follows: Mauritania, 58 kg/ha; Burkina Faso, 54 kg/ha; Ghana, 53 kg/ha; Nigeria, 50 kg/ha; Mali, 45 kg/ha; and Senegal, Benin, and Niger, about 38 kg/ha each. Country-level soil mining data, however, may hide hotspots requiring urgent attention (Dreschel and Gyiele 1999).

Using land for growing nonfood crops such as biofuels, sometimes in the context of land grabbing by multinational companies from small-scale farmers, presents opportunities for diversification in response to climate change and increased incomes of rural communities and increased national GDPs (Ngigi 2009), but caution is required because these crops may compete with food crops for land, nutrients, and water, resulting in landless people and social unrest. Biofuel plants such as Jatropha are becoming popular in Mali and Ghana.

Use of Local and Indigenous Knowledge and Its Combination with Scientific Knowledge

The term indigenous knowledge refers to knowledge systems developed by a community in a particular place over time, as opposed to scientific knowledge. West African crop farmers have coped with changing environments, sometimes due to climate variability. Despite some successes of indigenous coping strategies, there is evidence of breakdown because of a rapidly changing environment in terms of land use, sociopolitical, and cultural stresses (IPCC 2007a). Dieye and Roy (2012) reported from a case study in the semi-arid north of Senegal that although crop farmers have a clear appreciation of changes in natural resources, few new adaptive/coping strategies to climate change beyond traditional ones were envisaged. Traditional responses may not be adequate at present and especially in the future climate change stresses, and may even lead to unsustainable responses in the longer term (DFID 2004). Rather than utilising indigenous knowledge on its own, or discarding it completely, its incorporation into climate change policies can lead to the development of effective adaptation strategies that are cost effective and sustainable. Indigenous knowledge provides suitable entry points for research and development of climate change adaptation practices (FAO 2008).

Climate Change and Conflicts

The underlying causes of conflicts are complex and may be political and social, but climate change may contribute to conflicts between states and within states because of competition for water use if the increased supply to meet growing demand cannot be assured (Niasse 2005; Urama and Ozor 2010). When water supply is short, pastoralists come into conflict with crop farmers. Such conflicts can be so serious that they result in deaths on both sides, as happened in Nigeria between the Fulani cattle herders and sedentary crop farmers over grazing land and water bodies. These kinds of conflicts amongst smallholders are frequent in other parts of the semi-arid zone of West Africa. The drying up of Lake Chad, to which climate change has contributed strongly, has led to confrontations between fishermen, farmers, cattle herders, indigenous Chadians, and Chadians from elsewhere (Urama and Ozor 2010). Land degradation through salinisation and consequent shortage of land might also encourage conflicts. However, Sayne (2011) observed that attributing conflicts to climate change in Nigeria calls for caution because the scientific, social, economic, and political implications of a changing climate in the country are poorly understood. Unresolved conflicts would certainly increase vulnerability to climate change.

3.2 Vulnerability and Adaptation of Agricultural Systems

3.2.1 Vulnerability and Adaptation of Crop Farming Systems

Scientific Evidence for Implications of Climate Change for Crop Farming in a Multistressor Context

Vulnerability to climate change is a state that is governed not only by climate change itself, but by multiple processes and stressors (CGIAR 2009). Poverty, access to land, soil nutrient mining, use of low-yielding crop varieties susceptible to pests and diseases, high postharvest losses, and poor access to credit and markets are all challenges facing the smallholder. The relative contribution of climate change to low agricultural productivity, taking all the other challenges into consideration, is difficult to assess quantitatively. Several GCMs including CSIRO-MK 3.0, MIROC 3.2, CNRM-CM 3, and ECHAM 5 have been used to outline scenarios of climate change by region, broad agroecology, and country. Although increasing temperatures in the Sahel are clearly indicated by the GCMs, there is some uncertainty in rainfall-related projections for West Africa. This uncertainty carries over when crop simulation models are integrated into GCM scenarios (Mertz et al. 2009).

The results of modeling studies have been reported for millet, sorghum, maize, rice, groundnut, beans, cassava, cocoyam, and cotton in West Africa (Huq and Reid 2005; Sarr et al. 2007; Nelson et al. 2010; Jalloh et al. 2013). Roudier et al. (2011), performed an analysis of 16 modeling studies and concluded that a wide spread of yield changes ranging from −50 to +90 %, with a median of −11 % for West Africa. The predicted impact is larger in the northern Sudano–Sahelian countries (−18 %) than in the southern Guinea countries (−13 %) and the negative impacts on the crop productivity increase in severity as warming intensifies. The negative impact on yield was attributed mainly to projected temperature increases, although rainfall (uncertain to predict) has the potential to reduce or increase this impact. Apart from temperature and rainfall, increases in the concentration of carbon dioxide in the atmosphere as a result of climate change may have direct impacts upon yield levels of certain crops.

Recently Jalloh et al. (2013) employed the same models and parameters for all 11 West African countries and predicted that there will be a significant continuous decline in crop yields between 2000 and 2050 if no adaptation measures are undertaken. CSIRO and MIROC models predict a general decrease in maize yields of 5–25 % over baseline in most parts of the countries which lie on the southern coast of West Africa and a yield increase of 5–25 % in the Sahel zone. Both models indicate a yield decline in the northernmost parts of Mali, Burkina Faso, and Nigeria. Table 4 shows predicted production changes by country, assuming increased use of inputs (including improved varieties) and improved management practices. The models predict 5–25 % drop in yields of sorghum across most parts of West Africa, with yield losses greater than 25 % in some parts of Togo, Benin, and adjacent areas of Ghana and Nigeria. Yields of rainfed rice are predicted to decline by 5–25 % in most parts of Cote d'Ivoire, Ghana, and Togo based on CSIRO and MIROC and in Nigeria based on CSIRO. For groundnut, the two models predict decreases in yields of 5–25 % across most parts of West Africa, but lower yield changes in Sierra Leone, Liberia, and Guinea. Yield increases of 5–25 % are predicted for some parts of northern Cote d'Ivoire, Ghana, Burkina Faso, and Nigeria.

Apart from crop yields, effects of climate change have been assessed in terms of crop revenues and length of growing period. Kurukulasuriya and Mendelsohn (2008) estimated a multinomial logit to predict the probability of agroecological zones. A model was then used to calculate baseline values of cropland and revenues and estimates of the impacts of climate change made on them. They reported reduction in crop revenue in West Africa of between US$9.2 billion (−17 %) and US$17.4 billion (−32 %) for the Parallel Climate model (PCM) and the Canadian Climate Centre model (CCC), respectively, by 2100. Jones and Thornton (2009) studied arid and semi-arid zones of sub-Saharan Africa, including West Africa and found that under scenarios in which the emission of carbon is high the number of reliable growing days (RGD) would drop below 90 days for several hectares of marginalised land. For a low-emission scenario the acreage would reduce by 50 %. The significance of the finding is that if RGD drops below 90, rainfall may be so inadequate

Table 4 Changes in area, yield, and production for maize in West Africa under A1B scenario

	2010			2050					
Country	Yield (tons/ha)	Area (thousands of ha)	Production (tons)	Yield (tons/ha)		Area (thousands of ha)		Production (tons)	
				Min	Max	Min	Max	Min	Max
Benin	1.08	748	810	1.87	2.08	886	929	1660	1911
Burkina Faso	1.41	458	646	2.20	2.61	408	424	900	1105
Cote d'Ivoire	1.11	745	824	1.98	2.09	787	825	1601	1661
Gambia	1.93	16	31	2.55	2.73	17	18	43	48
Ghana	1.52	825	1255	2.44	2.59	945	990	2311	2538
Guinea	1.15	138	159	2.14	2.29	161	168	344	386
Guinea Bissau	1.90	16	31	2.03	2.15	18	19	37	41
Mali	1.39	381	531	2.31	2.61	304	313	703	803
Niger	0.78	4	3	1.57	1.69	1	2	2	3
Nigeria	1.29	4696	6070	1.74	1.90	4405	4829	7664	9181
Senegal	1.98	132	263	2.76	2.90	144	151	398	439
Sierra Leone	1.92	10	20	2.98	3.10	10	11	30	33
Togo	1.11	477	531	1.78	2.01	318	334	567	661

Adapted from Nelson et al. (2010) and Jalloh et al. (2013)

Note: A1B scenario assumes fast economic growth, a population that peaks in mid-century, and the development of new and efficient technologies, along with the balanced use of energy resources

that maize cultivation, with the common varieties, will not be possible and even the cultivation of millet will be difficult.

Options for Strengthening Adaptive Capacity and Supporting Crop Farming

1. *Research approach and options*: The International Development Research Centre (IDRC) and the UK Department for International Development (DFID) through their shared programme, Climate Change Adaptation in Africa (CCAA), have reported success stories with the use in West Africa of Participatory Action Research as a tool for strengthening smallholders' indigenous adaptive capacity to climate change. The approach favours joint identification of climate change related problems and probable solutions, practical action, and shared learning among researchers and many of those most affected: farmers, village elders, meteorologists, agronomists, academics, local leaders, government officials, and civil society organisations (Gologo 2012). Another example of a participatory approach being used in adaptation to climate change in West Africa is the testing, with the UN Food and Agriculture Organisation

(FAO) support, of climate change best practices and technologies in Farmers Field Schools in Burkina Faso (GEF 2012) and in Liberia (Government of Liberia 2013). Nevertheless, the largest part of the knowledge obtained on best bet technological options has been through conventional research methods.

A number of research and development practitioners have advocated the use of one or more of the available adaptation options which are in accord with the aspirations of the National Adaptation Programmes of Action (NAPAs) and national documents, to improve the response of farmers to climate change and variability and support crop farming (Howden et al. 2007; Harrington et al. 2008; Ngigi 2009; Below et al. 2010; Adesina and Odekunle 2011; World Bank 2011; Farauta et al. 2012). Strengthening the capacity of farmers involves making adaptation options available to them and accessible by them as well as providing training and extension services and access to credit and markets (Zorom et al. 2013). They include use of stress-tolerant varieties; adjustment of cropping calendars and cropping systems, crop residue management, integrated soil fertility management, conservation agriculture, soil and water management, agroforestry, biotechnology, reduction of postharvest losses, value addition, weather forecasting and early warning systems, insurance for producers, and diversification and migration. Examples of research findings related to climate change adaptation in West Africa on some of these options are presented in the following subsections.

2. *Improved varieties tolerant to climate change stresses*: Plant breeders at Africa Rice, the Africa Rice Centre, have identified several traits that contribute to drought-tolerant and rice breeding materials, including some found in the indigenous African rice *Oryzae glaberrima*. Molecular markers are being identified which tag genes that contribute to drought tolerance, so as to speed up development of drought-tolerant lines. Gene pools of wild or weedy rice species *O. barthii* and *O. longistamata* are also being exploited (Manneh et al. 2007). African rice has combined the useful traits of *O. sativa* and *O. glaberrima* and developed interspecific lines (NERICAs). Many are weed competitive, tolerant to major pests and diseases, early maturing, and high yielding. Rice varieties with some tolerance to salinity are available (Rhodes 1995). The International Maize and Wheat Improvement Center and the International Institute of Tropical Agriculture (IITA) have developed and released in West Africa several new maize hybrids and open pollinated varieties which are drought tolerant and produce 20–50 % higher yields than other maize varieties under drought conditions (CGIAR 2010). To improve adoption rates by local communities, research institutions throughout West Africa where IITA and Africa Rice operate now engage in the participatory varietal selection, wherein farmers are actively involved in the development of improved crop varieties.
3. *Adjustment of planting date and cropping systems*: Kra and Ofosu-Anim (2010) did mathematical modelling of daily maximum and minimum temperatures for selecting the best planting date so as to minimise the total irrigation water requirements for maize in a situation of water shortage and competing uses. They showed that up to 96 % more irrigated areas could be brought under irri-

gation without additional irrigation water through optimum planting date selection in the coastal savannah zone of Ghana. In another modelling study involving Ghana, Burkina Faso, Niger, and Senegal, date of planting in combination with crop sequence was found to be an adaptation strategy worthy of further study. However, the implications of shift in date of planting and change of cropping systems for labour use have to be considered (Waha et al. 2013).

4. *Crop residue management*: Smallholder farmers in West Africa usually dispose of crop residues by burning, thereby releasing CO_2 into the atmosphere. Numerous reviews have pointed out the benefit of crop residue restitution of soil organic matter content, water holding capacity, and agricultural productivity in West Africa (Bationo et al. 1996; Bationo and Buerkert 2001; Schlecht et al. 2006). The practice is therefore considered climate smart. Rhodes (1995) used a nitrogen (N) balance model and predicted a relative loss in labile soil organic nitrogen over 10 years of 158 kg/N/ha for a system of fertiliser N plus maize crop residue restitution compared to 225 kg N/ha for fertiliser N alone in the semi-deciduous forest zone of Ghana. Gonzales-Estrada et al. (2008) showed that a crop simulation model and a household-level multiple criteria optimisation model could be used to identify a set of best practices that can sequester carbon (increase soil organic matter) and increase farm income in the Upper West Region (Guinea/Sudan savannah transition zone) of Ghana. There is spatial variability in soil organic matter content around homesteads and farms, especially in the Sahel, and field dispersion is an effective strategy to manage agroclimatic risk of crop failure (Rhodes et al. 1996; Akponikpe et al. 2011). In a study conducted in the Upper East Region (Guinea/Sudan savannah transition zone) of Ghana (MacCarthy et al. 2009), the Agricultural Production Systems Simulator model (APSIM) predicted that the amount of fertiliser N needed for sorghum in homestead fields (where crop residues are returned to the soil) would be half of that required in bush farms. Rate of residue application seems to affect the performance of APSIM; Akponikpe et al. (2010) concluded that the model performs satisfactorily for simulating millet response to fertiliser and manure in Niger when P is not limited, but only for low rates of crop residue application ($\leq$900 kg/ha crop residue).
5. *Integrated soil fertility management*: In its basic form, integrated soil fertility management (ISFM) stipulates the judicious combination of organic materials (animal manures, crop residues, green manures, or composts) with mineral fertilisers and use of N-fixing legumes to improve fertiliser use efficiency and soil and crop productivity (Vanlauwe 2004). For swamp rice cultivation, improving fertiliser efficiency by reducing losses of N_2O gas to the atmosphere is climate smart. However, the Participatory Action Research (PAR) was successfully used in Ghana's forest/savannah transition zone as an entry point, empowering communities to self-mobilise and self-organise into colearning and experimenting with ISFM technologies as an adaptation option to climate change (Mapfumo et al. 2013). Using participatory action research, ISFM was found to work in Ghana, Mali, and Burkina Faso, but it was concluded that best-fit options based on detailed analysis of the specific farming context, including

goals, resources, and biophysical environment were required instead of relying on blanket recommendations (CCAA 2012). Kato et al. (2011) also cautioned that adequate attention should be paid to biophysical conditions of the plots and the household access to labour endowments, farming equipment, and land tenure for ISFM to be scaled up and widely used in West Africa.

6. *Conservation agriculture and carbon sequestration*: The key principles of conservation agriculture are:
    (a) Minimising mechanical soil disturbance (involving use of herbicides to control weeds)
    (b) Maintaining permanent soil cover with organic mulch
    (c) Diversification of crop rotations

    CA resulted in increase in soil organic matter and carbon sequestration in Mali (Doraiswamy et al. 2007). Bayala et al. (2012) did a synthesis of reports on the effects of components of CA on yields of maize, millet, and sorghum in Burkina Faso, Mali, Niger, and Senegal. The practices compared were:
    (a) Parkland trees associated with crops
    (b) Coppicing trees
    (c) Green manure
    (d) Mulching
    (e) Crop rotation
    (f) Traditional soil/water conservation

    They found significant variability in cereal response with all practices, but the average effects of CA on crop yields were more positive than negative. Response to green manure and mulching were the best. The findings underscore the need of avoiding a 'one size fits all' mentality. Despite being widely promoted as climate smart, its uncritical use by smallholders should be avoided because of the implications of additional labour for weeding for women and the need for further fine tuning to the conditions of smallholders (Giller et al. 2009, 2011a).
7. *Soil and water management*: It is well known that good soil and water management are prerequisites for efficient use of water, especially in situations of declining rainfall in the Sahel and semi-arid zones (Ngigi 2009). Thus, these are invaluable in combating the effects of climate change. Technologies of soil and water management including provision of soil cover, minimum or no tillage, rainwater harvesting, and irrigation are available. However, very little information is available on the economics of soil and water management on farmers' fields. Reij and Smaling (2008) estimated the costs of establishment and maintenance of zaï pits for soil, water, and fertility management at US$250/ha/year and US$65/ha/year, respectively. Fox et al. (2005) found that the combination of rainwater harvesting and surface irrigation yielded a net profit of US$151 to US$622/ha for smallholder irrigation in Burkina Faso.
8. *Agroforestry*: The use of trees and shrubs in agroforestry systems helps to tackle the triple challenge of achieving food security, mitigating climate change,

and increasing the adaptability of agricultural systems (FAO 2010b; Torquebiau 2013). Recovery from extreme weather events or market failures is an attribute of agroforestry systems because of the diversified temporal and spatial management options. For these reasons agroforestry is said to be climate smart. Research on agroforestry in West Africa as related to climate change has focused on its carbon sequestration potential and effect on soil fertility (Asare et al. 2008; Takimoto et al. 2008). Thus, carbon sequestration by traditional agricultural parklands in Senegal was estimated at only 0.4 tons/ha/year with a potential of 20 tons/ha in 50 years. This finding led to the conclusion that in the West African Sahel, agroforestry seems more valuable for adaptation than for mitigation (Torquebiau 2013). In Mali, Takimoto et al. (2008) reported that the potential to sequester carbon in traditional agricultural parkland was greater than in live fences and fodder banks. Concerning the coastal zone countries, it was shown in Ghana that traditional shaded cocoa stored 155 tons/ha compared to 72 tons/ha for unshaded intensive cocoa (Asare et al. 2008). The productivity of the cocoa was higher in unshaded farms than shaded farms, indicating a tradeoff between cocoa productivity and carbon stocks. The fertility of the soil under shaded cocoa was greater than under unshaded cocoa.

9. *Biotechnology*: Genetically modified organisms (GMOs) constitute a technological option for adaptation to climate change for developing countries, for example, through improved effectiveness of insect pest management (Howden et al. 2007). The Economic Community of West African States (ECOWAS), West African Economic and Monetary Union (WAEMU), and Comité permanent inter-État de lute contre la sécheresse au Sahel (CILSS) are harmonising their regional biosafety regulations (Knight and Sylla 2011) and Burkina Faso, Mali, Ghana, and Nigeria have legislation allowing field trials of GM products. Burkina Faso is at the front in West Africa in the application of biotechnology for improving crop productivity. A survey conducted in 2009 in Burkina Faso showed that insect-protected biotech cotton increased yields by 18 % over conventional cotton and resulted in increased income of US$62/ha over conventional cotton (Vitale et al. 2010). By 2010/2011 yields had increased by 66 % (Knight and Sylla 2011). In addition, biotech cotton made farmers less dependent on fertilisers and better able to adapt to rainfall shortage in Burkina Faso. Biotech cowpea has recently been approved for confined field trials in Burkina Faso and Nigeria (Knight and Sylla 2011).
10. *Reducing postharvest losses, improving marketing, and value addition*: Agricultural productivity can be improved not only by increasing yields, but by reducing postharvest losses, which are considerable in West Africa. In Sierra Leone in the hot humid coastal zone, research (Government of Sierra Leone 2004) has shown a range of losses depending upon the produce: 20 % for rice and 40–50 % for fruits and vegetables. The recovery rate is 40–50 % of oil from palm bunches and 40 % for green coffee beans by traditional methods. Technology is available to reduce these losses substantially, for example, rapid drying after harvest to moisture content of 14 % or less, and use of mechanical rice and coffee hullers and oil palm mills. Value addition, through processing of

available improved methods (e.g., mechanical cassava graters for gari production) and improved infrastructure to access markets also reduces losses. The predicted temperature rise from climate change will increase postharvest losses of annual crops, and thereby vulnerability of farmers to climate change, if corrective measures are not undertaken.

11. *Assessment of 'best practice' technologies*: International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) researchers (Cooper et al. 2009) tested the hypothesis that in the medium term (2010–2050), ICRISAT is well placed to assist farmers in mitigating the challenges and exploiting the opportunities posed by climate change, through application of existing knowledge on crop, soil, and water and the redeployment and retargeting of the existing germplasm of its mandate crops. The ex-ante analysis involving the GCMs, APSIM, and the Decision Support System for Agrotechnology Transfer (DSSAT) showed that adoption by farmers of existing recommendations, even under climate change will result in substantially higher yields than farmers are currently obtaining. Other CGIAR centres covering West Africa – IITA, Africa Rice, International Maize and Wheat Improvement Center and the International Water Management Institute (IWMI) – have also developed improved technologies for their mandate commodities and published Best Practices (CGIAR 2008). CORAF/WECARD in collaboration with CTA has also published Best Practices developed by the National Agricultural Research Systems (CORAF/WECARD 2011). According to Lybbert and Sumner (2010), best practices should be regarded as providing a source of tactical responses (short term) to a changing climate as opposed to an acceptance of untested strategic responses (long term).
12. *Weather forecasting and early warning systems*: Modelling studies have been done to get a better understanding of the utility of weather forecasts to smallholders. Sultan et al. (2010) reported on the ex-ante economic value of seasonal forecasts in the Nioro Rip semi-arid zone of Senegal, using a bioeconomic model to simulate the decisions of farmers with access to a priori information on the quality of the next rainy season. They showed that predicting a wetter than average rainy season would expose farmers to a high risk of failure by favouring cash crops such as maize and groundnut that are very vulnerable to drought. On the other hand, for a drier than average rainy season forecast, farmers respond to minimise the climate risk by choosing crops such as millet and sorghum, which can tolerate higher rainfall in the case of the forecast being wrong. Roudier et al. (2012) showed for the Niamey Region of Niger that in response to forecasts, farmers were able to choose between millet cultivars, between levels of fertilisation, and between sowing dates. Seasonal forecasts improved farmers' situations in bad years and farmers benefited from improved incomes even when the forecast was not perfect. They concluded that improving forecasting systems by including the prediction of onset and cessation of rainfall would be of great value. In a case study in the savannah zone of Ghana, both men and women farmers reported that their use of weather forecasts over the radio is only occasional and they trust and rely on traditional methods (Naab

and Koranteng 2012). The IDRC/DFID programme showed through PAR how weather forecasting, taking into consideration indigenous knowledge, can be successfully used to strengthen farmers' adaptive capacity to climate change (CCAA 2012).

13. *Insurance*: Ngigi (2009) reported very little provision of formal insurance for smallholders in West Africa, but the situation seems to be improving. In Senegal, for example, the government has set up a national fund for agricultural insurance supporting 50 % of the premium. Index-based insurance (which correlates strongly with farmers' production outcomes) can serve as a buffer against climate extremes (Ngigi 2009). Muamba and Ulimwengu (2010) studied the viability of rainfall insurance in 12 districts in the northern region of Ghana for maize producers through a mathematical programming approach. They concluded that rainfall insurance may not work in all districts but may be satisfactory in districts which exhibit a positive correlation coefficient between maize yield loss and indemnity payments; and that rainfall may not be an ideal index for losses, and indexes such as area yield or remote-sensed vegetation may perform better in the design of optimal crop insurance. Although there is a need for further studies to find the most appropriate index-based insurance at community levels, an index-based insurance scheme is up and running. Some smallholder farmers in Ghana have been able to insure their crops against climatic risk through the Ghana Agricultural Insurance Programme (GAIP). At the start of the growing season, farmers pay GAIP a tenth of their cultivation expenses. A period of 12 consecutive days without rain triggers compensation payments to farmers. This insurance scheme is based on data collected daily from 19 automatic weather stations on wind, rainfall, humidity, and temperature. During the first year of implementation 136 farmers were compensated (Spore 2013).

    In summary, there is evidence of the availability, through research and development, in West Africa of several options for strengthening elements of the adaptive capacity and supporting crop farming, at least in the short to medium term, of smallholder farmers. These options are components of a climate-smart agriculture. How well they will work in the long term as climate change continues is uncertain. The research agenda and products of the national agricultural research and extension systems (NARES), CGIAR centres in West Africa, and other research organisations, although initially not intended to respond to climate change adaptation per se, are relevant to some of the short- to medium-term needs expressed in the NAPAs and National Communications.

Documented Adaptation by Crop Farmers

Research has been conducted in West Africa, which provides evidence of adaptation to climate change and/or adoption of recommended adaptation options by farmers. This adoption is a reflection of the realities of climate change and variability on the ground and the ability of farmers to make informed choices from a

Table 5 Some adaptation strategies to seasonal forecasts reported by farmers

Country	Adaptation strategy
Nigeria	Change crop types; reduce herd size; change grazing methods, change planting time; relocate
Burkina Faso	Plant short duration crops/varieties; plant drought-tolerant crops/varieties; use or do not use fertilisers; store/sell grain stocks; orient furrows across slope; acquire capital to purchase inputs; ration food

Source: Adapted from Roudier et al. (2012)

range of available options. Surveys or case studies of countries in West Africa have documented the following: shallow and hand dug wells to supplement the shortfall in water in the dry season (Ngigi 2009); soil moisture improvement technologies including zaï, half-moons, and mulching (Ngigi 2009; Nkonya et al. 2011); irrigation, drainage, and lowland cultivation (Adebayo et al. 2011; Nkonya et al. 2011; Zorom et al. 2013); adjustment of planting dates (Adebayo et al. 2011; Nkonya et al. 2011); agroforestry and crop rotation (Ngigi 2009; Adebayo et al. 2011); rainwater harvesting, collection of rainwater from zinc roofs for storage in tanks, and local earthenwares, bunds, contour bunds, dugouts, and small reservoirs (Panyan et al. 2011; Zorom et al. 2013); fertiliser and manure use (Nkonya et al. 2011; Zorom et al. 2013); diversification in the form of introducing new crops and livelihood changes (Nkonya et al. 2011); integration of livestock with crops and engagement in off-farm activities, for example, gold mining (Ngigi 2009); protection and planting of trees (Nkonya et al. 2011); migration of farmers in wetter areas (Ngigi 2009); and use of weather forecasts and early and/or drought-tolerant crop varieties (Nkonya et al. 2011; Roudier et al. 2012). Concerning weather forecasts, Roudier et al. (2012) cited examples of adaptation to weather forecasts reported by farmers (Table 5).

Gender-disaggregated research data are scarce, but Naab and Koranteng (2012) found that in the same village in the Upper West Region, in the savannah of Ghana, men reported that they used planting of trees, intercropping, crop rotation, and cultivation of lowlands to adapt to climate change and women reported tree planting, dry season vegetable gardening, compost and farmyard manure use, not burning bush and crop residues, and application of crop residues as adaptation/coping strategies.

The relationship of adoption to agroecologies and the determinants of adoption have been studied: thus, Adebayo et al. (2011) grouped technologies adopted by farmers in southwestern Nigeria in response to climate change in terms of agroecologies. They found that in swamps, the order of adoption was first constructed of drainages, being much greater than channelisation of beds, which was in turn greater than adjustment of planting date. In the forest zone, adoption of irrigation was much greater than afforestation, which was greater than use of fadamas (valley bottoms/lowlands). In the savannah zone ‘no adoption’ was much greater than irrigation, which was greater than adjustment of planting date.

Key determinants of adoption of drought-tolerant maize in the Bono State of northeastern Nigeria, in the northern Guinea savannah zone of West Africa, were shown to be access to technology, complementary inputs, extension services, and climate change information (Tambo and Abdoulaye 2012). They also found that off-farm income and wealth status of a household were important in adoption, implying that it would be difficult for resource-poor farmers to adopt adaptation technologies. Farmers identified costs of the technology package, in particular fertiliser inputs, as major constraints to adoption. Nkonya et al. (2011) reported that in the semi-arid zone of Niger, female-headed households were less likely to respond to climate change than male-headed, whereas in the same zone in Nigeria gender did not have a significant effect. Both in Niger and Nigeria having nonfarm activities reduced the likelihood to respond to climate change and there was a positive association between distance to markets and response to climate change. This suggests that marketing opportunities provide stimulus for maintaining or increasing productivity.

A word of caution was raised by Mertz et al. (2009), who in a study of the Eastern Saloum, Senegal, concluded that communities are highly aware of climate issues, but climate narratives are likely to influence responses when questions mention climate change. Changes in land use and livelihoods in the study area are driven by adaptation to a wide range of risk factors of which climate, though important, appeared not to be the most important. The wider applicability of this conclusion to savannah and forest communities in West Africa is untested.

Lessons from Adaptation Projects and Interventions in Crop Farming

A consistent lesson reported from climate adaptation research is that although climate change is a source of significant stress (and perhaps opportunities), it is only one factor among many with which smallholders have to contend. Several adaptation projects have been conducted or are ongoing in West Africa. Lessons reported by a selection of projects and successful interventions (Nkem et al. 2011; BNRCC 2012; CCAA 2012; Mapfumo et al. 2013) are grouped in Table 6 in terms of implementation, gender, weather, local knowledge and participation, partnerships, and institutions and policy makers.

Key Documented Barriers to Adaptation by Crop Farmers

Adoption and assimilation of adaptation strategies and options into national development plans has been slow. The documented barriers include economic capacity, information systems, technology development and dissemination, infrastructure/institutions, sociocultural perspectives, gender issues, environmental issues, extension services, incentives and conflicts among different interest groups, and inadequate policies or lack thereof (Ngigi 2009; Nkem et al. 2011; Nzeadibe et al. 2011).

Table 6 Lessons from adaptation projects and interventions in crop farming

Groups	Lessons
Implementation	• Sufficient time is needed to promote learning and action with full community participation, to enhance local adaptive capacities and strengthen the resilience of communities, and to learn from these actions
Gender	• Women and children are usually the most vulnerable groups and the most affected by climate change impacts • In ensuring awareness and sensitisation to the issues, it is important that all community members, both women and men, agree on and are clear about the process • More work needs to be done to overcome the social and cultural barriers for communities to fully embrace gender equality
Weather, local knowledge, and participation	• Farmers are better able to adapt to climate change and variability when they engage with and apply climate information • Scientific seasonal climate forecast information is mostly supply driven at the national level and does not reflect understanding of user needs • Integrating indigenous knowledge forecasts and scientific seasonal climate forecasts has worked well in many instances but could benefit from further analysis and policy support • Participatory Action Research is necessary to take into account local knowledge to adjust advice and frequency of forecasts to the specific realities of an area or community. Messages in the local languages greatly facilitate uptake • Choosing influential farmers as experimenters can increase uptake of tested soil and water management practices • Participatory technology testing is most effective when farmers are respected and their knowledge considered. In addition, farmers should have ownership of the process of reflection-action-evaluation-planning and its integration into ways of addressing their constraints • Participatory action research provides an entry point for building adaptive capacity of farmers
Partnerships	• Vulnerability assessments, identification of adaptation options, and the implementation of those options often depend on different areas of experience and expertise in order to minimise the risk of failure • Partnerships among relevant institutions including nongovernmental organisations (NGOs) and local communities can strengthen capacity and increase use of seasonal and indigenous forecasts • Project achievements derive largely from the strength and dedication of the entire project team, including the partner organisations and the participating community members with the support of their village heads
Institutions and policymakers	• Institutional barriers to adaptation are more important limitations compared to issues with scientific uncertainties surrounding adaptation options • Involving policy makers at the early stage of a project permits them to appreciate the benefits themselves and help identify resources to sustain useful practices identified through research

Economic Capacity, Information Systems, Technology and Technology Dissemination

Farmers need to have the money to adopt new technology, but smallholders in West Africa are poor, and therefore lack the capacity to adapt. Cost of adaptation packages (including good quality seeds and fertilisers) has been documented as a constraint to adaptation (Adebayo et al. 2011). Farmers can therefore be locked into a vicious cycle of poverty, little use of nutrient inputs, soil mining, and therefore degradation of the environment and increasing vulnerability to climate change.

At the regional level, the African Centre of Meteorological Application for Development (ACMAD) and the Agro-Hydro-Meteorology (AGRHYMET) Regional Centre provide broad information to national partners, but their work is based on inadequate data. The density of meteorological stations in sub-Saharan Africa is one eighth of the minimum recommended by the World Meteorological Organization (Tall 2010). Poor information systems, both at local and national levels to collect, process, and disseminate climate change information and weather forecasts hinder uptake. Poor availability and access to technology and a community's inability to modify the technology adversely affect uptake. It was shown in an earlier section that availability of crop technology for adaptation, at least in the short term, is not a problem; the issue is with regard to accessibility. National extension services are generally weak due to funding and skills constraints.

Infrastructure, Institutions, and Land Tenure

Poor physical infrastructure (irrigation water supply, water management structures, transportation and marketing systems, storage and processing structure, and communication) and inadequate social infrastructure/institutions such as inadequately funded research institutions and unempowered farmers' organisations, cooperatives, and water users' associations are widespread. For example, the Sierra Leone Agricultural Research Institute, with five operating research centres, was allocated approximately US$600,000 in 2013 for nonsalary recurrent expenses, which is 10.6 % of the nonsalary recurrent allocation to the Ministry of Agriculture, Forestry and Food Security (Government of Sierra Leone 2012). Furthermore, funds actually disbursed are sometimes less than funds allocated. With increasing population all over West Africa, access to land in the context of current land tenure systems is becoming very difficult. Poor access to credit for investments and inputs is also linked to the fact that the land under the traditional system cannot be used as collateral for loans. Ngigi (2009) drew attention to how ensuring land tenure for farmers increased water management and irrigated rice production in the Office du Niger, Mali.

Sociocultural Perspectives and Governance Structure

Two case studies conducted in Burkina Faso provide examples of how sociocultural factors can influence adaptation. It was shown that weather information necessary for adaptation sometimes circulates selectively; in a village in Burkina Faso, women were excluded and in two villages 'lower caste families' and families opposed to the village leader and herders residing at the edges of the villages did not receive forecast information (Roncoli et al. 2001). Nielsen and Reenberg (2010) studied two ethnic groups, the Fulbe and Rimaiibe, in the village of Bidi 2, northern Burkina Faso. They found that although the Fulbe were aware of the potential benefits of livelihood diversification – labour migration, development work, women's work and gardens – as they daily observed how these strategies of adaptation to climate change benefited the Rimaiibe by providing them with cash for household survival, they were unwilling to fully embrace them because they entail attributes deemed 'non Fulbe'. It is unknown how widespread this behaviour is in Burkina Faso or in West Africa, but it underscores the need for taking local factors into consideration in technology development and policy formulation.

There are vulnerable groups of both genders in rural communities in West Africa; but it is widely recognised that, in general, women are the most disadvantaged. Unequal access to land and water resources, limited involvement of women in water resources management systems, inadequate contribution to decision-making processes, higher illiteracy rates than men, and poor access to credit are all mitigating against innovation and adoption of climate adaptation practices and other agricultural technologies. Weak governance hinders the content of policies, policy formulation process, and implementation at the regional, national, and local levels with regard to climate change and adaptation (Ngigi 2009).

3.3 Agricultural Development and Climate Change Adaptation Policies

3.3.1 Climate Change Considerations in Continental Agriculture Sector Policies

The African Union/New Partnership for Africa's Development (NEPAD) Comprehensive Africa Agriculture Development Programme (CAADP) sets the overall framework and principles on agricultural development in sub-Saharan Africa, intended to be cascaded to the regional and national levels. CAADP contains broad themes of opportunities for investment to reverse the crisis facing African agriculture, which has made the continent import-dependent, 'vulnerable to even small vagaries of climate', and largely reliant on food aid (AU/NEPAD 2003). The 'vagaries of climate and consequent risks' that determine investment is also listed as one of the six challenges to achieving a productive agriculture. 'Land and water management', which is very important for adapting to climate change, is a Pillar of CAADP. In addition, the environmental initiative of NEPAD prioritises climate change as one of its ten programmatic areas.

3.3.2 Agriculture Considerations in Regional Climate Change Policies or Strategies

ECOWAS developed an Environmental Policy (ECOWAS 2008) whose overall objectives are to reverse environmental degradation and depletion of natural resources, ameliorate the quality of the living environment, and conserve biological diversity to ensure a healthy and productive environment. The strategic actions include promoting, monitoring of environmental change, and the prevention of risks by setting up a Regional Center Observatory, combating land degradation, drought and desertification, and sustainable management of coastal, inland, and marine ecosystems. Response to climate change was not one of the actions. Thus, in 2010 a Regional Action Program to Reduce Vulnerability to Climate Change in West Africa (ECOWAS 2009a, b) was adopted. It was agreed at the International Conference for Reduction of Vulnerability to Climate Change of Natural, Economic and Social Systems in West Africa of 2007 in Burkina Faso and the Ministerial Meeting on Climate Change of 2008 in Benin to develop and implement a programme of action to reduce vulnerability of West Africa and Chad to climate change. CILSS, the Economic Commission for Africa (ECA), and ACMAD were mandated to develop the programme.

The regional programme document noted that although urgent priority measures in the NAPAs are worthy of continuation and support, it is also important to complement them with concerted adaptation options at the regional level. The goal of the ECOWAS programme is, at the regional level, to develop the required mechanism, actors, and capacity to provide support to governments and communities as they adapt to climate change. The objectives are: (1) regional institutions are politically, technically, and financially supporting the states in their process to adapt to climate change; (2) national stakeholders in each country are adopting harmonised and coordinated approaches to adapting to climate change; and (3) climate change is mainstreamed into priority regional and multicountry investments, programmes, and projects. The coverage of the 10 development sectors including agriculture (crops and agroforestry) is envisaged, but the extent to which adaptation to climate change in the agricultural sector will be dealt with is not given and presumably will depend on national priorities.

3.3.3 Tradeoffs and Barriers to Mainstreaming Climate Change Adaptation into Agricultural Policy

ECOWAS's regional policy guidelines, the NAPAs (prepared under guidance from UNFCCC) and the policy documents prepared by Nigeria and Ghana all indicate that policy documents on climate change are separate from agricultural development policies and other plans/strategies. However, in general, the agricultural development policies/plans recognise directly or indirectly the need for responding to climate change without tying productivity targets to the projections of how climate change could affect agriculture.

There are benefits and disadvantages to mainstreaming adaptation to climate change into agricultural policies (ECOWAS 2009a, b). The benefits are: additional policies and their associated bureaucracy to be added to already stretched government institutions are not required; it does not increase duplication, potential incompatibilities, or conflicts among policies and agencies; adaptation initiatives fall within policies that are already established in agencies with expertise, experience, and stakeholder connections in policymaking; it focuses more directly on practical adaptation and mitigation initiatives than on climate monitoring, models, and predictions. The disadvantages are that many programmes and agencies have to be engaged; and it is difficult to distinguish accomplishments in climate change adaptation from other development activities responding to various stresses.

The United Nations Environment and Development Programmes (UNEP and UNDP) Climate Change and Development Project—Adapting by Reducing Vulnerability in Senegal, Togo, Benin and Ghana reported inadequate knowledge on climate change risks, level of vulnerability, and adaptation options at the local level; inadequate institutional capacity to address the challenges posed by climate change at the local level; weak partnership between central and local government; and lack of proactive, targeted, and cost-effective strategy that increases the long-term resilience of the population as barriers to mainstreaming adaptation into national development frameworks (Nkem et al. 2011).

3.3.4 Key Arguments for Policy on Adaptation to Climate Change

Technical interventions cannot be effective and sustainable without supportive governance measures concerning policy and legal issues (Ngigi 2009). Incentives and flexibility are enhanced by good governance, policy, and institutional responses. The benefits of adaptation to climate change are more local compared to mitigation whose benefits are more global; hence the need for national and local policies dealing with adaptation is crucial.

In Mali, a comprehensive macroeconomic policy and institutional reforms (including provision of short- and medium-term credit to farmers and access to land) have turned irrigated agriculture into a profitable enterprise, sustaining livelihoods of farmers and improving the national economy (Aw and Diemer 2005). Also, a case study in the semi-arid zone of Nigeria and Niger concluded that the support of the Nigerian government over several years for irrigation development and more recently small-scale irrigation increased agricultural production and reduced production risks in the drier northern states (Nkonya et al. 2011). Although the irrigation programmes were not implemented as part of an adaptation to climate change programme, they helped farmers adapt to climate change. Furthermore, the adoption rate by farmers of fertilisers was relatively high because of the government's substantial fertiliser subsidy and promotion of fertilisers for a long time. For Niger, the granting to users of the right to own and benefit from trees on their farms, through the Rural Code, contributed to the greening of the Sahel.

3.3.5 Key Barriers to Uptake of Research and Successful Policy Implementation

The linkage between research and policy is weak, and research therefore does not adequately inform policy. The reasons for this are many: very conscious of maintaining their objectivity, researchers traditionally get uncomfortable about close contacts with policy makers. Decision makers on their side may think of researchers as too academic and impractical or their findings not used for decision making. Other obstacles are the perceived uncertainties surrounding climate change and modelling (e.g., there is some inconsistency in the predictions made by GCMs) and the short-term perspectives of politicians related to their tenure in office. The time lag between the time the research is conducted and the findings are made known is very long and the presentation often too technical; sometimes outputs of research do not even reach national policy makers, natural resource managers, or farmers (Huq and Reid 2005). What approach in research-policy dialogue works best and under which situation is unknown. Policy making in West Africa, even when evidence based, is generally linear. IDS (2011) argues that the policy process is not linear where researchers' roles are limited to providing scientific evidence at the end of the research process. The policy process is a disputed space, a complex mesh of competing interests and negotiations, in which power and politics are central.

3.4 Gaps in Climate Change Adaptation Research and Policy in the Agricultural Sector

Several studies undertaken in West Africa on adaptation research and policy reveal incomplete detailed technical knowledge of how to adapt sustainably to climate change in agriculture and weakness in policy formulation and implementation (Thornton et al. 2007; Ngigi 2009; FAO 2008, 2010b; Sultan et al. 2010; CGIAR 2011).

3.4.1 Key Research Gaps and Challenges

Crops

Across the region, there is limited or inadequate knowledge in several thematic areas such as how in response to climate change, farmers will shift to different crops, affecting feeding habits, nutrition, and cultural norms; on conservation agriculture; on adaptation at the watershed level; and on the productivity of biofuel crops in water-stressed conditions. There are no improved varieties of Jatropha that are being promoted in Mali and Ghana as a biofuel crop. There has been little research on climate change and tree crops/agroforestry.

Cross-Cutting Gaps

The incomplete understanding of the wide-ranging processes underlying the performance of markets, ecosystems, and human behaviour contributes to the uncertainties associated with modelling the impacts of climate change on the agricultural sector (Nelson et al. 2013). There is little or no routinely reliable method on the predictability of the onset of the rainy season and intraseasonal variability and how to make weather forecasting work best for smallholders. There is also limited knowledge on the applicability of index-based insurance to smallholder situations. Other areas of limited or inadequate knowledge are: adaptation through control of plant diseases; thresholds in natural systems beyond which adaptation may be very difficult or impossible; assessment of the effectiveness of adaptation options and understanding likely adoption rates, tradeoffs, costs, and returns of adaptation strategies; effective ways of communicating climate change information and its consequences on livelihoods and the environment; women's strategic interests (access to land and credit, decision-making power, etc.) in responding to climate change and variability; and relative benefits of promoting regional versus global trade for crop products.

3.4.2 Key Policy Gaps and Challenges

The national policies in place in West Africa (specifically Nigeria, Ghana, and Senegal) are generally more robust for technological practices compared to non-technical risk management, for example, trade. International trade is expected to play a critical role in adaptation and would itself be affected by climate change but there is little understanding of how all of these will play out and what the appropriate policies should look like. That climate change and adaptation are not always mentioned in agricultural development policies and strategies is an important weakness. Also, some policies to the benefit of one sector have been to the detriment of another.

There are inadequate policies or lack of policies in several areas: dry season reserves and livestock corridors from encroachment by crop farmers, investors, and national parks; transboundary control of water resources; strengthening climate communication and information networks to improve timely delivery of weather information; built-in capacity for flexible policies that continuously respond to changes; collaborative learning processes and understanding of the context in which decisions are made and the capacity of decision makers to change; gender imbalance in access to factors of production; mainstreaming gender into all climate adaptation policies and strategies; and weak institutional capacity to generate and utilise adaptation technologies.

3.4.3 Options, Spaces, and Opportunities for Improved Uptake of Research

Policy spaces are places, areas, locations, and gaps where policy can be influenced. Examples of policy spaces and tools for policy engagement are informal expert consultations through national consultative groups used effectively to widen debate and common understanding on topics such as food insecurity and climate change and climate-smart agriculture, and creating informal spaces within otherwise formal processes (IDS 2011). Through its interaction with the Sectorial Permanent du Plan d'Action Pour la Gestion Intégrée des Resources en Eau (SP/PAGIRE) in Burkina Faso and the Water Research Commission (WRC) in Ghana, the CGIAR Challenge Program on Water and Food (CPWF) is promoting a 'visionary team' (mediators) to guide project activities and ensure uptake of the programme (Aduna 2011). The fact that researchers, trained in the conventional way of investigation and reporting, are becoming familiar with participatory action research and donors are keen to fund PAR are all opportunities for bridging the gap.

4 Central Africa

Sub-Saharan Africa is often cited as one of the world's most vulnerable regions (Slingo et al. 2005) because it maintains the highest proportion of malnourished population, has become more vulnerable, and is now the most exposed region in the world to the effects of climate change (World Bank 2009). A significant portion of its national economies is dependent on agriculture (Benhin 2008; Schlenker and Lobell 2010), and most of its available water resources (85 %) are used for agriculture (Downing et al. 1997). Farming techniques are also relatively primitive, the majority of the continent was already arid, and the smallholder systems that dominate the agricultural landscape have very limited capacity to adapt (Muller et al. 2011).

4.1 Overview of Agriculture in the Central African Region

4.1.1 Climate Challenges in the Region

Africa has experienced a greater warming trend than other regions; about 0.5 °C per century since 1900 (Hulme et al. 2001). In the agricultural sector, the Central African region faces tremendous challenges. A generally low agricultural investment portfolio means that agriculture is extremely sensitive to climatic fluctuations. Agriculture is primarily rainfed, and the onset of rainfall and precipitation levels have become highly variable, with some parts of the region experiencing decreases in annual rainfall that have made it impossible for farmers to be aware of when to plant or where to graze. Wildlife species have also been forced to migrate southward in search of water. Massive floods resulting in soil erosion in dry areas with fewer months of rainfall have made matters worse. New diseases have emerged and minor diseases have developed highly virulent strains. Deforestation is being enhanced by extensive agriculture to increase agricultural production, resulting in massive loss of biodiversity, depletion of water resources, and extensive environmental degradation. Lastly, political conflicts have destabilised some countries, adversely affecting food production and making the region extremely vulnerable to climate change. Agriculture is characterised by stagnant yields, land degradation, and recurrent droughts. Without a sound agricultural sector, the Central African region, already facing food insecurity and poor health, is unlikely to develop diversified economies that can cope with the impact of climate change. Consequently, the impact of climate change on agriculture and food security in the region over the next few decades will depend on progress in applied agricultural research and development (IPCC 2007b).

4.2 Review of Climate Change Adaptation Research in the Agriculture Sector in Central Africa

4.2.1 Adaptation of Crop Farming Systems to Climate Change in the Central African Region

In all countries of the region, the crops most affected by climate change are maize, cassava, groundnut, bean, yam, and upland rice, which require climate-smart practices for increased field productivity. Climate-smart crop production practices provide management options to farmers to both adapt to and mitigate climate change (FAO 2010b). Sustainable crop production seeks to reduce reliance on nonrenewable external inputs (e.g., inorganic fertilisers) and capitalise on and enhance natural biological processes (e.g., manures) to improve production in a more environmentally-friendly way which avoids degradation of natural resources. To cope with the challenges of climate change, crop production must adapt through, for instance, good selection of crop varieties, plant breeding, cropping patterns, and ecosystem management approaches, and become resilient to greater frequency and intensity of the changes.

By reducing the use of inorganic fertilisers, avoiding soil compaction or flooding to reduce methane emissions (prominent in paddy rice systems), and sequestering carbon (e.g., planting perennial crops and grass species), crop production can contribute to mitigating climate change by reducing GHG emissions. Because farmers are the primary custodians of knowledge about their environment, agroecosystems, crops, cropping patterns, and local climate patterns, adapting cropping practices and approaches will relate strongly to local farmers' knowledge, requirements, and priorities. Hence, sustainable crop production provides farmers with options for farming sustainably, taking into account the local ecosystem. Integrated approaches – such as crop–livestock systems, rice–fish systems, and agroforestry – diversify food sources and consequently strengthen the resilience of farmers' livelihoods, and also provide opportunities for mitigating climate change.

Climate change impacts on food crop smallholder farming in Central Africa are producing huge economic losses to growers. Although farmers now know that changes have occurred in the amounts of rainfall and onset of rains, changes have been rather abrupt, making nonresilient farming groups in the region face difficulties in adapting to them. Major crops such as sorghum in the drier zones of the region have been most hit, with productivity dwindling massively because of high sensitivity of existing varieties to drought. This has prompted plant breeders to breed short-cycle varieties which are adapted to drought conditions (IRAD 2008). In other countries new varieties of tomatoes, cassava, and groundnuts have also been bred to cope with the changing climatic conditions.

Autonomous Adaptation and Coping Measures

Food security and climate change can be addressed together by transforming agriculture and adopting practices that are climate smart. Unrecognised, a number of production systems considered climate smart are already being used by farmers and food producers in the Central African region to reduce GHG emissions, adapt to climate change, and reduce vulnerability. These include:

(a) *Conservation Agriculture*: CA includes minimal mechanical soil disturbance (i.e., no tillage and direct seeding); maintenance of a mulch of carbon-rich organic matter covering and feeding the soil (e.g., straw and/or other crop residues including cover crops); and rotations or sequences and associations of crops, including trees, which could include nitrogen-fixing legumes. CA offers climate change adaptation and mitigation solutions while improving food security through sustainable production intensification and enhanced productivity of resource use.

(b) *Agroforestry*: The use of trees and shrubs in crop and/or animal production and land management systems is practiced in many forms, including improved fallows, taungya (growing annual agricultural crops during the establishment of a forest plantation), home gardens, growing multipurpose trees and shrubs, boundary planting, farm woodlots, orchards, plantation/crop combinations, shelterbelts, windbreaks, conservation hedges, fodder banks, live fences, trees on pasture, and tree apiculture (FAO 2010b). For instance, *Faidherbia albida*, a tree commonly found in agroforestry systems in the Central African region, thrives on a range of soils and occurs in ecosystems from deserts to wet tropical climates. It fixes nitrogen and has the special feature of reversed leaf phenology, meaning it is dormant and sheds its leaves during the early rainy season and leaves out when the dry season begins (FAO 2010b). This feature makes it compatible with food crop production, because it does not compete for light, nutrients, or water during the rainy season. Farmers have frequently reported significant crop yield increases (6–100 %) for maize, sorghum, millet, cotton, and groundnut when grown in proximity to *Faidherbia*. As with many other agroforestry species, *Faidherbia* tends to increase carbon stocks both aboveground and in the soil and improves soil water retention and nutrient status. With maize being the most widely cropped staple in Central Africa, the potential for adopting this agroforestry system is tremendous.

The study showed that the use of nontimber forest products is one important coping mechanism practiced by farmers to adapt to climate change impacts on agriculture. The use of diversified and multipurpose tree species has been shown to enhance the adaptation of agricultural crops to climate change. By supporting the integration of high-value tree species, a programme in West and Central Africa funded by the International Fund for Agricultural Development (IFAD) helped farmers produce marketable forest products, enabling them to diversify their sources of income, improve their nutritional base, and restore the region's biodiversity (IFAD 2011). The programme led to a gradual reduction in slash-and-burn agriculture and deforestation in these humid tropical areas. To avoid damaging young trees, smallholder farmers have now stopped the practice of burning fields that have been left fallow for several years. Farmers have been trained on agroforestry tree propagation techniques and integration, and now plant trees on their farms. This has significantly reduced the need for them to deplete the forests by cutting down trees. In addition to the benefits of enhanced soil conservation and fertility, the greater number of trees also increases carbon sequestration. Using farmers' indigenous knowledge as well as local community participation in agricultural systems in the region has led not only to the improvement of soil quality (soil structure and soil organic matter), but also efficient water use and soil moisture retention. In some areas crop yields have been substantially increased through the use of such soil conservation and fertility measures (FAO 2011b).

(c) *Exploitation of wetlands*: Another finding was that farmers of the region cope with drought by exploiting wetlands for agricultural production. They adapt to drought conditions by using inland valleys and watersheds, especially in vegetable production and food crop cultivation.

(d) *Other cultural practices*: These include shifting planting dates, modifying cropping patterns and rotations, mulch and cover cropping, crop diversification or the uptake of pre-existing crop varieties, using high-quality seeds and planting materials of adapted varieties, using integrated nutrient management, integrated pest management, integrated weed management, water and irrigation management, landscape-level pollination management, organic agriculture, and land fragmentation of riparian areas and forest land within the agricultural landscape. All of these help to offset some negative impacts of climate change at different levels in the farming systems of Central Africa.

Use of Genetic Resources and Enhancement

Genetic makeup determines a plant's or animal's tolerance to shocks such as temperature extremes, drought, flooding, pests, and diseases. It also regulates the length of growing season/production cycle and the response to inputs such as fertiliser, water, and feed. The preservation of genetic resources of crops and breeds and their wild relatives is therefore fundamental in developing resilience to shocks, improving the efficient use of resources, shortening production cycles and generating higher yields (and the quality and nutritional content) per area of land. Generating varieties and breeds which are tailored to ecosystems and the needs of farmers is crucial. The selection of clones and crop cultivars with tolerance to biotic and abiotic stresses (e.g., drought, high temperatures, flooding, soil aluminium toxicity, high soil acidity, insect pests, and diseases) are providing an opportunity for genetic variation to enhance the improvement and development of new crop varieties which offer hope in adaptation to climate change. National and international research institutes and NGOs in the region are also promoting the use of indigenous and locally adapted crop genotypes and selecting, multiplying, and popularising these crop varieties and landraces adapted to, tolerant of, or resistant to adverse climatic conditions.

Response of Crop Species in Adaptation to Climate Change

The greatest benefits in food-insecure regions such as Central Africa are likely to arise from more expensive adaptation measures, including the development of new crop varieties (which takes a long time) and uptake of costly new technologies such as the expansion of irrigation infrastructure (especially for irrigated rice cultivation). Farmers of the subregion agree that among the roots and tubers, cassava (the basis of the diets of most populations) is the hardest hit, and its field yields and disease resistance have been most affected by climate change. High-yielding cassava varieties which were yielding upwards of 35 tons/ha under on-farm conditions have seen their yields reduced to a bare 15 tons/ha. New diseases including the cassava root rot have developed in synergy with root insects such as the African root and tuber scale (*Stictococcus vayssierei*). African cassava mosaic disease, endemic in the region, has developed more virulent strains such as the Ugandan variant. At the same time, a minor cocoyam leaf spot (caused by *Phytophthora colocasiae*) has turned into a yield-devastating blight for the crop. The severity of maize and sorghum *Striga* has made these crops less productive in the north, leading scientists to produce extra-early maize and sorghum varieties to curb hunger in that agroecological zone. In the forest region, plantain fungal diseases have increased in severity because of progressively heavy precipitation in that ecozone. Maize has been seen to be the most vulnerable cereal, followed by rainfed rice. Groundnut and common bean are the grain legumes most affected by a changing climate in the subregion. All these have seen substantial losses in agricultural production. There is a need to support research in the region to enable farmers to adopt measures and strategies for adaptation of their agriculture to these climate-induced changes.

A recent study showed substantial yield increases for bambara groundnut, soybean, and groundnut, and little or no change and even decreases of maize and sorghum yields, varying according to the climate scenario and the agricultural region in Cameroon. The yields of maize and sorghum are expected to decrease by 14.6 and 39.9 %, respectively, across the whole country. The results also show that the effect of temperature patterns on climate change is much more important than that of precipitation. Findings call for monitoring of climate change/variability and dissemination of information to farmers, to encourage adaptation to climate change (Tingem et al. 2008). Taking the 'no regrets' principle in considering specific adaptation strategies for three crops, maize, sorghum, and bambara groundnut, showed that changing sowing dates may be ineffective in counteracting adverse climatic effects because of the narrow rainfall band that strictly determines the timing of farm operations in Cameroon. In contrast, the possibility of developing later maturing new cultivars in some regions proved to be very effective in offsetting adverse impacts, giving the highest increases in productivity under different scenario projections without management changes (Tingem et al. 2009).

Role of National Governments

Governments of the Central African region must recognise that the projected impacts of climate change have to be included and be given a high priority in their countries' development agendas, because in order to reduce their vulnerability to disasters, planning in land-use systems, natural resource management, and even the design of road, water, and energy infrastructure must be done. This should lead to reform in public policy, development of technological measures, and an adaptation to management systems. In the region, provision of financial resources and willpower from governments will assist in building adaptive capacity and adaptation management, all of which are necessary for adapting the agricultural systems to climate change.

4.3 Agricultural Policies for Climate Change Adaptation

Climate change is viewed as one of the gravest threats to the future of humanity. Debates and commitments relating to climate change in Africa date back to the G8 summit in Gleneagles, Scotland in 2005 (Niang 2007). During that summit, it was noted that Africa was having difficulties in achieving the Millennium Development Goals (MDGs) by 2015. Decisions were made to support the reduction of African countries' vulnerability to climate change by strengthening the existing institutions and climate centers in Africa through the Global Climate Observing System (GCOS), and a commitment was made by the World Bank to take account of climate risk in its investment portfolio. West Africa, confronted with desertification, has several institutions with clear and distinct mandates on climate change issues, including the Permanent Interstate Committee for Drought Control in the Sahel (CILSS), the Agro-Hydro-Meteorological (AGRHYMET) Regional Centre, the Centre for Medical and Health Research (CERMES), research institutes, universities, and NGOs. In Central Africa, where the chief concerns are linked to climate change as it affects agricultural production, deforestation, depleting water resources, loss of biodiversity, and environmental degradation, subregional institutions are still in gestation. In a summit of the African Union African heads of states were asked to integrate climate change issues into their national development policy agendas, and since then an interest in climate change has begun to develop, especially at the level of the Economic Community of Central African States (Niang 2007). This view was reinforced at a meeting of the Assembly of the African Union in Addis Ababa, Ethiopia, during which a decision was made that specifically urged all of the governments in the region to integrate climate change considerations into development strategies and programmes at national and regional levels and to implement the Plan on Climate Change and Development in Africa.

4.4 Gaps in Climate Change Adaptation Research and Policy in Agriculture in the Central African Region

In the Central African region there are at least five areas of concern reflecting huge gaps in climate change adaptation research, namely: (a) adaptation in forestry, where forest ecosystem goods and services are found to be indispensable in planning adaptation in all other sectors (Nkem et al. 2007); (b) adaptation in agriculture; (c) adaptation in water resources; (d) adaptation in public health; and (e) adaptation in urbanisation. Much work has been done on climate change adaptation in forestry (especially on mitigation efforts and the reduction of GHG emissions resulting from deforestation and forest degradation), and it is here also where international partners have put more emphasis, probably because of the importance of forest resources in the region. But even here, there are still areas of concern, such as the GHGs (fluorocarbons) utilised in the domestic fridges, which are manufactured in developed countries but sold to developing countries.

4.4.1 Gaps in Agricultural Research and Policy

In agricultural research, the main gaps relate to identifying how to tackle climate change scenarios (precipitation, floods, temperature, and drought) on crop farming and making the necessary government policies to implement adaptation. Major gaps in agricultural research are: (a) the adaptation of annual crop (maize, sorghum, millet, and wheat) cultivar responses to drought in drier zones given the shortened water regimes in the Sahel, and the need for new crop varieties required by growers to bring resilience in the agricultural community in that zone; (b) tackling emergent crop diseases in the wake of a changing climate; (c) countering increases in small animal diseases and pests in the forest–savannah transition areas in response to global warming and regional climate change; and (d) addressing fragile, highly depleted soils which are very vulnerable to climate change (Knox et al. 2012). Policies on these issues, accompanied by appropriate funding, need to be made, especially as climate change adaptation studies in agriculture are just beginning to be perceived as high priority issues and unavoidable threats to food security.

4.4.2 Policy Gaps in Climate Change Adaptation

Adaptation policy in the region appears to be low because of the apparent low commitment of governments to support adaptation. As the main stakeholders, governments should be ready to play the major role of rallying all other stakeholders; bring them to the negotiating table so as to make a clear evaluation and identification of adaptation issues and strategies; and fund the adaptation activities. The research results obtained should be transferred to the end-users through appropriate mechanisms and workable stakeholder training.

4.4.3 Research Policy Gaps in the Region

Research policy gaps also exist. Research activities could be formulated, but if not funded, adaptation will not be enhanced. In developed countries industry funds most of the research; in Africa, the main research support comes from governments, making the latter a very important factor in the adaptation development process. Research must therefore undertake the necessary advocacy to attract government funding for its initiatives.

4.4.4 Research and Policy Gaps in the Various Countries of the Region

(a) *Inadequate scientific infrastructure and manpower*: Many national research systems are not sufficiently staffed and do not have the appropriate infrastructure. Because funding is usually inadequate, the governments of the region could pool resources together and establish regional institutions, centers, or laboratories of excellence to serve the countries of the region, especially for complex issues such as climate change. Scientists could also be trained or retrained in climate change research and on current areas including GIS, remote sensing, climate forecasting, monitoring, and evaluation, and these skills could similarly be shared in the region. Unfortunately, because national institutions cannot adequately fund research, many research scientists have resorted to doing consultancies and other things to occupy themselves and make ends meet.

(b) *Improvement of extension systems*: Regional extension systems need to be reinforced. It should also be regional policy to include civil society in the public extension services so as to tap into their competence, willingness, and availability in the dissemination of climate- and adaptation-related results.

5 Southern Africa

There is a growing need for the development of climate change response strategies and policies at different levels, from local to subregional scales, in sub-Saharan Africa. Global scientific inquiries have revealed unequivocal evidence that the world's climate is changing and presenting new challenges to almost all spheres of development, as well as threatening the sustainability of current human livelihood systems (IPCC 2007b; World Bank 2009). Most of the changes in climate have been attributed to anthropogenic factors related to industrialisation and high external input agricultural systems that characterise most of the world's developed nations. Reports of the Intergovernmental Panel on Climate Change demonstrate that although climate change is a global phenomenon, its effects and impacts will be unevenly distributed across the world's geographical regions, ecosystems, and human communities (IPCC 2007b). Empirical research has shown that Africa's farming systems are highly diverse and heterogeneous (Giller et al. 2011b), revealing complexities associated with any efforts to target development solutions. This implies critical challenges for decision makers in formulating relevant climate change response strategies and adaptation policies. It is currently unclear if the research on climate change conducted in Southern Africa in recent years has generated sufficient empirical evidence to inform policymaking processes at the local, national, and regional levels.

5.1 Overview of Agriculture in the Region

5.1.1 The Role of Climate Change Challenges

In its fourth assessment report the IPCC projected that Southern Africa will experience longer dry seasons and increased rainfall uncertainty (IPCC 2007b), and this will demand matching adaptation measures. Overall, an analysis of the IPCC data provides evidence of temperature increases of 0.1–1 °C between 1970 and 2004 in countries that include South Africa, southeast lowveld areas of Zimbabwe, and southern as well as coastal parts of central Mozambique. During the same period, corresponding temperature increases in the rest of Zimbabwe, Malawi, and many parts of Zambia, Botswana, and Namibia averaged between 1 and 2 °C. Such magnitudes of temperature change are anticipated to have a significant influence on the functioning of biological systems including terrestrial and freshwater aquatic ecosystems. An analysis of the IPCC projections (IPCC 2001, 2007a) strongly suggests that Southern Africa will suffer negative effects in three main areas; (1) influence on freshwater resources in lakes and dams; (2) breakdown in the resilience of dominant ecosystems; and (3) influence on productivity patterns of food, fibre, and forest products.

Southern Africa falls within the regions where a decrease of 10–30 % in water availability and runoff from rivers is anticipated by the middle of the twenty-first century. This is likely to increase water scarcity in a region already suffering severe water stress for both agriculture and domestic use. Increased frequency of droughts coupled with warmer temperatures and climate-induced floods is likely to force major changes in land use patterns with a high likelihood of overexploitation of resources drawn from major natural ecosystems (Campbell 1996). The majority of rural communities is poor and depend on natural resource pools derived from forest and aquatic systems, including nontimber forest products. Such disturbances are projected to influence the structure and functioning of ecosystems as ecological interactions and geographical distribution of species are altered. The negative effects of climate change are therefore likely to be exacerbated by human actions, with even greater consequences for biodiversity and ecosystem services as traditional water and food supply systems are also stretched by a growing human population. The need to enhance food production while maintaining the agricultural resource base and the resilience of the agroecosystem will be an increasingly important topic in discussions on the development of the Southern African region in the foreseeable future (Ajayi et al. 2010; Giller et al. 2006).

The IPCC projections suggest that there will be a decrease in growing season length and an expansion of semi-arid and arid zones in the context of agricultural production in Southern Africa. More importantly, localised (specific areas) increases in temperature of 1–2 °C are projected to result in decreased crop productivity, significantly increasing the risk of hunger in many communities (IPCC 2007b). Southern Africa is therefore one of the regions where yields from rainfed agriculture could be reduced by up to 50 % by 2020, potentially heightening prevailing conditions of food insecurity and malnutrition. This calls for adaptation options that may include changes in crop type and cultivars as well as planting times for key crops. However, many of the region's communities are known to be among the world's most vulnerable due to multiple stresses (IPCC 2007a; Casale et al. 2010). For instance, access to improved crop seeds and fertilisers is a major challenge for many smallholder communities in Southern Africa (SADC 2012). The agricultural sector in the region still suffers from lack of access to appropriate information, knowledge, and technologies by different farmers, and this may greatly limit the scope for adaptation.

5.1.2 State of Knowledge on the Implications of Climate Change for Other Key Challenges (and Opportunities) for the Agricultural Sector in the Region

One of the major challenges in rainfed agricultural systems such as those dominating in Southern Africa is the lack of awareness by farmers, agroservice providers, and policy makers about past, current, and future changes in climate and their implications. The summary report targeted to policy makers has already revealed a lack of evidence and good examples from Africa regarding impacts and adaptation options (IPCC 2007b), suggesting a need for deliberately supporting empirical research to address these knowledge gaps. Available findings from empirical research strongly suggest complex interactions and relationships between agriculture and natural resources (including environmental service functions) in driving livelihood systems in both rural and urban environments. The current and potential impacts of climate change and variability on these systems are therefore less clearly understood given the limited knowledge on major variables explaining these complexities. However, findings from the limited research studies available to date provide some insights on potential areas of development where climate change impacts are likely to have ramifications beyond agriculture and in turn constrain adaptation. Such areas include: (1) changes in dynamics of rural–urban interconnections; (2) a shrinking natural resource base and environmental degradation, with poor and declining soil fertility as a critical underlying factor; (3) increased resource use conflicts and breakdown of traditional social safety-net systems within/across communities; (4) diminishing marketing and trading opportunities in agricultural produce and derived industrial products; and (5) land ownership disputes.

Numerous research studies over the years have helped to explain the intimate relationship between environmental resources (or natural resource pools) and livelihoods in many rural systems (Campbell 1996; Kepe 2008) and the interconnections between rural and urban livelihood systems in Southern Africa (Andersson 2002). The architecture of urban development in most Southern African countries has tended to discriminate against women, as formal employment historically favoured men who provided much of the labour force during the colonial past. Arguably, this has precipitated a women-dominated (or at least biased) farm labour force, particularly in smallholder areas. However, the working husbands away in urban areas often make strategic farming decisions for these households. Rural communities are therefore often dependent on such services as information and remittances from family members employed in urban areas (Cavendish 2000), whereas urban communities are often subsidised by rural-based family members and relatives in terms of food provision and sometimes income (Andersson 2001). These social collaborations have tended to provide the much-needed social safety-net mechanisms for coping with multiple stress factors including climatic-induced problems. However, the potential value of these collaborations in supporting climate change adaptation has not been critically assessed in the wake of increasing rural-to-urban migration. Conversely, it may be the lack (or collapse) of such social collaborations that triggers conflicts and heightens vulnerability across the rural urban divide. There is also evidence to suggest that similar social collaborations underpin traditional social safety nets that may have helped to reduce vulnerability of different social groups (e.g., livestock owners versus nonlivestock owners) within smallholder communities (Rufino et al. 2011).

Communities in Southern Africa have long been developing strategies and mechanisms for coping with frequent droughts, seasonal crop failure, and perennial challenges of food insecurity, which are often associated with poor and declining soil fertility. Most of the communities fall back on common natural resource pools during poor cropping seasons (Woittiez et al. 2013), yet emerging evidence from the IPCC suggests dwindling opportunities for communities to rely on these resource regimes as water resources are projected to decline (IPCC 2007a). Although indigenous knowledge regulating the use and sustainable management of these resources has not been given due attention in research and development, there is evidence of significant contribution to household nutrition, food security, and income (Shackleton and Shackleton 2004). Previous studies in the region have revealed that most smallholder communities derive up to 35 % of their annual income (Cavendish 2000), and that poorer households get up to 40 % of their calorie intake during drought years (Woittiez et al. 2013) from common natural resource pools. Kalenga-Saka and Msonthi (1994) found high nutritional values of wild fruits drawn from miombo woodlands in terms of macronutrient elements and energy, and Grivetti and Ogle (2000) found high concentrations of essential micronutrients in a range of fruits from similar environments. High dependence on rangeland products such as fruits and vegetables during times of food scarcity has also been commonly reported elsewhere in Africa (Muller and Almedom 2008). However, the studies have also shown that access to these resources is highly differentiated according to gender, age of household heads, wealth status, and composition of households (Woittiez 2010). Poorer households, who often comprise a high proportion of women-headed families, rely more on the common pool resources and therefore the negative impact of climate change on the natural resource base has strong implications for their livelihoods (Woittiez et al. 2013).

Such studies reveal diverse livelihood benefits derived from forests and rangelands (Kepe 2008). Although social, economic, and political factors often comprise the major factors driving conflicts related to issues of access and distribution of natural resources, it is also apparent that conflicts may arise due to multidimensional and competing resource uses and ownership claims. Such conflicts occur not only within and among communities (e.g., for land and water), but also between people and both domestic animals and wildlife (Giller et al. 2008). There is clear evidence that communities attach value to common natural resource pools (forests, rangelands, etc.) beyond current considerations (Kepe 2008; Shackleton et al. 2001), but it is still unknown how these values are likely to change as relationships and interactions among cropping and natural subsystems are altered in time and space by increasing pressures of climate change and variability. Climate change impacts are exerting additional pressures on an already diminishing natural resource base for most communities, calling for extraordinary adaptable solutions to sustain agricultural productivity and develop new income opportunities for the young and growing populations. This may require new forms of production technologies and institutions as the size and quality of land and environmental resources decline.

5.2 Climate Adaptation Research in the Agricultural Sector

5.2.1 Vulnerability and Adaptation of Crop Farming Systems in the Region

Scientific Evidence for Implications of Climate Change

The IPCC projections of increasing air temperatures in Southern Africa are confirmed by a number of empirical research studies from Malawi, South Africa, and Zimbabwe. Yearly average air temperatures in South Africa were found to increase at a rate of 0.13 °C per decade between 1960 and 2003 (Kruger and Shongwe 2004; Abraha and Savage 2006). However, some of the downscaled models projected temperature increases of 2–3 °C, particularly in the interior of the country (Johnston et al. 2012). In Zimbabwe, Unganai (1996) found an increasing trend in mean maximum temperatures of 0.1 °C per 10-year period between 1933 and 1993, with an overall increase of up to 0.8 °C. However, localised temperatures in areas such as the capital, Harare, increased by up to 1.2 °C over the same period, suggesting uneven distribution of the warming even at local scales. The downscaled models used by Unganai (1996) also predicted that a doubling of atmospheric CO_2 mean air temperature would increase by 2–4 °C. Almost a decade later, Mugabe et al. (2012) used four downscaled global circulation models (GCMs) derived from the IPCC and predicted a 1.5–2 °C increase in annual maximum temperatures for the period up to 2050 in most of the country, based on two of the models (CSIRO and MIROC). One of the other two models suggested a 2.5–3 °C increase for most of the country and a possibility of 3.5 °C in the country's western areas within the same period. Climatic data from Malawi showed that mean and maximum air temperatures increased by 2.3 and 2 %, respectively, between 1970 and 2002, and projections up to 2050 also suggest increased warming. The same GCM models used in South Africa and Zimbabwe predicted increases in air temperature of 1–1.5 °C for the northernmost parts of the country, and 1.5–2 °C for the rest of the country (Saka et al. 2012). Although the predicted temperatures vary with geographic areas within countries and also with the specific model used to make the projection, the bottom line is that all models predict a significant warming in the region. This is already consistent with observed patterns from historical field data analysed in each of the countries.

The observed and projected increases in air temperatures have generally been linked to a significant decrease in rainfall in Southern Africa. Unganai (1996) analysed long-term rainfall figures between 1900 and 1993 and concluded that there was a 10 % decline in rainfall over the period. However, the major challenge for cropping systems is likely to come from deteriorating quality of rainfall seasons. A critical analysis of rainfall data from over 40 different stations in Zimbabwe revealed no changes in total annual rainfall, but rather highly significant increases in within-season variability (Mazvimavi 2010). This is confirmed by an emerging body of empirical research suggesting that critical challenges for cropping systems will arise more from increased intraseasonal variability in rainfall rather than the mere total amount received per season (Rurinda et al. 2012). Episodes of floods characterised sometimes by a whole seasonal total received within a single month, followed by conditions of drought within the same season, have been common in Southern Africa.

Several studies have revealed that a combination of increased rainfall variability and increasing ambient air temperatures will in turn cause a significant decline in yields of major staple crops, particularly maize (Makadho 1996; Phillips et al. 1998; Kiker 2002; Dixon et al. 2003). Most of the regional studies have therefore used simulation modeling to evaluate the potential effects of projected rainfall variability in the production of major crops, particularly the staple maize that has a strong bearing on food security. In South Africa, each 1 % decline in rainfall is predicted to cause a 1.1 % decline in maize and a 0.5 % decline in winter wheat production (Bilgnaut et al. 2009). Gbetibouo and Hassan (2005) also predicted reduced yields for a variety of crops including maize, wheat, sorghum, sugarcane, groundnut, sunflower, and soybean due to increased rainfall variability and warmer ambient temperatures. Taking advantage of a wide network of field trials by international and national research networks across Africa, Lobell et al. (2011) used a dataset of more than 20,000 historical maize trials in combination with daily weather data and showed that for each degree day spent above 30 °C final maize yield was reduced by 1 % under optimal rainfed conditions, and by 1.7 % under drought conditions. Furthermore, maize yields are projected to decline by up to 20 % in the next 50 years in Malawi (Ibrahim and Alex 2008; Lobell et al. 2008), and by 10–57 % by 2080 in Zimbabwe mainly due to increased rainfall variability (Fischer et al. 2005; Lobell et al. 2008). A revelation from these various studies is that the highest losses in production will be in areas traditionally considered to be of high agricultural potential, with serious implications for an already food-insecure region. Major losses in production of staple cereals will be due to a rainfall-induced shrinkage in areas suitable for production: that is, the loss of current high potential agroecologies.

Researchers have also used different simulation models to evaluate the implication of the IPCC-based projections (mainly SCIRO and MIROC models). For example, in South Africa, the Decision Support System for Agro-technology Transfer (DSSAT) crop model projected significant maize yield reductions in the current medium to high potential areas by 2050 in relation to the 2000 yield levels (Johnston et al. 2012). Yield increases were, however, projected for some of the country's provinces that include Northwest and areas that are currently considered too cold for maize production in the Free State and Eastern Cape provinces. On the other hand, significant wheat yield increases were projected for the Free State and Mpumalanga provinces (ibid). Using the IMPACT global model for food and agriculture, the area suitable for maize production in South Africa was projected to decline by 25 % between 2010 and 2050, raising concern that the country could become a net importer of maize if no countermeasures are taken. The model, however, showed that sugarcane was the most resilient crop and showed potential for increased yield across large areas in the country (ibid). Similar work in Malawi using DSSAT showed that most of the central and northern regions of the country will witness 5–25 % increase in maize yields in the period to 2050, whereas the southern region will have large areas facing threats of a 5–25 % yield decline (Saka et al. 2012). However, the areas with a potential for more than 25 % maize yield increase were mainly found in the western areas of the country's southern region. Over the same period, the IMPACT model projected no significant changes in areas grown to maize, but a significant decrease in area under cassava, causing a decline in total production despite prospects of a 50 % increase in yield for the crop. There is therefore a high probability that the country will be a net importer of cassava within the 40-year period under consideration. The model, however, projected a doubling of cotton production due to increased yields, although the land shortage is expected to limit any possible expansion in the cotton production area (Saka et al. 2012). In Zimbabwe, similar DSSAT projections based on SCIRO and MIROC models produced inconsistent results on both maize and sorghum yields. With SCIRO, significant areas in the country were projected to suffer a 5–25 % maize yield loss for the period up to 2050, and many areas were expected to witness a 5–25 % increase in yields under the MIROC scenario (Mugabe et al. 2012). Using the CERES-Maize mode in earlier studies, Makadho (1996) concluded that maize production would become an unacceptably riskier agricultural activity for most smallholder farmers in Zimbabwe mainly due high ambient temperatures triggering moisture stress during grain filling. These findings and projections suggest new challenges in managing cropping systems in the future, and have a bearing on potential adaptation options to reduce vulnerability of the cropping subsector in agriculture given the multiple challenges that farmers face.

The foregoing discussion shows the value of modeling in informing future options for climate change adaptation in agriculture, however, it also reveals the glaring knowledge gaps arising from lack of field data on how farmers' current decision-making process may or may not influence the projected outcomes. For example, analysis of interseasonal rainfall variability (Tadross et al. 2005) and intraseasonal rainfall patterns (Tadross et al. 2009) in Southern Africa highlight major challenges of supporting farmers' strategic (long-term), tactical (between seasons), and operational (within season) decisions to minimize/avoid risk or take advantage of any emerging opportunities at local scales. Tadross et al. (2009) projected an increase in mean length of dry spells and a reduction in rainy day frequency in Southern Africa, making farmer choices of planting dates and selection of crop types/varieties critical. The study suggested that early planting may not necessarily be a solution in certain seasons due to prolonged dry spells, yet late planting may also render crops susceptible to diseases and pest outbreaks induced by the late rains. Studies by Tadross et al. (2005) provide insights on how improved understanding of climatic factors controlling critical seasonal rainfall events such as onset and cessation could improve targeting of adaptation options. Decision-making processes for many in Southern Africa, particularly the smallholders in Malawi and Zimbabwe, are undermined by numerous constraints that include lack of timely access to affordable agricultural inputs, volatile output markets, lack of access to climate information, and lack of access to land and improved production technologies. These factors add to the complexity problems defining the scope for the vulnerability of farming households drawing livelihoods primarily from rainfed cropping systems.

Causes of Vulnerability

As noted above, the definition, and therefore conceptual understanding, of the term 'vulnerability' is often different within and among different groups of practitioners in research and development (Casale et al. 2010; Miller et al. 2010). However, there is a general consensus that farmers in Southern Africa and other parts of sub-Saharan Africa are exposed to different stress factors associated with global environmental (e.g., climate change), economic, and sociopolitical change processes, and that the response capacities of these communities are limited. Agriculture accounts for the livelihoods of the majority of Southern Africa's population, either directly or indirectly through employment in agro-based industries. One can argue that the major causes of vulnerability to climate change and variability in the region are inherent in the very traditional problems known to constrain agricultural systems, with the emerging impacts of climatic change presenting a new context for interpretation of these challenges. Farmers in the region, as elsewhere in Africa, are often faced with multiple stress factors that in effect can define the complex interactions underpinning their adaptive capacity (O'Brien et al. 2009; Casale et al. 2010).

There are more commonalities than differences in the major causes of vulnerability to climate change on households and communities in many Southern African countries. These can be classified as outlined below, and the multiplicity of stress factors defining the context of the adaptive capacity of diverse communities against the effects of climate change and variability is also explained.

1. *High dependence on climate-sensitive crop production systems*: The predominantly maize-based (including other cereals and leguminous crops) and rainfed cropping systems of Southern Africa are dependent on season quality on a year-to-year basis, and susceptible to weather extremes of droughts, floods, storms, and extreme temperatures (Dixon et al. 2003; Unganai and Murwira 2010). For example, any negative effects of climatic factors will affect over two thirds of Zimbabwe's rural population who live directly on proceeds from agriculture. In Malawi, about 85 % of the population (51 % of whom are women) are based in rural areas where they depend on rainfed crop production (Government of Malawi 2002). South Africa also presents a good example of contrasting scenarios showing how the heavy dependence on climate-sensitive agricultural systems may be a major source of vulnerability. The Western Cape and Gauteng provinces, which have high levels of infrastructure development, high literacy rates, and low shares of agriculture in total GDP, are relatively low on the vulnerability index. In contrast, the highly vulnerable regions of Limpopo, KwaZulu Natal, and the Eastern Cape are characterized by densely populated rural areas, large numbers of small-scale farmers, and high dependency on rainfed agriculture (Hachigonta et al. 2013). More than 70 % of the South Africa's poor population resides in rural and informal settlements where their livelihoods are dependent primarily on crop production. Overall, the region's overdependence on maize may in itself be a source of vulnerability for millions of people, although this may also present opportunities to draw on technology advancement in crop improvement and management of crop interactions that involve maize. During the past decade, researchers have begun to explore mechanisms for getting smallholder farmers out of the 'maize poverty trap' (Nyikahadzoi et al. 2012; Mapfumo 2009, 2011). A major revelation from this research is that: unless there is sufficient maize on the market, communities will continue to grow the staple crop despite the high rates of production failure. Intensification of the

maize-based systems are therefore considered a pathway to diversification (out of the maize trap) into alternative high-value crops, but this calls for supporting policies on intensification and diversification (Mapfumo 2009).

2. *Poor and declining soil productivity*: Granite-derived soils dominant in many parts of Southern Africa present some of the world's most challenging soils in terms of their inherently low nutrient supply capacity, low soil organic carbon contents, and poor water retention capacity (Mapfumo and Giller 2001; Mafongoya et al. 2006). Poor soil fertility is one of Africa's major developmental challenges (Sanchez et al. 1997; Bationo 2004). The poor and declining soil fertility under maize monocropping inevitably results in a diminishing land quality with several concomitant externalities including agricultural extensification (Mapfumo 2009) and conflicts related to access to land resources (Rukuni et al. 2006; Lahiff 2007). Pressure on existing land resources due to low use of external nutrient inputs resulted in alarming rates of nutrient mining, declining crop yields, and accelerating land degradation as farmers encroach into marginal and fragile lands for cultivation (Stoorvogel and Smaling 1998; Mtambanengwe and Mapfumo 2005). A combination of unproductive soils, poor access to fertilisers and alternative nutrient resources, and increased climate variability is a recipe for absolute disaster for crop production in Southern Africa.
3. *Land degradation and a diminishing natural resource base*: Low productivity levels on croplands often result in annual food deficits at household and community scales (FAO 2010b; Nyikahadzoi et al. 2012), leaving many households to rely on food aid and/or food gathering from common resource pools such as forests, woodlands, and rangelands (Kepe 2008). However, increasing population pressure and a general decline in productivity and size of these common lands have increasingly contributed to land degradation and desertification. For instance, between 1990 and 2010 Malawi lost about 17 % of its forest cover to agricultural expansion, growth of human settlements, and harvesting of domestic fuel wood against low levels of reforestation (FAO 2011c). Poor performance of cropping systems due to climate change will, therefore, not only increase the threats of land degradation, but also undermine the provision of ecosystem services that have traditionally supported livelihoods of many poor households (Kazombo-Phiri 2005; Davies et al. 2010).

In South Africa, the most sensitive regions to climate change are Limpopo, KwaZulu Natal, and the Eastern Cape, because of severe land degradation and reduced natural production capacity. According to Meadows and Hoffman (2002), the Eastern Cape, KwaZulu Natal, and Limpopo possess a combination of physical and socioeconomic factors (both contemporary and historical) that have led to significant and in some cases irreversible, levels of deterioration in the rural environment. The least sensitive regions are the Western Cape, Gauteng, and Free State. A common feature of these regions is that they have a low percentage of subsistence farmers and have the least populated rural areas. Research findings from different countries indicate that smallholder communities in Southern Africa strongly rely on natural resource pools to sustain their livelihoods during drought years or poor cropping seasons (Mapedza et al. 2003;

Frost et al. 2007). Any threats on this resource base due to the negative impacts of climate change will therefore render many households even more vulnerable (Woittiez 2010).

4. *Lack of timely access to crop production inputs and to output markets*: Numerous studies have shown how poor access to crop inputs such as seeds, fertilisers, herbicides, and equipment has remained a perennial problem for the majority of predominantly smallholder farmers in Southern Africa (Kazombo-Phiri 2005; Government of Malawi 2008; Mtambanengwe and Mapfumo 2009; SADC 2012). Smallholder cropping systems, upon which most of the vulnerable communities depend, have mainly been centered on a subsistence mode of production in which endogenous input components are maximised while external inputs are minimised. Many of the farmers, by design, therefore live beyond the reach of markets, yet agricultural development policies are hinged on the principles of (assumed) market participation. Transformation of these subsistence farms into commercially-oriented production systems driven by market objectives (Delgado 1999) therefore effectively demands structural and process changes in knowledge systems, technology development and delivery, institutions, and policies.

   Climate change and variability exert further demands for such transformations, bringing to the fore questions on potential links between vulnerability and functioning (or failures) of agricultural markets at different scales. The rise of smallholder agriculture in post-independent Zimbabwe (before the recent socio-economic and political crisis) (Rukuni et al. 2006), and experiences from Malawi's recent subsidy programme (Dorward and Chirwa 2011) present some key lessons on the value of input–output market access. However, such efforts to increase productivity and commercialise smallholder agriculture have also increased the necessity for external input use, with disproportionate livelihood effects against poorer households and communities in remote areas (Nyikahadzoi et al. 2012; Mapfumo et al. 2013). Due to increased rainfall variability, use of purchasing crop inputs has not only become riskier, but also critically dependent on timing of operational decisions by farmers. There is evidence that farmers with better access to seasonal climate forecasts are better able to make appropriate farming decisions at the farm level and get better harvests (Patt et al. 2005). However, lack of access to inputs often remains an overriding constraint (Patt et al. 2005; Mapfumo et al. 2013). Development of models for supporting access and efficient use of agricultural inputs by diverse categories of farmers and supporting their timely responses to climate forecasts is therefore a major challenge for development researchers and practitioners in their planning of adaptation interventions. Empirical evidence is critically lacking on how timely access to agricultural inputs and output markets can reduce or heighten vulnerability of farming communities under current and future changes in climate change.

5. *Lack of access to information and knowledge*: One major cause of vulnerability in the agricultural sector is the lack of access to agricultural information and knowledge of farmers and local-level service providers (e.g., local extension agents) on climate forecasts, early warning systems, improved agricultural tech-

nologies and practices, and available options for adaptation. The limited information accessed in most African rural communities has also tended to discriminate against women and socially disadvantaged sections of local societies. Farmers depend more on their indigenous (local) knowledge systems and own social networks than conventional scientific knowledge systems for decision making (Nyong et al. 2007; Mapfumo et al. 2010). Farmer decisions on what crops/cultivars to grow, when to plant, as well as when to sell how much of their crops, are therefore not informed by robust (science-based) evidence. However, the value of indigenous knowledge in development (Pawluk et al. 1992; Tanyanyiwa and Chikwanha 2011) is worth recognition. Communities have historically managed to adapt to climate and other environmental stresses, albeit with severe tradeoffs. However, there is a general lack of supporting evidence on how local knowledge systems may or may not be sufficiently understood, or are simply not adequate to inform farmer decisions on sustainable adaptation options to match the magnitude of current and future challenges due to climate change and variability. The nature and magnitude of emerging impacts of climate change are likely to present adaptation demands that are beyond the scope of current local knowledge systems, potentially rendering most of the communities vulnerable. Studies in Zimbabwe and South Africa have shown that farmers have a varied understanding of the major causes of climate change and variability, the current and potential impacts and the need for adaptation suggesting a general lack of equal access to quality, climate, and agricultural information by farmers (Gbetibouo 2008; Dutta 2009; Mtambanengwe et al. 2012). The usefulness of seasonal climate forecasts has often been undermined by lack of credibility, coarseness of scale, and institutional barriers, among other factors (Patt and Gwata 2002).

There is increasing evidence that participatory action research and learning-based research and development approaches enhance access to information/knowledge by farmers in general, and the hitherto marginalised social groups in particular, allowing them to experiment with new technologies and potential adaptation options (Mapfumo et al. 2013). Evaluation of work of SOFECSA in Zimbabwe showed that about 73 % of the farmers preferred interactive farmer-learning platforms to access information on integrated soil fertility management (ISFM) and other agricultural knowledge (Gwandu et al. 2013). In contrast to findings from related studies in the health sector in the region, six farmers' least preferred sources of information included nongovernmental organisations (NGOs), newspapers, and magazines (ibid). There is also evidence suggesting that participatory workshops enhanced use of climate forecast information by farmers (Patt et al. 2005). Lack of access to information renders irrelevant the role of climate early-warning systems, leading to poor preparedness against climatic hazards such as droughts and floods (Unganai and Murwira 2010).

6. *Weakening of local institutions and traditional social safety-net systems*: Farming communities have always coped with multiple stresses as they struggle to sustain their livelihoods, probably accounting for some of the diversity and complexity of agriculture and natural resource management systems that have kept them

going for generations. However, it has become evident that collapsing components of traditional social safety-net systems will likely increase the vulnerability of households and communities. These include the following: (1) breakdown of rural–urban links (Andersson 2002); (2) weakening extended family systems (Casale et al. 2010); and (3) weakening of local institutions that have traditionally supported social collaborations and minimised conflicts to achieve food security (Mapfumo et al. 2013), enhanced management of crop–livestock interactions (Rufino et al. 2011), and regulated use of natural resources such as forestry (Campbell 1996). High-profile development projects that hold high promises (e.g., through environmental conservation and economic benefits), as well as interventions anchored on compliance with donor-driven, but frequently changing buzzwords, have sometimes tended to heighten vulnerability rather than reduce it (Büscher and Mutimukuru 2007; Andersson et al. 2012). Many food aid and relief programmes championed by governments and NGOs have also apparently contributed to erosion of the core values of local social safety nets, often rewarding laziness among communities and weakening their adaptive capacity (Mapfumo et al. 2013). Casale et al. (2010) demonstrated the strong links between external sources of vulnerability such as lack of employment or income and internal sources such as a lack of adequate education that in turn undermine the ability to secure employment. These examples suggest the vulnerability of local institutions to external pressures, which in turn further exposes communities and households to emerging threats of climate change. This also points to the intricate poverty traps that commonly characterise livelihoods of poor communities in developing countries, which if not unravelled and clearly understood in the context of climate change, may instead result in the development of adaptation options that undermine some of the current and future sources of resilience. Dercon (2007) defined a poverty trap as an equilibrium outcome or situation from which one cannot emerge without outside assistance/intervention, and this is often caused by market failures which force farmers into low risk–low return livelihood options (Dercon 2009).

7. *Poor and diminishing capital resource base*: Most households and communities lack the capacity to use or create new off-farm livelihood opportunities due to their current levels of poverty, and it is unlikely that they will be able to respond to additional livelihood pressures, or even take advantage of any opportunities associated with climate change and variability. For instance, Malawi is one of the world's poorest countries, ranking 160 out of 182 countries on the Human Development Index. According to the United Nations Development Programme (UNDP) Human Development Report for 2009, about 74 % of the population still lives below the income poverty line of US$1.25 a day and 90 % below the US$2 a day threshold. The proportion of poor and ultrapoor is highest in rural areas of the southern and northern parts of the country (Ellis et al. 2003; World Bank 2008). Lack of education coupled to physical exclusion from major national economic initiatives due to poor infrastructure present major barriers to climate change adaptation. Communities often lack access to infrastructure such as land, roads, bridges, health and education facilities, and water supply struc-

tures, and are often not the primary beneficiaries of financial services such as microcredit, microinsurance, and microsavings (World Bank 2008; Unganai and Murwira 2010; Government of Zimbabwe 2013). The communities are, therefore, practically trapped, with limited alternative livelihood options outside agriculture for most of the rural communities.

8. *High prevalence of HIV/AIDs, malaria, and other diseases*: Labour productivity in the agricultural sector in Southern Africa has continued to be severely compromised by the scourge of HIV/AIDS. The region has witnessed prevalence rates as high as 25–40 % in many of the countries, creating a great strain on the health delivery system and indirectly affecting another livelihood system (Casale et al. 2010). For example, it is projected that farmers in areas such as the Limpopo, KwaZulu Natal, and the Eastern Cape provinces are unlikely to cope effectively with the potential impact of climate change and variability due to high unemployment and HIV prevalence, and low infrastructure development (Government of South Africa 2004; O'Brien et al. 2009). There are numerous reports of labour constraints as family members spend significant time looking after the sick. Weakening institutional arrangements and social networks have also been found to aggravate the risks associated with loss of labour in the agricultural sector (SADC 2003; Casale et al. 2010).

Options for Strengthening Adaptive Capacity and Supporting Crop Farming-Based Livelihoods

Building adaptive capacity of farming communities in Southern Africa will require a consideration of the diverse farmers' production objectives and resource endowments, and understanding of differential impacts of pending climatic threats on different social groups within and across communities (e.g., women, youth, the elderly, migrant households, and the disabled) in order to appropriately target adaptation options across temporal and spatial scales. Sustainable adaptation options are likely to be those rooted in local knowledge systems and institutions. Strategies for building adaptive capacity in Southern Africa are therefore likely to differ significantly between the large-scale commercial and smallholder sectors. The commercial sector is often characterised by a big capital base and high organisational capacity drawn from their diverse private, corporate, and public ownership structures. Typically, the farmers have larger cash flows and greater diversification, can afford longer planning horizons that take advantage of easy access to credit, and have the capacity to make capital investments and respond to market fluctuations (Thomas et al. 2011). Building their adaptive capacity is therefore likely to involve support mechanisms and policies that enhance technology development and adoption, crop diversification, innovative insurance strategies, and improved financial and risk management (Challinor et al. 2007). In contrast, the smallholder farmers present a more complex scenario because of their heterogeneity (Giller et al. 2011b) and their intricate but resource-constrained livelihood systems. Thus, climate adaptation interventions for smallholder communities will necessarily require fostering capacity for multidimensional responses (sociopolitical, economic, and ecological) and change processes that can transform both agricultural and livelihood systems.

Research studies in Malawi, South Africa, Zambia, and Zimbabwe under the IDRC-DFID funded CCAA programme demonstrated the potential role of a combination of participatory action research (PAR), field-based colearning, participatory technology development approaches, and innovation systems in building the adaptive capacity of different smallholder communities (Twomlow et al. 2008; Majule et al. 2011; Mapfumo et al. 2013). Interventions that significantly influenced social change processes with positive feedback on local institutions were those that enabled access to improved crop types/cultivars and ISFM technologies to address food security concerns and enhanced market participation by farmers (Mapfumo et al. 2013). The interventions demonstrated that PAR and farmer colearning platforms could be coupled to support smallholder farmers to self-mobilise and self-organise for collective action processes that included natural resources management, joint acquisition of agricultural inputs, and marketing of produce. These processes promoted farmer-to-farmer sharing of information and knowledge on ISFM as an adaptation option (Gwandu et al. 2013), and contributed to enhancement of household food self-sufficiency (Nyikahadzoi et al. 2012). Lessons can be drawn from these limited CCAA projects to provide insights on appropriate approaches for building adaptive capacity of the poor and socially disadvantaged (hence more vulnerable) communities. The following are options for crop-based climate change adaptation by smallholder farmers in Malawi, South Africa, and Zimbabwe, as suggested from the various studies:

- Enhancing interactions between planting time and soil fertility management technologies for optimising crop yields under variable rainfall and changing temperature regimes (Crespo et al. 2011; Zinyengere et al. 2011; Mapfumo et al. 2013).
- Promoting timely access to sufficient quantities of quality crop production inputs by farmers in order to enhance the timeliness of farming operations in response to the dictates of prevailing climatic factors. This includes access to fertilisers, seed, herbicides, and farming equipment.
- Improving access to and use of soil, water, and natural resources management technologies, including ISFM technologies (Mafongoya et al. 2006; Mtambanengwe and Mapfumo 2009), conservation agriculture (CA) options (Thierfelder and Wall 2010; Unganai and Murwira 2010), land reclamation/restoration options (e.g., agroforestry and indigenous legume fallows), natural resources management approaches (Mapfumo et al. 2005; Akinnifesi et al. 2008; Nezomba et al. 2010), and integrated water management strategies and techniques (Theu et al. 1996; Nyamangara and Nyagumbo 2010; Maponya and Mpandeli 2012). However, the relative contributions of these options to climate change adaptation processes still require quantification.
- Crop diversification into stress-tolerant crop types and cultivars, including mixes of perennial versus short-cycle cultivars; cash crops versus subsistence crops; root and tuber crops versus staple cereals; and high-yielding crop types and cul-

tivars to take advantage of known windows of favorable climatic conditions (e.g., rainfall and temperature) (Bryan et al. 2009; Dinar et al. 2008). Crop improvement research to develop stress-tolerant crop cultivars is therefore a necessity (Bänziger et al. 2006).

- Switching to more water-efficient crops such as sorghum or millet or changing production entirely from crops to livestock (Kiker 2002; Makadho 1996).
- Integrating stress-tolerant nitrogen-fixing legumes into the cropping systems to enhance soil productivity and improve household nutrition and income (Kasasa et al. 1999; Mpepereki et al. 2000; Waddington and Karingwindi 2001; Mapfumo 2011).
- Development of irrigation infrastructure, including construction of small to medium dams in smallholder farming areas to complement rainwater (Matarira et al. 2004; Bryan et al. 2009).
- Developing mechanisms for enhancing efficiency of resource targeting at field, farm, and community scales (Giller et al. 2006; Tittonell et al. 2012) including options for mineral fertiliser management in response to within-season rainfall patterns, and strategic management of mineral and organic fertiliser combinations (Ncube et al. 2007; Kanonge et al. 2009; Chikowo et al. 2010).

Building research and extension capacity at different levels for technology development, adaptive testing, and participatory monitoring and evaluation of change processes associated with the above options will apparently provide a major avenue for their implementation. The government facilitated the provision of financial aid, credit, insurance, and market incentives to both commercial and subsistence growers which may enable farmers to respond adequately to more challenging cropping environments (Bryan et al. 2009). Other suggested supportive measures include: promotion of diversified employment opportunities, new institutional arrangements, and communal risk-sharing measures to conserve resources (Challinor et al. 2007). Running comprehensive HIV/AIDS programmes can also enhance agricultural labour productivity and redirect resources towards other adaptation options.

Documented Adaptation by Farmers in the Region

Farmers have responded to climate variability through a variety of crop management strategies, although most of these efforts may qualify more as coping than as adaptation strategies. This can be attributed to the fact that farmers have long been living with climatic problems such as droughts, flooding, and within-season rainfall variability, but in recent years the awareness of the magnitude of the problem has been raised. This may therefore explain the limited practical evidence available on adaptation measures that have been pursued by farmers to date. Most of the available examples are notably related to food security, suggesting reactive rather than anticipatory or planned adaptation actions by most farming communities. Tropical Southern Africa is dominated by miombo ecosystems (Campbell 1996) and a number of rural institutions have evolved over time to regulate harvesting and distribution of livelihood benefits among rural communities (Clarke et al. 1996; Shackleton and Shackleton 2004;

Magombo et al. 2012). Smallholder communities have continued to depend on their indigenous knowledge to extract wild fruits and other nontimber forest and rangeland products, particularly during years of poor harvests and drought (Frost et al. 2007; Woittiez 2010). An important source of adaptation from these activities is the evolution of functional community-based natural resource management regimes (Mutimukuru et al. 2006; Roe et al. 2009). This has not only given rise to better opportunities for community mobilisation and organisation towards natural resource conservation, but has also increased consciousness among external stakeholders in development about the value of local institutions and the role they can play in anchoring solutions to emerging environmental threats.

Commonly documented adaptation options employed by farmers directly in management of crop systems include (re)introduction of mixed cropping, and planting of short-season maize varieties and other crops to allow early harvesting and shortening of hunger periods (Stringer et al. 2009). Farmers have also tended to move towards mixed crop–livestock farming (Magombo et al. 2012). Detailed case studies from southern Mozambique (Milgroom and Giller 2013) and northeast Zimbabwe (Rufino et al. 2011) showed how local institutions have evolved out of environmental marginality to yield social collaborations that offer options for adaptation to climate variability by smallholder communities in semi-arid zones. Collaborations that provided for land and draught power (cattle) exchange allowed Mozambican farmers to stagger their plantings and maximise staple cereal production during favorable seasons. In Zimbabwe, such collaborations minimised conflicts between cattle owners and non-owners, allowing for draught power sharing and livestock grazing arrangements that helped offset climate-induced constraints (Rufino et al. 2011). Across most of the region, farmers have also responded by seeking off-farm income opportunities. However, these are often restricted to selling of livestock, domestic assets, and natural resource-derived products, and temporary migration to urban areas or diasporas (Matiya et al. 2011). Table 7 briefly outlines notable research studies that provide relevant insights on adaptation. Notwithstanding the above examples, it was generally evident that concrete examples of adaptation by farmers are critically lacking, whether by their mere absence or by lack of research capacity to identify and document them. A number of adaptation options have been suggested for Southern Africa, including those mentioned above, however, these have largely been at the research level. There are few, if any, studies clearly documenting the adoption of these adaptation options by farmers at scale. Most of the farmers' current responses to climatic shocks have been of a short-term nature, and often punctuated by external but temporal response measures such as food aid and relief programmes.

Lessons from Adaptation Projects and Interventions in the Crop-Farming Sector in the Region

Major lessons on adaptation in Southern Africa are currently limited to few intervention projects, mainly those conducted under the IDRC-DFID funded CCAA (Twomlow et al. 2008; Mapfumo et al. 2010; Majule et al. 2011), DFID (Brown

Table 7 Selected examples of climate change adaptation studies and interventions conducted in Malawi, South Africa, and Zimbabwe

Outline on research based on climate change adaptation studies and their interventions
• Combined use of participatory action research (PAR) and learning centre approaches to revitalise local institutions supporting traditional social safety nets and uptake of integrated soil fertility management (ISFM) technologies and improved agronomic practices (e.g., managing planting date × nutrient management interactions for different crop types and cultivars) by smallholder farming communities in Makoni and Wedza districts of eastern Zimbabwe (Mapfumo et al. 2013). The studies enabled quantification of the contributions of forest and rangeland resources to farmer livelihood during climatic stress (Woittiez et al. 2013)
• Assessment of local climate change adaptation strategies used by farmers in Malawi, such as crop diversification, temporary migration, selling of assets, eating of a wild tuber plant called *Nyika*, small-scale irrigation, and application of organic manures for soil fertility enhancement. These options were promoted at scale by the government, donor community, and civil society in order to build adaptive capacity of communities and resilience of the farming systems against the effects of climate change and variability (Matiya et al. 2011; Magombo et al. 2012). Prioritised interventions included diversification into early maturing and drought-tolerant maize and sorghum varieties (Magombo et al. 2012)
• Initiatives by Practical Action and Lutheran Development Services focused on mainstreaming of climate change adaptation and disaster risk reduction at district, provincial, and national levels through use of community-based approaches so as to empower local communities in decision-making processes in Zimbabwe. This enabled adoption of a livelihoods-centred approach to disaster risk reduction, which marked a policy departure away from postdisaster emergency response (Brown et al. 2012)
• Coping with drought and climate change project in Chiredzi district in southeast Zimbabwe (Government of Zimbabwe/UNDP/GEF 2009; Unganai 2009). Focusing on developing adaptation strategies for smallholder farmers, the project employed principles of participatory decision making, planning, and implementation. One of the key objectives was to promote access and use of medium- to long-term climate forecasts to inform decision-making processes in cropping and water management as well as off-farm activities
• Promotion of conservation agriculture (CA) and related farming practices by various development partners as an adaptation strategy in drought-prone areas. Apart from provision of inputs, smallholder farmers have received new knowledge that enabled them to try new options for adaptation (Mutekwa 2009; Gukurume et al. 2010; Gukurume 2013)
• In South Africa, large-scale commercial farmers have shown promise to adapt through technology development and adoption, crop shifting and diversification, insurance, and improved financial management (Challinor et al. 2007)
• Activities of the Zvishavane Water Projects (Zimbabwe) demonstrated that building on farmers' indigenous knowledge, skills, and experience through soil and water conservation technologies such as water harvesting activities enabled farmers to adapt to harsh climatic conditions prevailing in this area (Mutekwa 2009). Provision of climate forecast information in a language that is understandable to farmers on warnings of poor season, commencement of season, and adequacy of rains also proved a useful entry point for informing decision-making processes (Unganai 2000; Patt et al. 2005)

et al. 2012) and the UNDP/Global Environment Facility (GEF) Coping with Drought and Climate Change Projects7 (Unganai 2009). The CCAA also supported a project that focused on Building Food Security and Social Resilience to HIV/AIDS. Most other climate change projects have generally been exploratory (assessments), and have largely helped to create awareness among communities and development stakeholders, as well as characterising and developing an understanding of the major elements of vulnerability to climate change (Casale et al. 2010; O'Brien et al. 2009). However, these limited development research studies provide valuable insights and lessons to inform future development planning and policy processes for climate change adaptation in crop-based farming systems. The following are some of the key lessons:

- Adaptive testing of emerging practical options for climate change adaptation at scale in the agricultural sector is increasingly necessary, building on available data. Most of the adaptation options suggested for the crop-based farming systems in Southern Africa, such as staggered planting, crop diversification, integrated soil fertility management and irrigation, show promise at experimental scales (Mapfumo et al. 2010; Brown et al. 2012; Rurinda et al. 2013).
- Food insecurity and poverty are in themselves fundamental sources of vulnerability that will severely limit the scope for adaptation. Most smallholder communities typically have limited access to agricultural inputs, soil fertility management technologies, agricultural water, and resource conservation approaches (Mapfumo et al. 2013). This limits their adaptive capacity.
- Farmers, particularly in the smallholder sector, will require technical support to make critical decisions on how to allocate limited resources among crop production, natural resources management, and off-farm employment (Giller et al. 2006; Twomlow et al. 2008). Detailed studies on the tradeoff analysis of these production (livelihood) objectives are necessary to inform planning of adaptation interventions at scale, and to guide adaptation policy processes.
- Climate change adaptation research interventions that employ PAR and field-based farmer learning platforms will likely attract effective participation by diverse social groups from among the farmers, including women and the socially disadvantaged (Mapfumo et al. 2013; Mashavave et al. 2013).
- Increasing farmer access to seasonal climate forecasts coupled with technical agricultural information and access to improved seeds, soil fertility technologies, and crop production practices will strengthen the adaptive capacity of many poor farming communities (Gwandu et al. 2013).
- Investments into integrated approaches to soil fertility management, soil and water conservation techniques, and land reclamation will broaden climate change adaptation options across diverse agroecologies and benefit many rural and urban communities in Southern Africa (Tittonell et al. 2012). This could form a basis for participatory development of 'climate-smart' crop production options.
- Failures of current development interventions to strengthen local institutions and indigenous knowledge value systems may increase current vulnerabilities and compromise future adaptation processes (Roncoli et al. 2011; Mapfumo et al. 2013).
- There is a general absence of large-scale, well-directed research and development programmes to promote locally-adapted crop types/cultivars/varieties that have traditionally supported livelihoods in Southern Africa.

- Based on available studies, it can be inferred that policymakers must create an enabling environment to support adaptation by increasing access to climate information, credit lines, insurance, and markets (input and output) to reach small-scale subsistence farmers with limited resources to confront climate change.

Key Documented Barriers to Adaptation

Major barriers to adaptation processes in Southern Africa revolve around lack of research and development capacity to develop, test, and deliver adaptation processes, as well as the absence of responsive policies that are specifically tailored to meet the emerging climatic challenges. The launching of CCAA was in recognition of the major gap. UNDP (2008) cited limited analytical capability of local personnel to analyze the threats and potential impacts of climate change effectively, so as to develop viable adaptation solutions. Thus, traditional and contemporary agricultural policy frameworks, developed under these inherent deficiencies, are unlikely to deliver adaptation processes without undergoing substantial changes. For example, with no ready access to good quality seasonal climate forecasts (Patt and Gwata 2002; Mtambanengwe et al. 2012) and knowledge on available adaptation options (Kandlinkar and Risbey 2000), farmers will find it difficult to make decisions and plan against future climate stresses. Agroecologies in Southern Africa are generally semi-arid and characterised by poor within-season rainfall distribution (Tadross et al. 2009), yet the majority of farmers have no access to conventional forms of insurance. Farmers' perennial problems with the lack of timely access to crop production inputs, including seed, fertilisers, herbicides, draught power, and equipment (Nyikahadzoi et al. 2012; Mapfumo et al. 2013) have largely been attributed to lack of access to lines of credit (Mano and Nhemachena 2007; Nhemachena and Hassan 2007). This is apparently a major disincentive for farmers to invest in organising their local institutions and capacities to demand new knowledge and adopt improved technologies. Instead, poor institutional arrangements and deterioration of social safety nets (Nyikahadzoi et al. 2012; Mapfumo et al. 2013), against a declining resources base, are sinking farmers deeper into a subsistence mode of production and making them more vulnerable. It is, therefore, essential that fundamentals of sustainable crop production and food self-sufficiency be first addressed, in order to reduce risk of external input use and stimulate innovations towards market participation by farmers.

Another hindrance to crop-based adaptation interventions is lack of access to land and poor infrastructure. Poor roads and bridges make access to rural areas difficult, hence compromising the delivery of farm inputs (e.g., fertilisers and seeds), access to external learning platforms by farmers, as well as access to markets. This is aggravated by extreme poverty, poor health, and malnutrition of vulnerable groups, who are also often illiterate, making it difficult furthermore to build adaptive capacity at the local level. High prevalence of HIV/AIDS puts a major drain on family energy, cash, and food (Casale et al. 2010), undermining time and other resource investments (e.g., labour, cash) in food production and pursuance of other livelihood opportunities. This failure in other key sectors of rural development will put a strain on climate change adaptation.

5.3 Agricultural Policies for Climate Change Adaptation

5.3.1 State of Knowledge on Policies and Strategies for Climate Change Adaptation in the Agricultural Sector

In all the three focus countries in this study, the major policy and strategic considerations for climate change adaptation are variables contained or implicitly implied within and outside agricultural policy frameworks. However, there is a clear reflection that the major national policy documents are informed by the international and regional conventions and discourse on climate change, particularly those derived from UNFCCC, NEPAD, and SADC.

Climate Change Considerations in National Agriculture Sector Policies and Strategies

In Malawi, climate change adaptation is covered in several government agricultural policy and strategy documents including the Food Security Policy 2006, National Agricultural Policy (2010–2016), Agriculture Sector Wide Approach (ASWAp) of 2010, National Water Policy (revised 2005), National Disaster Risk Management Policy, National Land Resources Management Policy and Strategy and National Irrigation Policy, and Development Strategy of 2000 among others (Government of Malawi 2006, 2011). Out of these documents, the National Agricultural Policy, which is mirrored by the ASWAp, explicitly provides action points for climate change adaptation. The ASWAp is a response to Millennium Development Goal 1 and to CAADP Pillars 1 and 2 (Government of Malawi 2011). It broadly focuses on agricultural growth and poverty reduction, but specifically addresses food security and risk management and sustainable land and water management. It is thus consistent with the National Agricultural Policy, which provides for the specific actions in relation to climate change adaptation:

1. Improving vulnerability assessments to provide early warning on food security. The ASWAp goes on to highlight a need for insurance against weather.
2. Enhancing food security and developing community-based seed and food storage systems.
3. Improving crop production through the use of appropriate technologies. The ASWAp emphasises the use of improved crop varieties that are tolerant to drought, and developing/implementing strategies for drought preparedness.

4. Increasing resilience of food production systems to erratic rains by promoting the sustainable dimba production of maize and vegetables in dambos, wetlands, and along river valleys. In this regard, the ASWAp emphasises protection of catchment areas and fragile areas including wetlands and rivers, as well as increased use of irrigation and development of small dams for water harvesting.
5. Developing a framework to ensure that all agricultural projects and programmes undertaken in the sector have had environmental impact assessments as required by the Environmental Management Policy and Act and the related international instruments.
6. Mainstreaming gender and HIV/AIDS issues.
7. Strengthening the capacity of all stakeholders in issues of mainstreaming environmental management in the agricultural sector.

The National Water Policy focuses on water resources management and development and recognises the increasing incidence of droughts and floods. It calls for better catchment management to maintain/enhance ecosystems functioning and preserve biodiversity, including protection of wetlands. The National Irrigation Policy and Development Strategy focus on irrigation development to reduce dependence on rainfed agriculture. However, it does not recognise potential negative impacts of climate change variability in irrigation development. It explicitly calls for measures to reduce impacts of climate change to minimize economic and cultural disruptions and dislocations of the most vulnerable people. Other documents, such as the National Gender Policy of 2000 in Malawi, do not offer clear action points on adaptation, although the latter recognises women as one of the most vulnerable groups to climate change and variability.

South Africa provides some of the major contrasts in agricultural policies and strategies for climate change adaptation, most likely due to the relatively low contribution of agriculture in the country to national GDP and therefore a different focus on the major pathways to economic development. The key guiding policies and strategies for agriculture in South Africa are contained in the Integrated Growth and Development Plan 2012 (Government of South Africa 2012). The document responds to the country's macroeconomic Medium Term Strategic Framework by addressing three of the twelve targeted outcomes: to achieve decent employment through inclusive economic growth; to have vibrant, equitable, and sustainable rural communities contributing towards food security for all; and to protect and enhance the country's environmental assets and natural resources. The policy document recognises the critical challenges of climate change, and clearly embraces the need for substantial public and private investments in irrigation; support of crop varieties and animal breeds that are tolerant to heat, water, and low soil fertility stresses; and imperative to build roads and marketing infrastructure to improve small farmers' access to critical inputs as well as to output markets. The policy framework also dovetails well with the Comprehensive Rural Development Programme (CRDP) of the Department of Rural Development and Land Reform (DRDLR). The CRDP focuses on three main pillars, namely land reform, agrarian transformation, and rural development (Government of South Africa 2009). The CRDP addresses several critical developmental issues that focus on reducing vulnerabilities of the socially diverse rural communities, and is relevant to enhancing climate change adaptation processes including:

1. The empowerment of rural communities, especially women and the youth, through facilitating and mediating strong organisational and institutional capabilities and abilities to take full charge of their collective destiny.
2. Capacity-building initiatives, in which rural communities are trained in technical skills, combining them with indigenous knowledge to mitigate community vulnerability, especially with climate change, soil erosion, adverse weather conditions and natural disasters, hunger, and food insecurity.
3. The establishment of business initiatives, agroindustries, cooperatives, cultural initiatives, and vibrant local markets in rural settings.
4. Revitalisation and revamping of old, and the creation of new, economic, social, and information communication infrastructure and public amenities and facilities in villages and small rural towns.
5. Empowerment of rural communities to be self-reliant and able to take charge of their own resources.
6. Development of mitigation and adaptation strategies to reduce vulnerabilities with special reference to climate change, erosion, flooding, and other natural disasters.
7. Increased production and sustainable use of natural resources, including related value-chain development in crop farming (exploring all possible species, especially indigenous plants, for food and economic activity).

The above policy and strategy documents evidently build on the Integrated Food Security Strategy for South Africa (Government of South Africa 2002), which was launched with the overarching objective to eradicate hunger, malnutrition, and food insecurity by 2015. Some of the key specific objectives of the strategy were to:

(a) Increase household food production and trading.
(b) Improve income generation and job creation opportunities.
(c) Improve nutrition and food safety.
(d) Increase safety nets and food emergency management systems.
(e) Improve analysis and information management systems.
(f) Provide capacity building.

The strategy involved a wide range of interventions that included food production, infrastructure development, storage and transportation of food, social security grants, food emergencies, and microfinancing. However, lessons drawn from the initiatives and their contributions to climate change adaptation thus far have not been clearly reflected in the new policy documents.

In Zimbabwe, the agriculture sector policies and strategies are provided for in the Comprehensive Agriculture Policy Framework 2012–2032 (Government of Zimbabwe 2012), which supersedes the Zimbabwe Agricultural Policy Framework 1995–2020, which was rendered nonfunctional by the government's land reform programme of 2000. The new policy framework was necessitated by the need to address the country's new challenges and opportunities in the agricultural sector, in line with the national macroeconomic policy contained in the Zimbabwe Medium Term Plan 2011–2015. The major policy objectives as outlined in the document include:

- Assure national and household food and nutritional security.
- Ensure that the existing agricultural resource base is maintained and improved.
- Generate income and employment to feasible optimum levels.
- Increase agriculture's contribution to gross domestic product.
- Contribute to sustainable industrial development through home-grown agricultural raw materials.
- Expand significantly the sector's contribution to the national balance of payment.

Surprisingly, the policy framework is largely silent on climate change, and does not put any emphasis on specific challenges related to rainfall variability, increasing temperatures, and frequent droughts and occasional floods affecting the sector. This is despite the apparent recognition by the government of the high vulnerability of this national livelihood pillar to the pending negative impacts of climate change and variability. Climate change is only mentioned explicitly under crop diversification, with a specific focus on breeding of drought-tolerant crops, apparently offering a limited scope for adaptation. This implies that climate change adaptation is not considered a development issue within the agricultural sector. However, a National Policy and Programme for Drought Mitigation is also in place, which provides for provincial and district programmes to access funding from international organisations for purposes of drought mitigation. The policy framework has also guided the establishment of regional early warning systems and drought monitoring centers (Chagutah 2010). The country's National Water and National Irrigation Policies, along with a number of other policies, are also under development as the country recovers from more than a decade of sociopolitical and economic crisis. These emerging policies offer opportunities for addressing some of the deficiencies on climate change adaptation in the new agricultural sector policy document.

Climate Change Considerations in Regional Agriculture Sector Policies and Strategies

All countries in Southern Africa are members of the African Union and SADC. Malawi, South Africa, and Zimbabwe are therefore all signatories to major regional treaties and protocols that guide economic development to safeguard natural resources and the environment for the benefit of the region's diverse populations. One of the African Union's major development initiatives is NEPAD (AU/NEPAD 2003), and all the countries subscribe to its programmes. Particularly relevant to the regional agriculture sector is CAADP, which implicitly embraces climate change issues under its strategic Pillars 1 and 3. Pillar 1 of CAADP seeks to extend the area under sustainable land management and reliable water control systems. Pillar 3, on the other hand, aims to increase food supply and reduce hunger across the region by raising smallholder productivity and improving responses to food emergencies. Although the two pillars strategically address some of the fundamental sources of vulnerability to climate change and vulnerability by communities in Southern Africa, their design formulation was apparently not from a climate change adaptation perspective. CAADP is also consistent with the joint efforts of the European Union member states to fulfil the United Nations' Millennium Development Goals.

SADC has developed a Regional Agricultural Policy (RAP) (SADC 2012) which seeks to harmonise policy for agriculture and natural resources and strengthen the interventions so far guided by the SADC Regional Indicative Strategic Development Plan (RISDP) of 2003. One of the major areas of focus for the RAP is to reduce vulnerability in its broad sense. The policy document specifically identifies the regional agriculture sector as vulnerable to climate change and variability, and recognises the critical need for adaptation. The policy also draws on the momentum of earlier protocols on agriculture, although these are not explicit on how to address climate change adaptation challenges. These include:

- The SADC Dar-Es-Salaam Declaration on Agriculture and Food Security of 2004, which prioritised sustainable food security as well as environment and sustainable development.
- The SADC Maputo Declaration of 2003, which required countries to commit at least 10 % of their national budgets to agriculture.
- The Maseru Protocol of 1996 (eventually launched in 2008), which sought to establish a SADC Free Trade Area to enable member states to liberalise trade through the removal of tariffs and nontariff barriers. South Africa is one of the countries that have fully implemented this Trade Protocol, allowing 99 % of imports from within SADC to enter the South African market free of customs duties (Government of South Africa 2012).

These regional protocols and policy strategies offer opportunities to broaden the scope for climate change adaptation and draw on integration of major adaptation processes that may be warranted at the transborder and regional scales.

The Common Market for Eastern and Southern Africa (COMESA), to which Malawi and Zimbabwe, but not South Africa, are members, is a regional organisation with a principal focus on agricultural development as a means for achieving economic growth, industrial takeoff, agricultural trade, and employment creation. In 2002, the organisation passed a COMESA Agricultural Policy aimed at harmonising national policies of member states towards a COMESA Free Trade Area FTA. Subsequently, the COMESA Nairobi Declaration of 2004 on Expanding Opportunities for Agricultural Production, Enhanced Regional Food Security, Increased Regional Trade and Expanded Agro-Exports through Research, Value Addition and Trade Facilitation was a milestone in pursuance of regional integration. Positive outcomes of these policy initiatives include the Maize without Borders Policy Platform. The COMESA policy initiatives may offer a conducive policy environment for broad-based climate change adaptation and disaster risk reduction management interventions in the region.

Agriculture Considerations in Climate Change Policies and Strategies

The development of climate change policies and strategies of national governments in Southern Africa is essentially a work in progress, as both awareness and understanding of processes is still gathering momentum, courtesy of the UNFCCC processes. Malawi and South Africa have already completed development of their climate change response policies and strategies. The national strategy for Zimbabwe is under preparation. A National Climate Change Office has been established under the Ministry of Environment and Natural Resources. A national interministerial task force on climate change was also formed. Invariably across the three countries, the climate change policies and strategies are housed in the national ministries of the environment.

The Government of Malawi, through the Environmental Affairs Department of the Ministry of Environment and Climate Change Management, launched its National Climate Change Policy in 2012 (Government of Malawi 2012) with the objective to ‘reduce vulnerabilities and promote community and ecosystem resilience to the impacts of climate change’. Climate change adaptation is ranked first out of eight key priority areas. The Malawi National Adaptation Programme of Action (NAPA) of 2006 (Government of Malawi 2006), which was developed as part of the UNFCCC process, is embraced by the new policy. All five prioritised adaptation options under the NAPA are strongly related to agriculture and aimed at increasing resilience of vulnerable communities to climate-related risks and disasters:

1. Improving community resilience to climate change through the development of sustainable rural livelihoods
2. Restoring forest in Upper, Middle, and Lower Shire Valleys catchments to reduce siltation and the associated water flow problems
3. Improving agricultural production under erratic rains and changing climatic conditions
4. Improving Malawi’s preparedness to cope with droughts and floods
5. Improving climate monitoring to enhance Malawi’s early warning capability and decision making and sustainable utilisation of Lake Malawi and lakeshore areas resources

However, lack of funding has been a major constraint to implementation of the Malawi NAPA, at least up to 2013. The National Disaster Risk Reduction Framework of 2010 provides for strengthening of early warning systems, addressing a critical area for development processes in agriculture.

In South Africa, the National Climate Change Response Strategy was developed in 2004, with the main objective to ‘support the policies and principles laid out in the Government White Paper on Integrated Pollution and Waste Management, as well as other national policies including those relating to energy, agriculture and water’ (Government of South Africa 2004). The strategy recognises the vulnerability of the agricultural sector, including rangelands, forests, and crops. The document also puts significant emphasis on mitigation. Unlike in Malawi, where adaptation in the agricultural sector is an obvious priority area, the sector is apparently not as emphasised in South Africa. This is most likely due to the relatively low contribution of agriculture to the national GDP.

5.3.2 Review of Key Arguments for Policies on Adaptation to Climate Change in the Agricultural Sector

The majority calls for supportive policies on climate change adaptation in the agricultural sector in Southern Africa arise from the increasing realisation of the threats to food security at household and national levels, supply of industrial raw materials, and national employment. This is particularly critical for countries such as Malawi and Zimbabwe, where the livelihoods for the majority of the national population are dependent on rainfed agricultural systems (e.g., Government of Malawi 2012; Government of Zimbabwe 2012). Consistent with CAADP and the strategic policy objectives of SADC and COMESA, agriculture is viewed as the main vehicle for economic growth in Malawi and Zimbabwe, where the national agricultural policy frameworks deliberately seek to enhance its contribution to GDP. Although South Africa's agriculture and forestry sector constitute a small proportion of the national GDP (around 3 %), the government still recognises its critical role in national and household-level food security; ensuring social and economic growth and development through job creation; and contributing to the rural socioeconomic development, particularly among the country's rural communities (Government of South Africa 2012). For example, about 70 % of total grain production in South Africa consists of maize, a climate-sensitive crop in the context of Southern Africa. Predictions of yield declines in excess of 20 % will therefore have a significant negative impact on the country's rural poor. There are also fears that any changes in rainfall and temperature may cause significant changes in areas uniquely suitable for specialised production of cash crops for export (Government of South Africa 2004).

5.3.3 Review of Key Policy Actors and Networks Involved with Adaptation to Climate Change in the Agricultural Sector

The majority of policy-related interventions on climate change adaptation in Southern Africa has been at a research level, out of which fewer than 50 % have focused on policy in a significant way. However, there has been significant involvement of development partners, NGOs, international research organisations, and regional policy networks in many of the research projects (Table 1), providing leverage for possible policy advocacy and dialogue processes. However, the total number of completed and ongoing projects for which there is published evidence is very small in relation to the magnitude of the problem. Most of the policy-related projects have also focused mainly on awareness raising (Table 8), most likely because of lack of empirical evidence at the local level.

5.3.4 Key Barriers to Uptake of Research Evidence for Policy Formulation

There is generally no documentation of evidence-based policy-making processes and their impacts in most of the countries in Southern Africa. Addressing these deficiencies is particularly important in the development of climate change adaptation policies, which have ramifications across different development sectors. Notable barriers to uptake of research evidence in Southern Africa include the following:

- Disconnect between UNFCCC processes and local-level evidence of the nature and causes of vulnerability of livelihood systems as well as mechanisms for adaptation.
- Lack of strategic incentives and appropriate institutional and policy mechanisms for involving different levels of policy makers in development research processes.
- Most of the literature revealed a lack of dialogue between research and development practitioners and policy makers as a major barrier. Interventions that broke this barrier, such as CCAA projects and the Government of Zimbabwe/UNDP/GEF Coping with Drought and Climate Change project, recorded positive outcomes.
- Limited research capacity to generate the necessary evidence: Most of the research studies are (for various reasons) isolated in time and space, requiring significant effort by researchers to consolidate (e.g., meta-analysis of existing data from different but related studies) and/or synthesise and discern key policy messages.
- Limited capacity of policy-making bodies to assimilate empirical research outputs. Those studies involving participatory action and colearning processes provide evidence that the capacity of policy makers at different levels can be enhanced, including their capacity to demand research results as opposed to the current dominance of supply-driven policy briefs and research findings sent to policy makers.

5.4 Gaps in Climate Change Adaptation Research and Policy in the Agricultural Sector

The study revealed several research and policy gaps that if addressed could enhance climate change adaptation processes at different levels in Southern Africa. Overall, the critical lack of empirical research and development studies/interventions covering diverse contexts already accounts for many of the glaring knowledge gaps.

Table 8 State of knowledge of stakeholder involvement on adaptation to climate change in the agricultural sector in Southern Africa

Country	Stakeholders	Category	Work done	References
Zimbabwe	Lutheran Development Services	Research/Policy	• Building adaptive capacity and sustainable livelihoods of smallholders in Makuwerere Ward, Mberengwa through gulley reclamation, conservation farming, and documentation of climate change initiatives and policy recommendations related to climate change	Brown et al. (2012)
Zimbabwe	SOFECSA	Research	• Learning centre concept (farmers self-mobilise and come up with technologies to adapt to climate change, e.g., staggering of crops, growing of small grains and different crop varieties) • *Zundera Mambo* concept (social safety net): chief supports communal production of staple maize and maintains a strategic grain reserve for the disadvantaged during years of crop failure	Mapfumo et al. (2013)

(continued)

Table 8 (continued)

Country	Stakeholders	Category	Work done	References
Zimbabwe	Department of Meteorological Services; FAO	Research	• Mid-term forecasting and provision of forecast information to smallholder farmers	Chikoore and Unganai (2001)
Zimbabwe	Government of Zimbabwe; United National Environment Programme (UNEP); UNDP; GEF	Research	• Assessed vulnerability of smallholder farmers in Chiredzi District and developed adaptation strategies • Addressed vulnerability drivers; climate risk management through enhancing use of early warning systems and developing community drought preparedness plans	Brown et al. (2012)
Zimbabwe	Practical Action	Research/Policy	• Mainstreaming livelihoods approaches to disaster risk reduction so as to ensure policy makers at district, provincial, and national level adopt a livelihood-centered approach to disaster risk reduction	Brown et al. (2012)

Country	Stakeholders	Category	Work done	References
South Africa	Rawsonville Cooperative; Oxfam Partner Organisation	Research	• Helped seasonal and unemployed workers increase their income through growing gourmet mushrooms and planting crops that survive in cold weather	Vincent et al. (2011)
Malawi	Alliance for a Green Revolution in Africa (AGRA)	Research/Policy	• Supporting agriculture development across the chain, from funding projects on seeds and soils to markets and policies	www.agra-alliance.org
Malawi, South Africa, Zimbabwe	African Agricultural Technology Foundation (AATF); ASARECA	Research	• Crop development and technology transfer for African farming systems through crop breeding	www.aatf-africa.org, www.asareca.org

(continued)

Table 8 (continued)

Country	Stakeholders	Category	Work done	References
Malawi, South Africa, Zimbabwe	Action Aid International; ACT; Africare; African Technology Policy System (ATPS); Bureau for Food and Agricultural Policy (BFAP); CGIAR; FAO; Forum for Agricultural Research in Africa (FARA); World Agroforestry Centre (ICRAF)	Research/Policy	• Integration of disaster reduction into schools • Integration of vulnerability and adaptation to climate change into sustainable development policy planning and implementation • Training programmes on climate change adaptation for policy makers • Natural resources management including water harvesting techniques • Modeling of climate change effects on crops, especially maize, and access to technology • Information dissemination through radio plays • Conservation agriculture	Mumba and Harding (2009), www.africare.org, www.bfap.co.za, www.cgiar.org, www.fara-africa.org

Country	Stakeholders	Category	Work done	References
Zimbabwe	National Agricultural Extension Services (AREX)	Research	• Facilitates smallholder farmers to adapt and cope better with climate variability and change through use of NGOs' global experiences on climate change adaptation and research in agriculture and meteorological services in developing countries	Mapfumo et al. (2013)
Mostly Africa	Environnement et Développement du Tiers-Monde (ENDA)	Policy	• Lobbying, policy dialogue, and multilateral agreements on climate change • Community-level climate change adaptation programmes, multiscalar activities	www.enda.sn

(continued)

Table 8 (continued)

Country	Stakeholders	Category	Work done	References
Malawi, South Africa, Zimbabwe	National universities including the University of Zimbabwe, University of Free State and Bunda College of the University of Malawi	Research	• Researchers and students conduct work on climate change adaptation and colearn with smallholder farmers to be innovative and use ‘best-fit’ techniques in their fields • Education and training workshops: a programme of policy research and teaching fellowships with related curriculum • Development and strategic matching of African and international institutions, where outside knowledge and resources can enhance given areas of expertise • Researchers are working with planners and farmers to develop modeling scenarios that will improve access to climate information and offer a range of options to help them prepare for a water-scarce future • Climate change adaptation for improved livelihoods in Malawi	Denton et al. (2010), Synnevag and Lambrou (2012)

Country	Stakeholders	Category	Work done	References
Malawi	Ministry of Agriculture and Food Security	Research	• Dissemination of climate-smart agricultural technologies such as reduced tillage, agroforestry trees, legumes and improved maize varieties through the research and extension system	Synnevag and Lambrou (2012)
South Africa	IDRC in collaboration with researchers from the University of Cape Town, University of Kwa-Zulu Natal, and University of Free State	Policy	• Development of a model that will allow policy makers to make informed adaptation decisions based on a combination of regional climate change models that can measure impact on water levels, farming systems, and urban water use • Enable capacity building among water managers, academic community, and general public with regard to climate change variability, vulnerability, and possible adaptation strategies	www.idrc.ca/ccaa
South Africa, Malawi, Zimbabwe	FANRPAN	Research/Policy	• Food security and the impacts of CC. Also some work on vulnerability • Research into adaptation strategies and building research capacity	www.fanrpan.org

(continued)

Table 8 (continued)

Country	Stakeholders	Category	Work done	References
Malawi	Red Cross	Research	• Disaster relief and climate change adaptation	www.redcross.org
South Africa	SouthSouthNorth	Research	• Community-based capacity building, e.g., drought-resistant Rooibos tea varieties	www.southsouthnorth.org
Africa	World Wide Fund for Nature (WWF)	Research	• Nature conservation, natural resource management	www.worldwildlife.org
Zimbabwe	Zimbabwe Regional Environment Organisation	Research/Policy	• Capacity building through installation of wind power for home use and irrigation pumps, helping rural villages to cope with water shortages • Scaling up local adaptation needs to national and international policy	www.zeroregional.com

- *Building empirical evidence of climate change impacts and application of adaptation options*: The current body of knowledge within the region is too thin to inform the formulation of comprehensive climate change policy frameworks and implementation plans. The intricate nature of economic, governance/political, technical, and sociocultural factors determining vulnerability and adaptive capacities of households, communities, and institutions make climate change adaptation one of the most complex subjects of development research in the region. Implications for capacity building in terms of methodologies, approaches, technical expertise, and research infrastructure are therefore bigger than can currently be served by tradition.
- *Harmonisation of concepts, methods, and tools for vulnerability assessment*: A number of vulnerability assessment studies have been conducted, but it remains unclear if different methods are necessary for understanding climate change. The concept of vulnerability in the context of climate change is clearly defined in IPCC reports, but conclusions have been made in some climate change literature based on somewhat different concepts. This has implications for how policymaking processes are subsequently influenced.
- *Identifying critical variables for improving quality of seasonal forecasts and early warning systems*: Most of the national policy and strategy documents emphasise the importance of seasonal weather forecasting and early warning systems, but there is no clarity on critical variables to be monitored, and the requirements for matching instrumentation and associated expertise at the national and regional levels to improve the quality of data on forecasts.
- *Lack of data and empirical studies to inform budgetary processes for adaptation*: There was limited evidence on quantification of the costs of adaptation processes for specific communities. Operationalisation of adaptation action plans is therefore in itself a major challenge, and is likely by be constrained by poor justification of both actions and budgets.
- *Understanding microlevel impacts of climate change and variability in agricultural systems*: Climate change and variability impacts on agriculture have tended to be reasoned on the basis of traditionally known factors regulating biophysical (physical, chemical, and biological) and socioecological (interactions) processes. However, one of the impacts of climate change may be an alteration of these regular processes (e.g., soil processes, biodiversity, hydrological cycles, human systems behaviour). Specialist process research is therefore necessary to understand microlevel impacts of climate change and variability in agricultural production systems. Examples in agriculture include revisiting the current understanding of:

  - Dimensions of crop–soil–water interaction patterns to enhance efficiency of resource use and targeting. For example, increasing efficiencies in the use of available nutrient and water resources in crop production systems is likely to be a major determinant of adaptation options in Southern Africa where production is constrained by a combination of poor fertility soils and water scarcity.

  - Emerging patterns and causes of postharvest losses in crop production systems.
  - Emerging patterns in agrobiodiversity such as climate change and variability impacts on pollinators, soil processes, crop–pest and crop–disease interactions.
  - Options for designing efficient management systems for forestry to reduce overexploitation and postharvest losses.

- *Role of traditional institutions in fostering and maintaining resilience*: Families and communities in Southern Africa have also survived in marginal environments because of strong institutions supporting extended family lifestyles and vibrant rural–urban interconnections. Development policies in the region have been exceptionally silent in recognising the contribution of these institutional arrangements on the resilience of livelihood systems at local, national, and regional (transborder) scales. The dynamics of these social collaborations (and conflicts) in response to climate change and variability effects (direct or indirect) have not received due attention, yet they underpin cross-generational survival strategies for the majority of people in the region. This is despite clear evidence that effective climate change adaptation options are likely to be those rooted in indigenous knowledge systems and built through the local practices. Comprehensive research on these issues is likely to generate key development insights that can inform cross-cutting policies, especially those related to gender and HIV/AIDs. Currently there is a strong show of will on gender mainstreaming in agriculture and natural resources management, but the content on the mechanisms is critically lacking.
- *Critical analysis of resource use efficiencies and tradeoffs for current and alternative adaptation options*: Institutional mechanisms regulating interactions among cropping and natural resources (including wildlife and forestry) management schemes within rural communities and between rural and urban/peri-urban communities need to be evaluated. This indicated that climate change can influence resource access and sharing arrangements, and sociopolitical conflicts related to resource governance, as well as the relative impacts of technological interventions/access. Further understanding is required on how climate change and variability may enhance or upset some of the key traditional sources of resilience for diverse farming communities.
- *Understanding emerging gender dynamics in the context of climate change adaptation*: Evidence is only beginning to emerge which suggests changing gender roles in response to impacts of climate change and variability, and interventions that yield a critical analysis on the direction and magnitude of such changes as well as effects on livelihood systems is required. This may help to inform the discourse on gender and climate change in agriculture. Current policies indicate increasing awareness of gender issues among stakeholders, but there is no clear evidence of contents. Studies are lacking on how the evolution of what are depicted as local cultures and social values today within the predominantly vulnerable communities have been shaped by environmental marginality and past

sociopolitical systems. Such studies could provide key insights on the current value systems as an outcome of past adaptation processes, or lack thereof.

- *Development of options for commercialisation of smallholder agriculture*: There is a need for expanded research programmes with options for sustainable agricultural intensification, and on understanding circumstances where extensification may hold promise now and in the future. Outcome of analyses of tradeoffs between extensification and intensification options is likely to be critical in informing future policy directions. Currently, there is also a glaring knowledge gap and no data on climate change and variability effects on production and trade of industrial export crops that include cotton, rice, coffee, cashew and macadamia nuts, tobacco, groundnut, tea, sugarcane, and horticultural crops (especially flowers).
- *Development of 'climate-smart agriculture' systems*: This is an area that has gained momentum in research over the past few years, but the conceptualisation and application of the underlying principles has generally been informed by speculative arguments with no supporting empirical evidence. This is likely to misdirect policy-making processes on the potentials and limitations of emerging agricultural technologies and their suitability to diverse local contexts. For example, a wide range of ISFM and CA technologies have been developed and tested under different agroecologies in the region, but their potential role in climate change adaptation has largely not been studied in sufficient detail to inform policy.
- *South African agriculture in transition*: Improvement of agriculture's contribution to national GDP is not a major objective of South African agricultural policy at present, and this has implications for the dynamics of vulnerabilities and therefore on relative adaptive capacity of the country's rural communities to climate change. Currently, 95 % of the country's marketable crop is produced in the large-scale commercial sector. Perceptions about the declining importance of farming in South Africa may possibly send an 'out of fashion' message to the country's youth, with strong implications for the future of national and regional food security as well as the economics of industrial development.
- *Analysing tradeoffs between irrigated and rainfed systems*: Although irrigation development is emerging as a major area of focus for national policies and strategies, the potential negative impacts of declining rainfall patterns on agricultural water have tended to be ignored in policy formulation. There are no clear indications that due consideration is being given to options for increasing productivity in rainfed cropping systems. With no empirical evidence to back up some of the policies supporting big investments in irrigation infrastructure development, costly miscalculations could be made.
- *Critical analysis of implications of past research and development intervention programmes on current and possible future manifestations of vulnerabilities*: Current discourse seems to imply that existing livelihood systems inherently lack resilience regardless of the differences in community exposures to multiple stress factors other than climate change and variability. However, there is little empirical evidence demonstrating how, and to what extent, past intervention pro-

grammes have really reduced vulnerabilities of the poor and disadvantaged rural communities. The changing context of development interventions due to climate change may also require governments to revisit some of the past development policies that may be now rendered relevant. Climate change also brings to the fore possible weaknesses in current approaches and methodologies for measuring vulnerability and impact in development (e.g., against the changing context of development interventions and multiple stress factors).

- *Generation of context-specific adaptation options*: There is limited empirical data upon which generalisations of potential impacts of climate change in a country can be made to inform local adaptation processes, yet adaptation is well known to be a local phenomenon. This strongly suggests a need to generate site-specific data and empirical evidence that can inform technical interventions and policy processes at the local level. This also brings to the fore the importance of engaging local-level decision makers as probably more important agents of change than national and regional stakeholders.

6 Conclusions

The concluding remarks outlined below are with respect to the key questions.

1. *What is the role of climate change challenges in the context of the multiple challenges and opportunities facing the agriculture sector in the African region?*

   The African continent is particularly vulnerable to the impacts of climate change affecting key economic drivers such as water resources, agriculture, and disaster risk management, among others. The impacts include water stress and scarcity; food insecurity; and high costs of disaster management as a result of increased frequency and intensity of droughts, floods, and landslides associated with the El Niño phenomenon.
2. *What is the current state of knowledge on adaptation to climate change in the agricultural sector in the African region?*

   There is a considerable amount of research on climate change adaptation in the agricultural sector in Africa. From the analysis of adaptation work, agricultural research appears to be a crucial area of adaptation to climate change in order to deal with changes in the length of growing seasons, increased droughts, and periodic waterlogging as well as increased temperature and salinity in the area. National Agricultural Research Centers and the private sector in areas expecting more droughts in the future should be supported to enable agricultural adaptation, taking on board climate-smart agricultural practices. CA is best suited for smallholder farmers in the region.
3. *What is the current state of knowledge on whether and how research findings are integrated in agriculture sector policies in the African region?*

   Despite a considerable number of climate change adaptation research projects in the African region, there is little evidence regarding how the generated knowledge is made useful or integrated in the agricultural development plans of the respective countries. The link between agricultural research in the context of climate change and policy-making processes needs to be strengthened. This implies that the various agricultural policies and initiatives within the African region are based on the knowledge generated to enhance adaptation. This can be achieved through proper packaging of research findings in a user-friendly way and sharing those findings through research-policy dialogues.

4. *What are the major gaps in research on adaptation to climate change in the agricultural sector?*

   Analysis of knowledge generated from adaptation research on the agricultural sector shows that little has been done to ensure that climate-resilient approaches are integrated into the sector. This includes the use of climate-smart agriculture. More research is also needed to show the interlinkages of the agricultural sector and other related sectors such as water and energy. Integrated approaches are needed in development interventions aimed at promoting adaptation to climate change. Smallholders are exposed to global environmental change and economic globalisation, leading to competition between smallholder produce and highly subsidised produce from industrialised countries. Combining local and scientific knowledge systems is important for making climate information relevant locally and for empowering communities, and is further necessary to enhance adaptation in the agricultural sector.
5. *What is needed to ensure that research findings are better integrated into agriculture sector policies?*

There is a need to ensure that findings from agricultural research for climate change adaptation are well packaged and made user-friendly to various categories of stakeholders. There is also need for a mechanism to link stakeholders at the grassroots and other levels, vertically and horizontally. The aim is to develop a regional climate change policy and strategies to respond urgently to the adverse impact of climate change that includes addressing the challenge of food insecurity as a result of the extreme climatic conditions associated with climate change.

7 Recommendations

7.1 Tackling Climate Change in the Context of Multisector Challenges

A comprehensive approach involving coordination of activities in the crops and forestry sectors is recommended, taking cognisance of the cross-cutting issues of water, energy, and gender. Interdisciplinary research, as appropriate, is therefore required. Fundamental to success in adaptation is good governance in the form of rule of law, decentralisation, and participation of citizens in decision making that creates the environment for social cohesion, rapid agricultural growth rates, and GDP growth that translate into improved human development.

7.2 Improving Adaptation to Climate Change by Smallholders

Improved access by smallholders to best bets, through diagnosis of problems and on-farm demonstrations/adaptive trials and improved dissemination systems, improved credit systems by way of strengthening rural banks and microcredit schemes, and improved access to markets through better infrastructure (storage, feeder, and major road networks) are required. Training on the options for adaptation to climate change is required. For sustainability, local communities should have ownership of interventions in adaptation.

7.3 Filling Gaps in Research on Adaptation to Climate Change

Both conventional scientific research and participatory action research should be employed as appropriate as they complement each other. Conventional research is more proactive and can therefore forestall disasters. The right balance between research for developing short-term and long-term strategies should be kept. There is a need for research at various levels on both the mitigation and adaptation aspects of climate-smart agriculture, their interactions and tradeoffs. The complementary roles of indigenous knowledge and scientific knowledge should be recognised at all levels of adaptation.

7.3.1 Technical Research on Crops

The tentative research themes and topics include: crop improvement for yield and tolerance to biotic and abiotic stresses; effects of climate change on incidence of crop pests and diseases; fine tuning conservation agriculture to diverse biophysical and socioeconomic conditions for improved smallholder uptake; increasing quality and adding value to crops products; nutritional value of processed products; improving efficiency of agricultural water use in the crops sector; reclamation of land degraded by salty water; prolonging the growing season; climate change and tree crops; screening and matching agroforestry species and plant populations with ecological zones and agricultural practices; and agroforestry and use of biochar as technologies for soil improvement and climate-smart agriculture.

7.3.2 Socioeconomics and Policy Research

Research is recommended on the policy process and political factors influencing priorities and affecting adaptation; land use patterns and adaptation; land use regulations; costs and returns of adaptation options, quantity, and value; ex ante evaluation of adaptation options, effectiveness of adaptation options, adoption rates and determinants of adoption; analysis of existing marketing structures to improve efficiency and determine how regional integration of markets and access to global markets will be important in responding to climate change; gender considerations in adaptation to climate change and variability; and effect of knowledge of climate change and variability on achievement of national development goals including poverty reduction and food security at national and regional levels. Improved modelling capability would facilitate technical and socioeconomic research.

7.3.3 Risk Management Dealing with Stocks, Weather Forecasting, and Insurance

Risk management should involve feasibility studies of buffer stocks (grain reserves), improvement in the quality of meteorological data collection and weather forecasting tools and techniques, and therefore early warning systems to reflect the needs of farmers; and innovative insurance schemes for smallholder crop farmers. The latter should include rainfall indices for crops.

7.4 Improving Policy Formulation and How Research Findings Can Be Better Integrated into Agricultural Policies

National policies on agricultural development and climate change adaptation should be evidence based and provide an enabling environment for maintaining or improving the productivity of land, water, and labour under a changing climate. This will involve policies to facilitate access by smallholders to credit and markets, policies to improve institutional capacity and infrastructure, smart subsidies, insurance schemes for smallholders in crops, and crisis management. Sustainable food security must be made the central concern. Farmers should be provided with financial incentives to adopt climate-smart agricultural practices. The linear 'research to policy model' should give way to more participatory approaches. To be useful in supporting policy formulation, strategies for adapting food systems to climate change and variability must be elaborated in the context of the policy processes. Better still, policymakers must be brought into the research loop very early.

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Causes and Prevention of Cherry Cracking: A Review

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Abstract Cherry fruit is considered to be quite sensitive to cracking and is the major limiting factor for profitable cherry production in most of the cherry-producing regions of the world. At times, the cracking severity can reach up to 90 %. Although most of the fruit cracking is attributed to direct and possibly localized water uptake through the fruit skin, there are many other interactive factors that can contribute to cracking including the variety grown, skin properties, climate, and so on. The cracking in cherry has been categorized in three distinct forms: stem end cuticular fractures, nose or apical cracking, and the third, side cracking, which is a large crack usually deep into the pulp on the cheek of the fruit and is considered to be most damaging. The type of the crack developed may depend on the particular etiological factor and the shape of the fruit. However, the problem can be minimized to a great extent by knowing the cause and accordingly, adapting certain management practices, of which irrigation management, protective covers, and mineral supplements are of prime consideration.

Keywords Cherry cracking • Rain • Water uptake • Protectants

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1 Introduction

The fruits of several species have a tendency to split during or just after rain, but none seems to be quite as sensitive to rain-induced fruit cracking as sweet cherries. In India, the Kashmir region is one of the principal cherry-growing areas of the country, but fruit cracking is the major problem limiting profitable cherry production. In some years with some susceptible varieties, the problem is extremely severe, with approximately 80–90 % of the fruit cracking (Bhat et al. 2008). However, it has been shown that as little as 25 % cracked fruit can render harvesting uneconomical on account of the escalating costs of harvesting and handling of the fruit (Looney 1986). Furthermore, as cracked fruits are very susceptible to the entry of fungus rot, just a few cracked fruits may destroy the entire crop of susceptible varieties.

Although most fruit cracking is attributable to direct and possibly localized water uptake through the fruit skin, a smaller proportion of fruits crack even when fully protected by rain shelters. Studies of other crops, for example, grapes, tomatoes, lemons, and apples, indicate that water uptake to the fruit from the root system, causing internal turgor pressure to build up, plays an important role in the cracking mechanism. Also, another consideration is what causes some fruits not to crack even if they are exposed to environmental conditions that should cause cracking. Although many studies have dealt with this complex phenomenon, the basic mechanisms involved in fruit cracking remain unclear.

2 Types of Cracks

Rain-induced fruit cracking in sweet cherries takes three distinct forms: stem end cuticular fractures, calyx end cuticular fractures, and large cracks usually deep into the pulp on the cheek of the fruit. The first two occur at either end of the cherry fruit, shallow cracks close to the point of stem attachment, or at the stylar scar or apical end of the fruit. These cracks are commonly referred to as “stem” and “nose or apical” cracks, respectively (Figs. 1 and 2).The small fine cracks in the base and apical end of cherry fruit may occur either at a very early stage or many days before fruit maturity and harvest. These fine cracks at an early stage of fruit development (which usually cork over and seal before the fruit ripens) decrease the market value of fruits. Verner (1937) found that there is a sugar concentration gradient from the stem to the apex. His conclusion was that the higher osmotic concentration of the fruit juice at the apical end accounted for more rapid water absorption of the rain drops through the fruit skin resulting in earlier cracks in this part of the fruit. Later, he also noted that the drop of water usually adhered to the apex of the cherry fruit and in this way the apical end of the fruit has a longer period for potential water absorption. According to Sawada (1934), the shape of the fruit can play an important role in cherry fruit cracking. Cultivars with kidney- or heart-shaped fruit have a deeper stem cavity and the rain drops can stay there for a longer time giving the

Fig. 1 Stem end cracking in sweet cherry

Fig. 2 Calyx end cracking in sweet cherry

possibility for more water absorption through the skin. It means that if a variety is genetically determined (based on the structure and thickness of the cuticle and sugar content) for moderate susceptibility to splitting and it has a kidney, blocky, or heart shape, maybe it will have stem end type splitting. It is in agreement with the work of Belmans et al. (1989) who found that "Hedelfinger" cherry fruits cracked at the stem end only. A third type, deep cracks originating from the cheeks and extending over the bulk of the fruit in any direction and often penetrating the entire fruit tissue to the pit, is the most damaging, both physically and economically. This type of crack is referred to as a "side" crack (Fig. 3). In plum, lateral splitting is irrigation affected and the stage of maturity has the major influence on the development of lateral splits (Uriu et al. 1962).

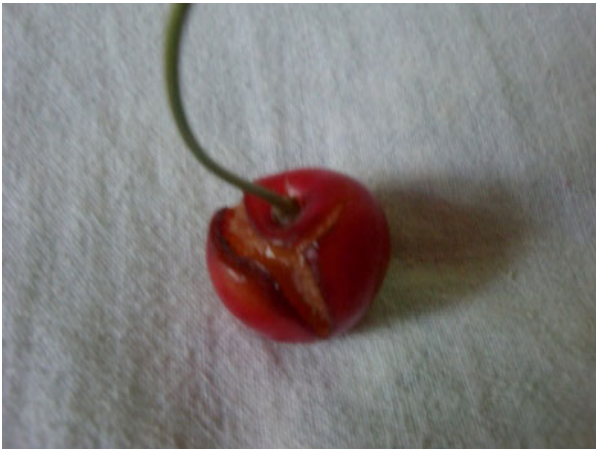

Fig. 3 Side cracking in sweet cherry

3 Causes of Fruit Cracking

There are many factors causing fruit cracking (Simon 2006):

1. *Genetically determined susceptibility of growing species and cultivars*
   Fruit characteristics. Varieties often differ greatly in their susceptibility to cracking. One is that varieties which take up more water, either in greater total amounts or at more rapid rates, from their fruit surface are likely to be more sensitive to cracking. Several factors govern the rate and amount of water taken up by the fruit from its surface.
   (a) *Fruit size*: Large–fruited cultivars have a greater tendency to crack than small fruited ones. Studies of Bullock (1952) and Way (1967), show that fruits of heavy crop loaded trees crack less than light cropping trees in the case of the same variety.
   (b) *Fruit firmness*: As cracking of cherry is caused by excessive uptake of water resulting in bursting of the skin, it seems logical that firm-fleshed cultivars are more susceptible to cracking. A study by Bhat et al. (2008), revealed that 93.52 % cracking was observed in firm-fleshed Misri Cultivar (*Bigarreau Noir Grossa*) and 87.18 % damage in case of cv. Double (*Bigarreau Napolean*).
   (c) *Fruit skin*: The skin of the sweet cherry fruit consists of a cuticle and several dermal cell layers. The size of the epidermal cells differs and a positive correlation could be found between the thickness of the inner wall of the epidermis and cracking (Kertesz and Nebel 1935). The fruit skin, its cuticle, and epidermis may be more of a barrier to water uptake into fruit in the resistant varieties (Webster and Cline 1994).The varieties that have skins with epidermal cells that are more strongly bound together are likely to resist cracking.

Wustenberghs et al. (1994) and Belmans et al. (1990) indicated that the cultivars having a thicker cuticle were more resistant to cracking than those with thinner ones. Concurrent with this the waxed cuticle does not stretch and fractures develop (Sekse 1995a). Such cuticular fractures would allow greater water penetration (Glenn and Poovaiah 1989).

(d) *Stomatas in the fruit skin*: Water uptake connected with stomata can be explained as uptake through cuticular fractures on the edges of guard cells (Glenn and Poovaiah 1985; Sekse 1995a). This may explain the results obtained by Vittrup Christensen (1972); large stomata could more easily develop fractures than could small.

(e) *Osmotic concentrations*: The very slight correlation found between the cracking index and the fruit sugar content indicates that osmotic effects account very little for cracking susceptibility of the fruits. Moreover, Sekse (1995a) discussed that soluble solid contents of the apoplastic part of the epidermal cells (i.e., the active osmotic agent) is only a small part of the pulp juice and may differ from that of the overall soluble solid contents of the pulp.

2. *Environmental influence*

It is widely accepted that tension caused by potential gradients between the soil, through the plant, and to the ambient environment is the major driving force for water movement through plants, in line with the cohesion tension theory of sap ascension (Zimmerman et al. 2002). Furthermore, fruit are natural reservoirs of water, which can be drawn upon when demand in the transpiration stream is high. Thus, flow to the fruit is influenced by multiple factors such as changing diurnal water potentials between the fruit and the leaf (Morandi et al. 2007), changing diurnal light intensity (Yamasaki 2003), and by source–sink interactions (Zhang et al. 2006). Cherry fruit are strong sinks (Ayala and Lang 2008) and therefore could influence the magnitude of diurnal flow patterns. As per the researchers, temperature plays a very important role in the rate of fruit cracking. In general, there was a linear increase in cracking with temperature increase from 10 to 40 °C. Permeability of the cell walls and biochemical processes of the cells are some factors affected by temperature. Richardson (1998) also found the increasing trend in the cracking index of cherry at 5, 15, and 25 °C water temperature. However, during dry periods, fruits usually have high turgor in the early morning, which then decreases throughout the day. More water is taken up when the temperature is quite warm following rains. Also it is well known in other fruits that sun-exposed fruits have a thicker cuticle than fruits growing in deeper canopy shade.

4 Prevention of Cracking

There are many reports in the literature suggesting that sprays of mineral salts, fungicides, and other chemicals reduce cherry cracking. However, in many cases it has not been possible to reproduce these results. Researchers agree that the appropriate cultivar and site selection are the most effective way to minimize the rain damage of a cherry orchard. The appropriate site should be with little or no rain incidence at or near harvest time.

5 Harvest Timing

The timing of harvest is primarily aimed at fruit maturity. However, both anecdotal and published evidence (Usenik et al. 2005; Simon 2006) suggest that growers consider timing of harvest as a cracking management strategy. It appears to be common practice for some growers to harvest slightly immature fruit when there is a high risk of rainfall occurring at harvest maturity, despite evidence that late harvest produces fruit with the most appealing taste, texture, and nutritional value (Diaz-Mula et al. 2009).

6 Covers

Regading rain cover protection, the covering needs to be started three weeks before harvest, often about the time when cherries start to change color and become sensitive to rain damage. Picking efficiency, yield, fruit size, and the quality of harvested fruit is improved greatly; it is about 20–60 % premium in years of persistent or heavy rainfall at harvest compared to uncovered orchards (Meli 1982). The expense of these structures is to some extent justified by the higher returns. However, the temperature under the covers may become too hot causing scorching or damage on leaves and shoots; the risk of disease infection is increased by the higher humidity.

7 Rootstock

The choice of rootstock used has traditionally been limited to availability, suitability to production systems, and site selection. Only more recently has the effect of rootstock on cracking been investigated (Cline et al. 1995; Hovland and Sekse 2003). In a trial examining the effect of rain covers and rootstocks, fruit grown on rootstock F12/1 showed no significant decrease in cracking, covered or uncovered. In comparison, fruit grown on rootstock “Colt” showed a significant decrease in field cracking both covered and uncovered (63 % and 5 %, respectively; Cline et al. 1995). Hovland and Sekse (2003) showed that rootstock influenced the development of cuticular fractures and cracking incidence when immersed in water and Simon (2006) commented that rootstock influenced cracking after immersion.

8 Mineral and Other Chemical Sprays

Calcium Calcium treatments in particular have played an important role in the prevention of cherry cracking. Calcium is known to be an important constituent of cell walls; the middle lamella of the plant cell walls is composed primarily of calcium and magnesium pectates (Salisbury and Ross 1991). As discussed by McCready and McComb (1954), calcium was easily absorbed by cherries after dips in $CaCl_2$-solution, which indicates that calcium is an important constituent of cell walls in cherry fruits. Thus in the long-term calcium has a positive effect on tissue structure, strength and elasticity of the fruit skin, and also has a positive effect on storage and shelf life.

Calcium spray reduces the differences in osmotic potentials between free surface water and the osmotically active solutes in the cherry fruits if sprayed before rains. However, this reduction (approximately 21 %) in osmotic potential does not seem convincing in explaining the effect of cracking reduction obtained when applying $CaCl_2$ to cherries. On taking into account that the calcium solution on the fruit surface usually will be diluted by rainwater, it becomes even less convincing. Moreover, Sekse (1995b) discussed the poor correlation often found between fruit cracking and the soluble solid contents of the fruit pulp; the soluble solid contents of the apoplastic part of the epidermal cells is only a small part of the pulp juice and it may be different from that of the overall soluble solid contents of the pulp.

Calcium treatments have been reported to influence the cuticular properties. Water diffusion was influenced by charged cations acting in cuticular pores (Schonherr 1976).

Aluminum Bullock (1952) studied different metallic salts and their effect on reducing fruit cracking. He found that aluminum salts had a stronger effect on reducing fruit cracking than calcium. Aluminum phosphate ($Al_3(PO_4)_2$) solution was sprayed in a 0.01–0.1 M concentration 8–18 days before harvest. Some other studies showed the same results. The spraying with aluminum salts did not spread in commercial orchards because of visible deposits left on the fruits and the risk of the spray's scorching.

Copper Copper salts have been used for spraying horticulture for a long time such as "Bordeaux mixture." Spraying with copper sulphate ($CuSO_4$) solution in 0.1 % concentration decreased the fruit cracking. However, as with aluminum, the problem with copper is the deposit left on the fruits and the risk of phytotoxic damage to leaves.

Boron Powers and Bollen (1947) showed that immersing fruits in a borax solution of 0.25 % concentration reduced fruit cracking by 50 %. Knoppien (1949) noted that spraying with a borax solution of 0.5–1.0 % concentration was effective in the case of one cherry variety and there was no significant cracking-reducing effect on others. As with sprays of many of the metallic salts, these boron treatments caused serious damage to leaves.

Hormones The effect of GA_3 applications on fruit cracking has been documented. Gibberellic acid (GA_3) is routinely used in commercial cherry production to increase fruit size and firmness, reduce surface marking, and delay ripening. It is generally applied at 15–30 ppm, 3–4 weeks prior to commercial harvest (Looney and Lidster 1980; Weaver 2005).

Webster and Cline (1994) showed that there was no effect of GA_3 application on cracking when the fruit surface was wet from rain, and that the occurrence of cracked fruit increased if fruit remained wet for 4 h after application. Other studies in Belgium revealed that GA_3-treated fruit had thickened cuticles, but a similar level of cracking to untreated fruit (Webster and Cline 1994). In contrast, research in Oregon found that GA_3 promoted large side cracks in fruit, but reduced the occurrence of stem cracks (Webster and Cline 1994). Usenik et al. (2005) found an increase in the cracking index for GA_3-treated fruit in only one out of three varieties but also noted that, across varieties, there was an increase in water uptake of GA3-treated fruit.

Paclobutrazol, a substance that prevents the synthesis of GA, has been found to increase calcium levels in fruit and shorten internodes (Webster and Cline 1994), with the implication that fruit firmness increases, and resultant increased leaf coverage acts as protection from rainfall. The same authors found that application of GA_3 did not affect the total or soluble levels of fruit calcium. No effect on fruit firmness from either soil or foliar applied paclobutrazol was seen in a study by Looney and McKellar (1987). However, when used in conjunction with GA_3 it was shown to increase fruit size, increase stem length, decrease soluble solids, and delay color development (Looney and McKellar 1987; Webster and Cline 1994).

The effects of napthalene acetic acid (NAA) application have been investigated in the United States of America and Spain where it was found to reduce water uptake through the fruit surface. When applied to fruiting trees at a rate of 1 mg/L, 30–35 days prior to harvest, NAA was found to reduce cracking incidence, however, when applied at the same rate 4–8 days prior to harvest the incidence of cracking increased (Webster and Cline 1994). Unfortunately these results have not been reproduced elsewhere despite several attempts (Webster and Cline 1994).

Overall, the effects of hormone application to cherries with the aim of reducing cracking incidence have yielded inconsistent and sometimes contradictory results. Nonetheless, studies have been conducted on different varieties, in different regions, and given that hormone application has been part of normal orchard practice, continued investigation is warranted.

Protectants Antitranspirants, such as Bioguard® (a calcium-based product), and Vapor Gard® (a terpene polymer providing a protective film) have been trialed in relation to fruit cracking, on the premise that they will limit water uptake as well as loss from the fruit (Hanson and Proebsting 1996). Antitranspirants are commonly used to reduce plant water stress (Landsberg and Jones 1981), however, they have also been shown to have a negative impact on the levels of soluble solids because they limit gaseous exchange (Webster and Cline 1994). Results have been inconsistent and unable to be reliably reproduced (Richardson 1998). Additionally, such applications have a tendency to leave surface residue (Webster and Cline 1994). Nonetheless, Bioguard® reduced cracking by 52 % in "Van" in South America (Torres et al. 2009).

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Climate Change and Plants

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Abstract Climate change with its escalating apparent widespread impacts is turning into a major environmental challenge in contemporary times as it poses a considerable threat to ecosystems, water resources, food security, and overall economic stability. The change in climate observed over the past 50 years is primarily attributed to unabated emissions of radiative gases. The implicit certainty about continuity of the changing climate trend in the future is likely to affect multifaceted sources of plant productivity, including level of temperature, atmospheric CO_2, and precipitation conditions, making it amply clear that plants will have to face the prospect of this change which can be both beneficial and detrimental. Many crops will show positive responses to changed levels of these climatic variables, but extreme levels will often negatively affect growth and yields. Predictions of climate change under various emission scenarios are likely to increase the concentration of CO_2 which will be associated with temperature increase and change in precipitation pattern and are likely to increase plant water stress in addition to the threat of increased pests and diseases, and can thereby engender adaptation challenges for plant productivity.

Keywords Climate change • Temperature • Carbon dioxide • Water stress • Plant productivity

1 Introduction

In twenty-first century, one of the most vehemently debated environmental issues is climate change. Strong scientific consensus highlights that substantial changes in climate are occurring mainly due to anthropogenic activities (IPCC 2007a, b) with clear evidence of an observed increase in average global temperatures and changes in patterns of precipitation (Fauchereau et al. 2003). Although still largely unresolved, the characteristics new climate is likely to have upon complete establishment, an expected tectonic shift of climatic belts has provoked extensive amount of research

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over the past two decades. Where, when, and how these changes would happen remains largely unsettled (IPCC 2007a) but these are expected to have far-reaching impacts on marine and terrestrial ecosystems in the decades to come. Plausible climate change scenarios include higher temperatures, changes in precipitation patterns, droughts, higher atmospheric CO_2 concentrations, and other weather extremes that will severely affect all forms of plant life both natural as well as cultivated (Jablonski et al. 2002; Challinor et al. 2005; Morecroft and Paterson 2006; Ziska and Bunce 2006; Fig. 1). Global atmospheric CO_2 has substantially increased from pre-industrial levels of 285 ppm to current level 384 ppm mainly due to anthropogenic activities far exceeding the natural range (180–300 ppm) seen over 6500 centuries and is predicted to approach to 448 ppm by the year 2050 (IPCC 2007b). Increased CO_2 levels may increase plant growth and productivity, both in terms of quantity and quality by increasing photosynthesis (Allen et al. 1987) and water-use efficiency, which could be an advantage to some plants grown in water-limited areas or when

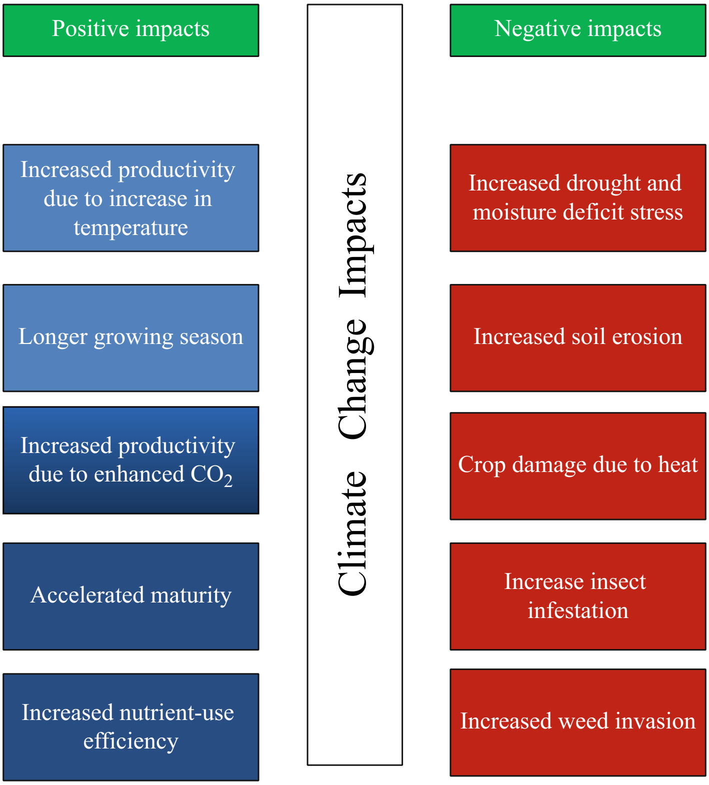

Fig. 1 Effect of climate change on plants

there are less than normal rainfall amounts (Hatfield et al. 2008, 2011), but not to others as they often show reduced content of nitrogen and protein.

The increase in levels of atmospheric CO_2 due to anthropogenic activities will result in an increase in average global surface temperatures by 0.6 ± 0.2 °C. Climate simulation models predict that by the end of the twenty-first century surface air temperature will increase by 1.1–2.9 °C "low scenario" or 2.4–6.4 °C under as "usual business scenario" relative to 1990 (IPCC 2007a, b). Temperature being one of the main climatic factors determining how efficiently plants will grow, its increase can be both beneficial and detrimental to plant productivity, but general trends indicate a reduction in yield of many plants especially cereals. A faster growth will be obvious due to warming in plants that are below their optimum temperature; however, at the same time, in some crops such as cereals warming reduces time for proper grain development thereby affecting yield (Hatfield et al. 2008). An increase in temperature will also cause northward movement of optimum latitude for many crops whereas a decrease in temperature would shift the same towards the equator, causing a shift in the growing areas of the world which will increase plant productivity in some areas, particularly in temperate regions, and at the same time will drastically decrease it in equatorial regions (Hardy 2003). Also, crops adapted to and showing luxurious growth in some regions, in the future will no longer be sustained there which can lead to changes in established feeding priorities in such areas (Krupa and Groth 1999). An increase in local temperature over a range of 1–3 °C will increase crop productivity, but above this range a decrease in same will occur due to its adverse effects on photosynthesis (Nobel 2005; IPCC 2007a, b), transpiration, and phenological stages (Mitchell et al. 1993).

The increase in CO_2 concentrations would also result in drastic shifts in the annual precipitation (timing and level) across the world (IPCC 2007b). A very high variation in precipitation is already being observed and it is becoming difficult to isolate trends, but in most regions there has been an increase in overall precipitation and heavy precipitation events, while at the same time a rise in drought occurrence has also been observed in some regions (IPCC 2007a; Allison et al. 2009). These extreme events such as droughts and heavy downpours that are projected to increase further are likely to reduce crop production because of the well-known negative effects of deficits and excesses of water on plant growth (IPCC 2007a), which can thereby greatly affect food supplies locally and globally (Brouwer and McCarl 2006). One among the various concerns with continued warming is the northward expansion of invasive weed plants that will increase the stress on native crop plants. In the southern hemisphere, weeds cause more damage to crops in comparison to the northern hemisphere (Bridges 1992). In general, this convergence of climate change with the explosive growth of population on a global scale will pose a serious threat to food security. Responses of crops to climate change vary with region and plant species as both are closely related to its varied patterns (IPCC 2007a, b). This chapter focuses on how climate change will affect plant productivity and what the likely responses of plants will be in such scenarios.

2 Effects of Climate Change on Plants

Climate change can affect plant productivity either by casting its effect on those biophysical variables that are involved directly in plant growth, such as temperature, precipitation, sea level, and CO_2 concentration, all of which have been and are likely to challenge plant productivity in decades to come or indirectly by affecting equally imperative factors arising from changing agroecosystem conditions such as soil properties, weeds, pests, and insects. The effects of these factors on plants and their likely adaptations of are described briefly here.

2.1 Average Temperature Increase

Climate change models have forecast an increase in mean temperatures for most regions across the world. The response of crops to temperature mainly depends on the specific optimum temperature for photosynthesis, growth, and yield (Conroy et al. 1994).

Elevated temperature accelerates various aspects of plant metabolism (Larcher 2003) and can affect crop yield primarily by causing rapid crop development (Badeck et al. 2004) thereby shortening duration of various aspects of plant metabolism (Larcher 2003), through changing the rate and timing of physiological processes, including organ development rate, respiration, and senescence (Farrar and Williams 1991); all this in most cases is associated with lower yields (Stone 2001). Secondly, the temperature has a profound effect on the rates of photosynthesis. A slight temperature increase will lead to increased plant growth if the ambient air temperature is below optimum for photosynthesis, but can have a negative effect on growth if the same is close to the maximum (Baker and Allen 1993). Crops with the C4 photosynthetic pathway (e.g., maize, sugarcane) have a higher optimum temperature for photosynthesis than C3 crops (e.g., rice, wheat), but even C4 crops show declines in photosynthesis at high temperature (Crafts-Brandner and Salvucci 2002).

Thirdly, an exponential increase in the air saturation vapor pressure will occur due to the increase in air temperature resulting in an increased vapor pressure deficit (VPD) between air and the leaf that will reduce water-use efficiency, as a result of which plants will lose more water per unit carbon gain (Ray et al. 2002).

Fourth, extremes in temperature directly damage plant cells. High temperatures for extended periods not only reduce plant biomass, but also adversely affect reproductive efforts of crops during critical reproductive periods (Polowick and Sawhney 1988), most predominantly during fertilization and flowering (Morison and Lawlor 1999) which can lead to severe sterility, reduced pollen germination and viability, fruit abortion adversely affecting seeds, thereby increasing risk of complete crop failure (Young et al. 2004; Teixeira et al. 2013). Also the increase in incidence of agricultural diseases is often associated with an increase in temperature (Ziska et al. 2011).

Plants respond to an increase in temperature by adopting various strategies. Plants under high temperatures tend to produce a robust root system to increase water uptake and smaller leaves to offset the leaf water loss (Gliessman 1998). Also, plants mitigate overheating by leaf drooping, leaf rolling, and vertical orientation (Larcher 2003; Nobel 2005) or by transient wilting (Chiariello et al. 1987; Nobel 2005); all these mechanisms, however, may lead to decreased photosynthesis. To counter high VPD, stomatal closure is the most rapid response of plants, however, it reduces the photosynthesis rate and can increase heat-related impacts. Plant hormones, such as indole-3-acetic acid (IAA), abscisic acid (ABA), and ethylene also are involved in plant response to high temperature (Nilsen and Orcutt 1996) for balancing transpiration through affecting stomatal conductance (Dodd and Davies 2004). High temperatures decrease IAA but increase ABA (Nilsen and Orcutt 1996) and ethylene evolution (Yu et al. 1980) which affects plant growth negatively and results in lower dry matter (Qaderi et al. 2006).

Higher temperatures in some cold climate marginal croplands will promote cultivation by shortening the freeze periods, but shortening crop duration, in general, will reduce crop yield in arid and semiarid areas (IPCC 2007a, b). An increase in mean temperature will result in decreased crop yield in subtropical and tropical regions (Parry et al. 2007; FAO 2008b) because of lower levels of soil moisture and increase in evapotranspiration rendering agricultural lands in tropics unsuitable for cropping (Bals et al. 2008). In cereal grains extended periods of high temperature have a negative effect on yield quality by reducing lipid and protein content (Lawlor 2005).

2.2 *Precipitation*

Water is one of the most critical inputs for crop production and its availability primarily is affected by two climatic variables, precipitation and temperature, and to some extent by potential evaporation. Precipitation is the principal source of fresh water resources, which, along with evaporation and temperature determine the soil moisture level (IPCC 2001). A change in pattern of precipitation is one of the most pronounced effects of climate change with precipitation becoming less frequent in some areas but more intense in others. This pattern of precipitation could become more variable and unpredictable, which can affect soil moisture levels (Boxall et al. 2008; Falloon and Betts 2006; Macleod et al. 2012). Increased precipitation by increasing soil moisture content can prove beneficial in semiarid and water-deficit areas, but in areas with excess water will exacerbate some problems. Heavy downpours at the time of harvest are found to reduce the yield quality of many crops. Climate model simulations suggest that high evaporation rates, a consequence of global warming, will cause higher precipitation rates in some regions of the globe such as the equatorial belt (humid tropics) and at higher latitudes (IPCC 2007a, b), and less precipitation in mid-latitudes, dry tropics, and semiarid areas. This change in climate is expected to make the temperate regions (wet areas) wetter and tropical dry areas drier (FAO 2008b), both of which are likely to affect crop yields. Precipitation variability, particularly increased precipitation under a warmer climate, is also expected to aggravate water pollution and will adversely affect the quality of surface and groundwater (Fussel 2009) and can thus affect plant growth.

Global climate change is also expected to increase drought severity and frequency in most regions of the globe in the future (Meehl et al. 2007, 2009; Karl et al. 2009) which are detrimental to plants, particularly at a time when rising temperature escalates ever-increasing water demands of plants (Wolfe et al. 2007). In some areas, reduced precipitation along with an increase in temperature will likely result in the loss of arable land due to decreased soil moisture, increased aridity, increased salinity, and groundwater depletion (Bals et al. 2008) which in turn will cause crop water stress due to reduction in availability of good quality water for them at certain times of the growing season (FAO 2008a, b). Stomatal closure and slowing down of carbon uptake are two strategies generally employed by crop plants to counter water stress, however, it raises the canopy temperature by lowering latent heat (Bernacchi et al. 2007) and increases heat-related impacts that will negatively affect crop production. Although this climatic variability threat can be reduced by irrigation, but there is every possibility of change in temporal and spatial distribution of reliable water resources on which irrigated farming systems bank due to changing climate. Climate change models predict that unabated emission of greenhouse gas will significantly affect the hydrological system, and hence river flow and regional water resources all of which are expected to have an overall negative impact on freshwater systems (Strzepek and McCluskey 2007) thereby making agriculture vulnerable because globally 70 % of available freshwater is used for irrigation purposes.

In such situations plants by accessing moisture below the surface with shallow depth may escape drought, however, high temperature and change in patterns of precipitation may also affect the rate of groundwater recharge (Bates et al. 2008), which will increase the crop's irrigation demand. Furthermore, the changes in the timing of the rainy season may mystify already established techniques for farmers to find out apt plantation dates. Finally, more events of heavy rainfall can lead to waterlogged soils and flooding which also are pathways for damaged crop production as they decrease levels of oxygen in the soil and increase vulnerability of roots to diseases (Falloon and Betts 2006).

2.3 Rise in Sea Water Level

The sea level will affect plant growth and productivity in some parts of the world. There has been an increase of 12–22 cm in global sea level during the twentieth century, and new observations now confirm that there has been an increase of about 3.4 millimeters (mm) in sea level per year in the last two decades (IPCC 2007a; Allison et al. 2009). Global warming at the current rate is expected to raise the sea level by half a meter by 2100 A.D. making low-lying agricultural lands vulnerable to inundation and salinization which can lead to loss of agricultural land and thus significantly affect crop production in these areas. Melting of polar ice and glaciers due to increase in temperature has led to an increase in sea level by 20 cm in the last part of the twentieth century (Douglas 1997). In addition to this there is every chance of greater exposure of arable land to wastewaters contaminating it to a severe extent (ESCAP 2009). All these factors are going to decrease crop production in times to come.

2.4 Soil

Effects of climate change on plants also include the effects on key resources of plant importance such as soil. The actual water available to plants depends upon soil type, its water-holding potential, and rate of infiltration. Other soil properties that affect plant productivity include nutrient and organic matter level, its structure (more prominently aggregation of the primary soil particles and macroporosity), pH levels, a microbial community, and concentration of phytotoxic elements or compounds for plant, animal, and microbial life. Several processes of soil degradation, soil erosion, acidification, toxification, salinization, compaction, and loss of organic matter that occur continuously in nature are highly sensitive to changes in climatic conditions. Climate change via a change in temperature and availability of water will affect the rate of soil organic matter accumulation. Soil erosion is one of the major environmental concerns and is a natural process occurring regardless of anthropogenic interference; however, human activities, including intensive agriculture, have accelerated its rate (Montgomery 2007). Soil erosion is mainly affected by the erosive effects of rainfall, snowmelt, irrigation, and wind, all of which will be directly affected by the change in climate. Climate change models predict that the erosive power of rainfall will increase (Nearing et al. 2005; Pruski and Nearing 2002a) which in turn will increase erosion rates on the order of 1.7 % for every 1 % increase in total rainfall (Pruski and Nearing 2002b). Excessive soil erosion will cause increased loss of soil organic matter and other nutrients, thereby reducing soil fertility and hence productivity (Cruse and Herndl 2009).

2.5 Weed Species

Plant weeds by competing for water, light, and nutrients reduce the quantity and quality of plant yield. Increase in temperature as a consequence of global climate change will affect weed species' success (Woodward and Williams 1987) and subsequently their distribution, growth and reproduction as well. Most invasive weeds are confined to subtropical and tropical areas (Holm et al. 1997) as higher latitudes because of the low temperature extremes are highly inhospitable to them. Global warming will facilitate and accelerate northward expansion of these weeds (Rahman and Wardle 1990).

Climate change will not only alter distribution of invasive weeds, but also will promote their access within plant communities (McDonald et al. 2009; Ibanez et al. 2009; Bradley 2009; Bradley et al. 2010b; Jarnevich and Reynolds 2011). Biogeographical models suggest that the increase in temperatures and change in precipitation may increase the potential expansion range of some species, such as cheat grass (Bradley et al. 2010a, b; Jarnevich and Stohlgren 2009; McDonald et al. 2009), particularly near the cooler margins of their range (poleward and upward in elevation). But for some species, such as knapweed, can reduce invasion risk in portions of their invaded range (Parker-Allie et al. 2009; Beaumont et al. 2009; Bradley 2009).

Weed invasion will also be affected by extreme climatic events such as floods and drought (Jimenez-Moreno et al. 2011; Diez et al. 2012). Although invasion is expected to be inhibited due to decreasing precipitation conditions, a long spell of severe droughts can act as disturbances that by decreasing biotic resistance from native species will provide invasion opportunities to exotic invasive species once precipitation returns. For example, *Eragrostis lehmanniana* rapidly invaded and became the dominant species of Arizona rangeland following a severe drought in 2004 and 2005 that led to the death of many native grasses and shrubs (Scott et al. 2010).

2.6 Insects and Pests

Generally, an increase in air temperature is beneficial to insect pests as it accelerates every aspect of their life cycle. Increased temperature in summers results in proportionately greater damage insects inflict on their host plants (Bradshaw and Holzapfel 2010; Norhisham et al. 2013) and in winters reduces their mortality. Increasing air temperature will result in reduced cold stress without substantial increase in heat stress (Bradshaw and Holzapfel 2006). There will be an overall positive effect on the expansion of geographical ranges of insects due to the increase in temperature (Walther et al. 2002; Parmesan and Yohe 2003; Parmesan 2006; Walther 2010). Increased air temperature will result in successful colonization of insects into their "earlier outside population range habitats" due to early maturation and migration (Bale and Hayward 2010). More outbreaks of pest populations will be favored with projected increase of extreme climate, particularly extreme precipitation events (Hawkins and Holyoak 1998; Srygley et al. 2010) by stretching current thresholds that otherwise keep some pests in check. All this will hamper proper growth of plants and will also affect their yield potential.

2.7 Rising Atmospheric Carbon Dioxide Concentrations

The present atmospheric CO_2 concentrations (384 ppm) are projected potentially to rise to 550 ppm by 2100 (IPCC 2007a, b), greater than 800 ppm under the business as usual scenario (Schmidhuber and Tubiello 2007). Elevated CO_2 concentration affects the photosynthetic process directly and evokes a wide range of morphological, anatomical, and biochemical responses in plants. These responses depend mainly on photosynthetic pathways operative in plant species and thus vary accordingly. The most common responses in plants include growth rate changes (Poorter et al. 1997), change in the pattern of allocation of resources (Bazzaz 1990), water-use efficiency (Eamus 1991), and the rate of nutrient uptake (Jackson and Reynolds 1996). However, without studying a species directly it is difficult to predict whether CO_2 enrichment will benefit it and the community in which it thrives. However, based on certain traits it is predicted that those species with C3 photosynthetic pathways respond favorably to elevated CO_2 concentration in comparison to C4 and CAM species. The increase in CO_2 concentration generally enhances plant growth and development by stimulating photosynthesis and improving water-use efficiency. Plants have been classified mainly into three groups, namely C3, C4, and CAM plants on the basis of the photosynthetic pathway operational in them and the variation in the physiological response of plants to carbon dioxide enrichment mainly stems from CO_2-fixing enzymes involved, namely ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco), phosphoenolpyruvate carboxylase PEP carboxylase, and to some extent carbonic anhydrase.

The present ambient atmospheric carbon dioxide concentration is a limiting factor for C3 plants when other factors affecting plant growth (light, water, temperature, nutrients) are optimal (Osmond et al. 1980; Downton et al. 1980) and any increase in its concentration will be beneficial to these plants. Rubisco, which is the primary enzyme involved in leaf photosynthesis in C3 plants is not CO_2 saturated at present-day atmospheric conditions, and can bind to either CO_2 or O_2. An increase in the concentration of CO_2 enables ribulose 1,5-bisphosphate carboxylase/oxygenase (Rubisco) to compete better with O_2 for binding sites of the Rubisco protein and thus can fix more CO_2 due to the increased CO_2:O_2 ratio (Ziska and Bunce 2006). Thus, CO_2 enrichment will momentarily enhance the relative growth rate by increasing net carbon uptake (Lambers et al. 1998) thereby increasing biomass and yield (Kimball 1983). The plants with C3 photosynthetic pathway may benefit in dry matter production of high CO_2 in three ways: (1) enhancement of leaf expansion by increasing leaf thickness, leaf area, and leaf area index (LAI; Bray and Reid 2002) due to accumulation of nonstructural carbohydrates (Lambers et al. 1998), (2) increase in the photosynthetic rate per unit leaf area, and (3) increase in water-use efficiency. Elevated levels of CO_2 accelerate growth and also bring in changes in inherent established timings of stages of plant development (Bowes 1993).

Experiments under idealized conditions revealed that a doubling of atmospheric CO_2 concentration increased photosynthesis by 30–50 % in C3 plant species (Ainsworth and Long 2005) and crop yield by 10–20 % (Gifford 2004; Ainsworth and Long 2005).

The CO_2 fixation in C4 plants is mediated by the enzyme phosphoenol pyruvate carboxylase (PEPcase) and CO_2 assimilation in these plants is saturated or almost saturated at low ambient CO_2. This is due to the fact that primary carboxylase enzyme, phosphoenolpyruvate carboxylase utilizes HCO_3^- as substrate for which O_2 is not a competitive substrate and also because of insensitiveness of the enzyme to changes in the CO_2:O_2 ratio due to lack of binding of O_2 to its catalytic site. In addition, this biochemical process operative in C4 plants raises the CO_2 concentration in their bundle sheath cells 10 times more than present in C3 mesophyll cells up to 2100 µmol l^{-1} (Von Caemmerer and Furbank 2003) which nearly saturates the carboxylation reaction and inhibits photorespiration. Consequently, rising CO_2 concentrations will not confer many additional physiological benefits to C4 plants, although some C4 plants respond positively in terms of yield (Poorter et al. 1997; Anderson et al. 2001) which can be due to higher water-use efficiency (Ghannoum et al. 2000; Sage and Kubien 2003) as a result of prolonged stomatal closure at high temperature (Long et al. 2004, 2006) which in part decreases stomatal conductance and transpiration (Ainsworth et al. 2003). Also, nitrogen limitations are exacerbated by high CO_2 levels, which favor many C_4 species over other plants as they have greater photosynthetic nitrogen-use efficiency (Sage and Kubien 2003). Elevated CO_2 conditions also result in enhanced photosynthesis in C4 plants under high irradiance conditions whereas little to less response under low irradiance conditions has been observed (Ghannoum et al. 2000). Under natural atmospheric conditions, doubling of atmospheric CO_2 concentration increases photosynthesis by 10–25 % in C4 species (Ainsworth and Long 2005) and crop yield by 0–10 % (Gifford 2004; Long et al. 2004; Ainsworth and Long 2005).

In general, an increase in the number of mesophyll cells and chloroplasts as well as extensively long roots and large stems are associated with elevated CO_2 levels (Bowes 1993). A gain in carbon might increase the length and thickness of roots (Lee-Ho et al. 2007), and can also stimulate the production of lateral roots (Pritchard and Rogers 2000). Elevated CO_2 causes shifts in biomass allocation to roots from leaves (Stulen and Den Hertog 1993). CO_2 enrichment can increase the flower, fruit, and seed number (Jablonski et al. 2002), resulting in greater individual and total seed mass (Jablonski et al. 2002); however, it decreases protein content in flower and seeds (Ziska et al. 2004). Elevated CO_2 alters plant chemical composition which affects growth (Poorter et al. 1997). CO_2 enrichment causes nonstructural carbohydrate accumulation, increase in soluble phenolic compounds, and decrease in concentration of minerals and organic nitrogen and phosphorus (Rogers et al. 1999). Plants exposed to elevated CO_2 have higher photosynthetic nitrogen use efficiency (PNUE) and higher nitrogen use efficiency (NUE; Tuba et al. 2003).

Atmospheric CO_2 enrichment, however, endows plants with a counteracting tendencies to several environmental stresses that otherwise will have deleterious effects on their growth and development (Fig. 2). An increase in CO_2 ameliorates the effects of following stresses:

2.7.1 Temperature

Increased levels of the atmospheric CO_2 meliorate, and at times fully compensate for the negative influences of raising the temperature (Aranjuelo et al. 2005; Gutierrez et al. 2009; Yoon et al. 2009). The increase in air temperature is one among the various environmental stresses that can adversely affect crop productivity, and reduce crop yield to such an extent to diminish critically our capacity to produce fuel and

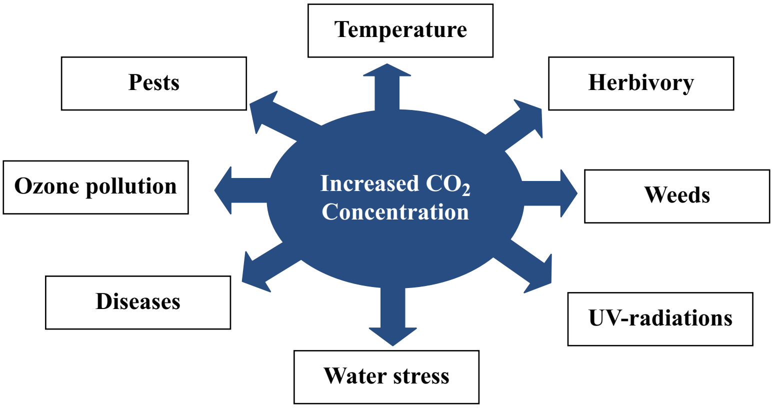

Fig. 2 Ameliorating effect of CO_2 against various stresses

feed food products. A rise in temperatures will cause northwards migration in many crops that can adversely affect agriculture. However, the rise in temperature increases the growth-enhancing effects of carbon dioxide. For example, results of 42 experiments on C3 plants revealed an enhancement in mean CO_2-induced growth from a value of zero at 10 °C to a value of 100 % at 38 °C (Idso and Idso 1994).

This increase in plant growth occurs due to the negative impact of high CO_2 levels on the growth-retarding process of photorespiration, which in C3 plants can “cannibalize” newly synthesized photosynthetic products by 40–50 %. Because at high temperatures this phenomenon is more pronounced, enrichment of atmospheric CO_2 offers greater potential to benefit plants as air temperatures rise.

CO_2 enrichment increases the optimum temperature for plant growth. Several studies depicted an increase by 5 °C in optimum temperature for growth when the air’s CO_2 was increased by 300 ppm (Berry and Bjorkman 1980; Stuhlfauth and Fock 1990). These observations have an important implication as they reveal that even the most extreme global warming conditions envisioned by IPCC won’t adversely affect the majority of plantation as C3 plants account for 95 % of all plant species and the rest of the planet’s vegetation (which is either C4 or CAM) have already adapted to warmer environments of earth that are predicted to warm much less in comparison to the other regions of the globe; consequently, temperature increase induced by elevated CO_2 will likely not lead to a very high reduction in crop yield.

2.7.2 Drought

Increasing atmospheric carbon dioxide will reduce agricultural sensitivity to drought, reduced soil moisture, and water stress (Manderscheid and Weigel 2007; Robredo et al. 2007, 2011). It has been suggested that there will be an increase in drought severity and frequency with an increase in greenhouse gases, causing crops to experience more frequent and more severe water deficit periods, thereby reducing crop yields (Robinson 2000; Karl et al. 2009). However, an increase in CO_2 will make crops less susceptible to water deficits induced by droughts even if their severity and frequency increases, as plant productivity stimulation induced by CO_2 is typically not negated by water stress. In fact, an increase in plant biomass stimulated by CO_2 elevation under water stress is often greater than well-watered conditions.

CO_2 enrichment during water stress stimulates development of larger than usual and robust root systems in plants that invade greater volumes of soil for scarce and much-needed moisture. Elevated concentration of atmospheric CO_2 also tends to induce stomatal closure, thereby reducing stomatal conductance resulting in less water loss via transpiration and, consequently, lowering the plant water usage overall, thus contributing to maintenance of favorable plant water status during drought (Chaplot 2007; Parry and Hawkesford 2010; Zhu et al. 2008).

2.7.3 Ozone Pollution

Elevated CO_2 also trims down and overrides the deleterious effects of ozone (O_3) pollution on plant growth and yield. Tropospheric ozone is a secondary air pollutant created by a chemical reaction between nitrogen oxides and volatile organic compounds in the presence of sunlight. Exposure of plants to elevated levels of ozone concentration reduces growth in plants. Because increase in temperature favors O_3 formation, there are apprehensions that global warming will further increase ozone concentration which could result in reduction of crop yields in the future (Karl et al. 2009) However, elevated CO_2 by reducing stomatal conductance also limits the indiscriminate ozone uptake through leaves and conveyance to internal tissues, which otherwise has a tendency to damage photosynthetic pigments and proteins, ultimately reducing plant growth and biomass production.

2.7.4 Weeds

On the whole, CO_2 enrichment does not increase the competitiveness of weeds over crops. CO_2 enrichment stimulates the growth of nearly all plant species, including those currently deemed as weeds by humans in monoculture. The majority of the most dangerous invasive weeds are of C4 type and out of the 86 plant species that provide 95 % of the world's food supply 72 are of C3 type—the most common arrangement of all crop/weed mixed-species stands—typically demonstrate that elevated CO_2 favors the growth and development of C3 over C4 species (Patterson and Flint 1995; Zhu et al. 2008). Therefore, the ongoing rise in CO_2 concentration on the whole should endow greater protection to crops against weed-induced reduction in growth and productivity.

2.7.5 Herbivory Stress

An increased level of CO_2 is also known to reduce sternness of herbivory and pest stress. Higher atmospheric CO_2 will reduce crop damage from insects and pathogenic diseases (Joutei et al. 2000). Pest damage to crops will slightly decrease or remain the same. In fact, the herbivory-consumed proportion of plant production will remain more or less the same in the carbon dioxide enriched world (Coviella and Trumble 2000; Coviella et al. 2000; Bidart-Bouzat et al. 2005). In one study, for example, a 34 % reduction in the number of offspring in the first generation and 49 % in the second generation of destructive agricultural bean plant mite *Tetranychus urticae*, was observed when fed on bean plants grown in 700 ppm CO_2 air in comparison to when fed on beans grown on 350 ppm CO_2 (Joutei et al. 2000). This CO_2-induced reduction in reproductive fitness in this invasive insect, which otherwise adversely affects more than 150 crop species globally, bodes well for society's capacity to cultivate the food crops to meet demands of the growing population of the Earth.

The increase in CO_2 concentration is found to induce several changes in morphology, anatomy, and physiology of plants that augment disease resistance in host plants by the following mechanisms:

1. An increase in net photosynthesis occurs that mobilizes more resources into host resistance (Hibberd et al. 1996a).
2. Reduction in stomatal conductance and density (Hibberd et al. 1996b).
3. An increased production of carbohydrate and wax with extra epidermal cell layers in leaves (Owensby 1994).
4. Increase in number and density of papillae and silicon accumulation at sites of penetration (Hibberd et al. 1996b).
5. Increase in biosynthesis and accumulation of phenolic compounds (Hartley et al. 2000).
6. Increase in biomass of roots (Malmstrom and Field 1997) and root functionality (Fleischmann et al. 2010).
7. Increase in concentration of tannin (McElrone et al. 2005).
8. Increased colonization of arbuscular mycorrhizal fungi in roots (Gamper et al. 2004).
9. Increased glyceollin biosynthesis (Braga et al. 2006) .
10. Whatever the underlying mechanism may be, elevated CO_2 levels significantly ameliorate the detrimental effects of pathogenic invasion stresses. Consequently, as the concentration of atmospheric CO_2 continues its upward climb, the planet's vegetation should be equipped better to deal successfully with damage that pathogenic organisms are traditionally known to cause society's crops, as well as to the plants that sustain the rest of the planet's animal life.

2.7.6 Other Benefits of Increased CO_2

Elevated levels of CO_2 enrichment have additionally been known to reduce the severity of UV-B radiation (Zhao et al. 2004; Tohidimoghadam et al. 2011), low and high light intensity (Sefcik et al. 2006; Rasineni et al. 2011), low levels of soil fertility (Haase et al. 2008; Jin et al. 2009), and oxidative stress (Yonekura et al. 2005; Burkey et al. 2007; Mishra et al. 2008). Elevated atmospheric CO_2 concentration enhances the quality of many phytoproducts having high nutritional and medicinal value by increasing the concentration of antioxidants (Wang et al. 2003; Ali et al. 2005), vitamins (Barbale 1970), and other phytonutrients (Schonhof et al. 2007; La et al. 2009; Oliveira et al. 2010). CO_2 enrichment increases antioxidant concentration by 71 % in strawberry (Wang et al. 2003) and an 11–15 % increase in digoxin in *Digilatis lanata* (Stuhlfauth et al. 1987, 1990).

3 Conclusion

Global climate change is unequivocal whose apparent impacts are projected to intensify further, particularly if the emission of radiative gases continues unabated. Climate change impacts with regard to the magnitude and pace in coming years will be determined critically by the choices that will be made about emissions of greenhouse gases. Reduction in levels of emissions of these gases will slow the appearance of climate change and lower their impact. Responses to the climate change challenge will certainly evolve over time, but there is a need to gain insights into the effectiveness of several adaptation responses and their interaction with each other to mitigate its effects. The exact consequences of a changing climate are difficult to predict primarily due to the complexity and incomplete understanding of atmospheric processes and also because of interactive relationships between various environmental variables, including temperature, water availability, radiation, ultraviolet and visible sunlight, salinity, and soil nutrition. Even in the most optimistic scenarios, it is highly unlikely that global yields will not register a net decline due to climate change, the question of relevance is that in the perpetual race to keep productivity at par with demand, how much of a headwind climate change could present. It will be impossible to unambiguously measure the effect of changes in climate on crop yield, but to trim down the uncertainties of global impact, better estimates of the response of crop yield will prove highly helpful. With climate change expected to increase the intensity and frequency of weather extremes, some crops may show an increase in their yield or range, but at the same time will increase existing risks of extinction of many threatened crops or lead to a reduction in productivity.

In order to explore in detail the impact of climate change on plant productivity, plant performance under simulated future climate, using all available techniques, physiological, biochemical, molecular, and ecological in large-scale multifactorial experiments should be given due consideration to determine how the multiple environmental factors, when altered in projected changed climate, could interact with each other to cast their effect on growth and metabolism of several plants. The available evidence related to climate change and crop physiology until now, however, indicates that climate change represents a credible threat to sustain global productivity growth at rates necessary to keep up with demand. To further enhance and establish climate change effects on crop productivity and to avoid or reduce unwanted impacts of climate change, formulation and implementation of adaptation strategies will be the most palpable measures.

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Fertilizers and Environment: Issues and Challenges

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Abstract About 50 % of the increase in agricultural produce during the twentieth century was achieved by application of inorganic fertilizers to crop plants. Fertilizer application is still an important farm input that is required to achieve challenging yield targets of the twenty-first century. However, fertilizer application is known to deteriorate the environment around us. Therefore, better fertilizer use efficiency (FUE) is suggested for economical yields and a safer environment. This chapter first introduces the concept of FUE for a safer environment and then, subsequent topics detail factors affecting FUE and known management practices to enhance FUE at agricultural farms. Future research challenges relating to FUE and the environment are identified. The chapter, as a whole, summarizes important literature for farmers, policy makers, and scientists.

Keywords Fertilizer use efficiency • Environmental pollution • Soil Fertility • Crop productivity

1 Introduction

In spite of decreased growth rate of the world's average population from 1.26 to 1.10 % since 2006, absolute annual increase is continuing to be large. According to a recent estimate by the Population Division of the United Nations, about 80 million people will be added annually to the world population until the mid-2030s.

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The major share of this increase is expected to take place in the developing countries. More food, feed, and cloth are required for these additional people (Evans 2009). It has been estimated that the world will need twice as much food within 30 years (Glenn et al. 2008).

Over the previous few decades, dietary patterns around the globe have changed due to income growth, urbanization, awareness, and consumer preferences. Diets have shifted away from staples such as cereals, roots, and tubers and pulses towards more livestock products, vegetable oils, and fruits and vegetables (FAO 2008). Total meat production in developing countries has increased from 27 million tonnes to 147 million tonnes between 1970 and 2005, and global meat demand is expected to increase by more than 50 % by 2030 (FAO 2011). This will further increase the pressure on agricultural land, especially in Asia, which has the world's highest population density per hectare of arable land. Nonetheless, biofuel production would also require more land replacing the food crops. As per estimates, if biofuel use grows by 50 % over the next 10 years then 21 million hectares of food crops would be displaced by bioenergy crops. This would imply greater intensification of agriculture to meet food demand.

Cultivated soils do not usually contain sufficient amounts of plant nutrients for high and sustained crop yields. Therefore, agricultural yield depends upon availability of nutrients applied through fertilization and yield of most crops has been reported to increase linearly with the amount of absorbing nutrients (Kaur et al. 2007). Plant nutrition is one of the major factors that control soil productivity and quality (Jaga and Patel 2012). Fertilizers maintain soil fertility and productivity through supplying essential plant nutrients and therefore make a vital contribution to economic crop production.

Intensive agriculture can have negative effects on the environment: it can upset the balance of the food chain, pollute ecosystems, and cause harm to flora and fauna. To keep food production at the same level as population growth, without using up or destroying the resources and environment, is a major task. The main challenges include increasing the area of productive land, increasing the yield per unit area of land, maintaining soil productivity and reversing the nutrient mining of soil, and breeding new crop varieties with higher yield potential and improved tolerance to biotic and abiotic stresses. One of the sources of pollution from intensive agriculture is the excessive use of fertilizers (Ju et al. 2014). Typically a crop plant uses less than half of the applied fertilizers (Connor et al. 2011). Remaining nutrients attach to soil particles, leach into ground or surface water, or cause air pollution such as oxides of N (Ongley 1996; Hietz et al. 2011).

Recovery of applied inorganic fertilizer by plants is low in many soils of the world and increased fertilizer use efficiency (FUE) or nutrient use efficiency (NUE) is the only option for sustainable agriculture (Fixen 2009). Plants use only about 50 % of applied N; the remaining 15–25 % reacts with organic compounds in soil, 2–20 % is lost through volatilization, and 2–10 % is reported to interfere with surface and groundwaters (Raun and Johnson 1999; Sonmez et al. 2007; Chien et al. 2009). Average FUE is reported up to 65 % for corn, 57 % for wheat, and 46 % for rice (Ladha et al. 2005; Chien et al. 2009). The recovery of applied P is even lower and on an average only 25 % or less of the applied P is taken up by crop plants in a growing season. Moreover, precipitation of applied P with Ca and Mg in calcareous soils (Rahmatullah et al. 1994) and with Fe and Al oxides in acidic soils further reduces P use efficiency (Vance et al. 2003).

Overreliance and imbalanced use of mineral fertilizers is reported to pose serious public and environmental hazards (Savci 2012). The impact of fertilizer on the environment must be scrutinized as public influence over production is increasing. Overuse of N fertilizers contributes several harmful effects on the environment. In soil, by the process of microbial nitrification, ammonium ion is converted into nitrate and thus a negative charge on nitrate favours its downward movement into groundwater. However, the time taken by nitrates to move from the root zone to groundwater varies significantly depending upon soil texture and climate. According to the World Health Organization (WHO), concentration of NO_3-N should not exceed 10 mg L^{-1} in drinking water. The main alleged health hazard due to nitrate ingestion in food and water is a blue baby disease of young babies. Nitrogen loss as gaseous substances generally occurs through volatilization and denitrification, and this leads to environmental pollution. Another negative aspect of increased fertilization is eutrophication of water bodies. Increased concentration of P promotes luxurious growth of higher aquatic plants and algae that degrade water quality (Conley et al. 2009). Eutrophication leads towards depletion in oxygen and proliferation of unwanted species. As a consequence, it reduces the number of living species such as fish in the aquatic environment (Ansari et al. 2011).

Decreased fertilizer recovery not only has heavy costs but also has serious environmental concerns. Thus, judicious application of fertilizers to soils and their use by plants is needed for sustainable and safer agriculture. Nutrient use efficiency accounts for the acquisition of nutrients from the soil, biomass generation from nutrients, and remobilization of nutrients to organs of agronomic interest (Baligar et al. 2001; Aziz et al. 2011a, b). Nutrient use efficiency can be described by four agronomic indices: partial factor productivity (PFP), that is, crop yield in kg per nutrient applied in kg; agronomic efficiency (AE), that is, a kg crop yield increase per kg nutrient applied; apparent recovery efficiency (RE), that is, nutrient taken up in kg per nutrient applied in kg; and physiological efficiency (PE), that refers to kg yield increase per kg nutrient taken up (Mosier et al. 2004). Fertilizer use efficiency can be enhanced by adopting best management practices that refer to application of nutrient at the right time, from the right source, at the right rate, and at the right place (Roberts 2008; Epstein 1972; Fageria 1992).

2 Fertilizer Use Efficiency and Environment

Agriculture in the world is dependent on manufactured fertilizers and demand of fertilizers for crop production is increasing in most of the countries due to cultivation of modern varieties and intensive cropping systems. Consumption of N, P, and K fertilizers for crop production increased from 31 million tons in 1961 to 183

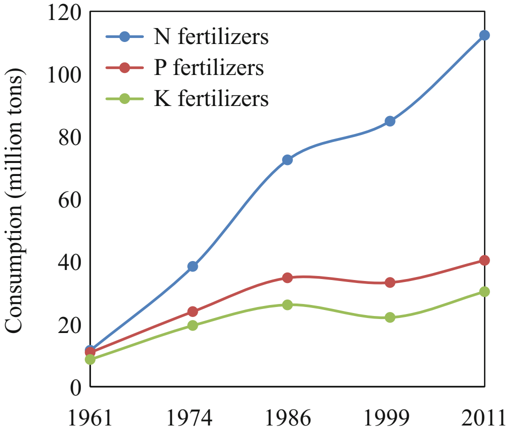

Fig. 1 Use of N, P, and K fertilizers. (*Source*: FAO 2014)

million tons in 2011 (FAO 2014). The greatest increase of consumption during the period was in N fertilizers (Fig. 1). The sharp increase in fertilizer consumption during the 1960s and 1970s can be attributed to the introduction of fertilizer-responsive cultivars of cereals, the Green Revolution cultivars. Even in the twenty-first century, the focus of plant breeders seems to be development of hybrids and varieties for greater yields. The new cultivars introduced have higher demands for nutrients as compared to old cultivars.

Energy and raw material, utilized for fertilizer manufacturing, often come from limited resources. A substantial amount of energy is consumed in the manufacture of fertilizers at industries and in transport of manufactured fertilizers to agricultural fields. From mining to manufacturing, various hazardous chemicals are introduced in the soil, water, and atmosphere. A detailed description of environmental hazards of the fertilizer industry is given in a technical report of United Nations Environment Programmme (UNEP 2000). Fertilizer manufacturing plants emit ammonia, fluorine (as SiF_4 and HF), oxides of N (NO_x and N_2O), oxides of S (SO_x), fertilizer dust, acid mists, and radiation in the atmosphere. Effluents of the industry also have these pollutants in toxic concentrations. Moreover, most of the solid wastes and by-products of the industry are pollutants. Therefore, manufactured fertilizers are a major cause of environmental pollution (Li et al. 2013; Ju et al. 2014).

Based on composition and purity of the raw material, fertilizers may be a source of pollutants in soils. As compared with N and K fertilizers, heavy metal contaminations were greater in rock phosphate and P fertilizers (Raven and Loeppert 1997). Toxic soil Cd concentrations in potato and sugar beet fields were related to long-term overuse of P fertilizers (Cheraghi et al. 2012).

Not all of the applied quantity of mineral nutrients is taken up by crop plants. More than 90 % of applied fertilizers may be lost in the environment leading to increased pollution of soil, water, and atmosphere. The situation gets worse when the applied nutrients, such as N and P, end up in water bodies causing eutrophication. Apart from runoff, N can also leach to groundwater and volatilize to atmosphere.

About 50 % applied N can be lost through ammonia volatilization and 25 % as nitrate leaching beyond the root zone (Zhao et al. 2011). Leaching of nitrate and contamination of drinking water resources increases health risks for humans and animals and volatilized ammonia is itself toxic and it also acts as a greenhouse gas and results in acid rains.

Due to pollution hazards of fertilizers during mining, manufacturing, and application, manufactured fertilizers are not safe for our environment (Table 1). Organic farming is suggested by some scientists as a sustainable and safer agricultural technology (Gabriel et al. 2010; Koohafkan et al. 2012; Strandberg et al. 2013). As desired yield levels are not achieved in organic farming, scientists have focused on integrated nutrient management strategies to improve fertilizer use efficiency (Bruulsema et al. 2008). Such strategies are not only good for better farm income, but also help us partially to decrease our dependence on manufactured fertilizers.

Table 1 Some fertilizer pollution reports from various world locations

Source	Location	Observations	Reference
N fertilizers	China	Aquifer have nitrate contamination about 20-100 mg L^{-1}	Zhao et al. (2011)
N fertilizers	India	Eutrophication, $NO_3 = 350$ mg L^{-1}	Pathak (1999)
N fertilizers	Poland	NH_4 concentration in pine tree bark 1699 mg kg^{-1}	Seniczak et al. (1998)
Rock phosphate	Pakistan	Contamination of Cr upto 105 μg g^{-1}	Javied et al. (2009)
Rock phosphate	North Africa	Concentration of Zn about 420 μg g^{-1}	Kongshaug (1992)
N fertilizers	Nigeria	$NO_3 = 20–100$ (mg L^{-1})	Uma (1993)
Phosphate fertilizer	China	Arsenic-contaminated soil with concentration about 1.6 to 20.3 mg kg^{-1}	Hartley et al. (2013)
Phosphate fertilizer industry	Lebanon	Zn = 92 (mg kg^{-1} soil)	Aoun et al. (2010)
Fertilizer N	China	Total N_2O emissions 980 (Gg N per year)	Liu and Zhang (2011)
Phosphatic fertilizer	China	Ar, Cd, and Pb contamination of 13.5, 2.6, and 300 mg kg^{-1}, respectively	Feng et al. (2009)
Single super phosphate	North Carolina	Contamination of Cd about 79.0 μg g^{-1}	Chien et al. (2009)
NPK fertilizer contain	China	Benzoanthracene 35.6 g kg^{-1}, Chrysene 33.9 μg kg^{-1}	Mo et al. (2008)
Fertilizer	Belgium	Polychlorinated dibenzo-p-dioxins 0.17 ng TEQ/k	Elsken et al. (2013)
Multinutrient fertilizer	Brazil	Contamination of Cr and Pb about 244 and 273 mg kg^{-1} soil	Nunes et al. (2010)
Rock phosphate	New Zealand	Contamination of Cd about 41 mg kg^{-1}	Loganathan and Hedley (1997)

Less fertilizer consumption at agricultural farms means less mining and manufacturing while there are still additional profits from crop production. By this, several issues of environmental pollution can be minimized. Therefore, increased FUE is a milestone towards a safer environment and greater agricultural profit.

3 Factors Affecting Fertilizer Use Efficiency

A fertilizer is considered efficient when maximum economical yield is obtained with the minimum amount of fertilizer application. Various soil, plant, fertilizer, and environmental factors that affect FUE are described below.

3.1 Leaching Losses

Nitrate (NO_3) fertilizers are susceptible to leaching losses (Almasri and Kaluarachchi 2004a, b). The extent of leaching is more in sandy soil compared to clayey soils. The situation is further aggravated when soil is bare than cropped soil. The main problems related to NO_3^- leaching are eutrophication of surface waters, increased production of nitrous oxide from receiving water bodies, and a higher concentration of NO_3^- in drinking water (WHO recommends <50 mg NO_3^- L^{-1} of drinking water).

According to Lehmann and Schroth (2003), nitrate leaching is lower in subsoil due to the increase in net positive charge, and the nitrate held in subsoil can be taken up by deep-rooted crops. Therefore, it is important to distinguish between nitrate movement within the soil profile (i.e., topsoil to subsoil), and leaching beyond the root zone, into the groundwater. Losses from ammonical fertilizers are higher during the summer season because of rapid oxidization by nitrifying organisms. The activity of the nitrifying organism can be reduced to minimize leaching losses. Various chemical compounds inhibit microbial nitrification of N fertilizers and reduce the leaching loss.

Phosphorus losses by subsurface leaching are negligible compared to losses by erosion and surface runoff. Subsurface leaching increases when P is in soluble organic form, as manure; the soil's capacity to bind inorganic P is saturated; preferential flow of water through channels and cracks in the soil prevents soluble P from getting in contact with the soil's adsorption sites. Furthermore, drained soils have a higher rate of subsurface leaching compared to undrained soils. Compared to inorganic P, dissolved organic P is more mobile in soil (Havlin et al. 1999; For detailed reading see Tunney et al. 1997).

Potassium can be lost in drainage water in sandy and acid soils and in high rainfall areas (Malavolta 1985; Havlin et al. 1999). Losses can be minimized by modifying the time of application with crop growth stage to maximum plant uptake period and also applying the fertilizer in split doses. However, in clayey soils, there are no leaching losses. Moreover, recently developed slow-release K fertilizers are not subject to leaching losses, for example, potash frits, potassium metaphosphate, and fused potassium phosphate.

Sulfate, added to soil as a secondary nutrient along with N and K fertilizers, is susceptible to leaching from the topsoil and accumulating in the subsoil. In the subsoil SO_4^{2-} is only available later in the season to deep-rooted crops. Leaching can also result in SO_4^{2-} losses to groundwater. Sulphate is also readily leached from surface soils; maximum losses are in soils dominated by monovalent cations such as K and Na and minimal in soils with high amounts of Al (Havlin et al. 1999).

3.2 Gaseous Losses

Gaseous losses of N from soils may be through (1) ammonia volatilization under high pH conditions in alkaline soils and (2) loss as N_2, N_2O, and NO due to denitrification. These losses are influenced by soil pH, fresh organic matter, moisture, temperature, and soil microbial diversity. Ammonia volatilization at high pH can be minimized by proper placement of urea. Cantarella et al. (2005) reported volatilization losses ranging 37–64 % of urea applied to maize crop at various locations. It is recommended to apply ammonical fertilizers at least 4–6 inches below the soil surface. Alternatively, urea should be used instead of nitrate fertilizer wherever there are high chances of losses of N by denitrification processes.

3.3 Immobilization

Immobilization is a major cause of reduced FUE as nutrients released from fertilizer become unavailable for growing crops over a certain period of time via chemical, physicochemical, and microbiological immobilization (Keeney and Sahrawat 1986; FAO 1972; Zhang et al. 2013). Ammonium and K ions are immobilized by strong adsorption by 2:1 type clay minerals such as vermiculite (Allison et al. 1953; Barshad and Kishk 1970). High soil pH further enhances this type of fixation. Practical soil fixation can be reduced by timely and proper placement of fertilizer. Fertilizer should be carefully selected so that it will have minimum interaction with the soil. Furthermore, the time and mode of application should be selected to ensure minimum immobilization of nutrients, such as preferable use of nitrate fertilizer may improve availability.

At low pH, the efficiency of water soluble P is very low. In acidic soils, P is known to react with Fe/Al oxides to form insoluble complexes (Vance et al. 2003). However, rock phosphate has shown increased solubility and availability under acidic conditions. In calcareous soils, applied P is invariably converted into tri-calcium phosphate, an insoluble P compound (Rahmatullah et al. 1994). Under such conditions water soluble P are relatively more efficient than water insoluble P such as rock phosphate.

Microbiological fixation of fertilizer N may be of concern when undecomposed organic matter of wider C/N ratio is present in the soil. However, this is a temporary type of immobilization. Application of a starter dose of N fertilizer to organic matter or by allowing enough time for complete decomposition of undecomposed organic matter may improve the N availability for the crop. Sulfate can bind to clays, and it is less mobile than nitrate but has higher mobility than phosphate.

3.4 Soil Compaction and Fertilizer Use Efficiency

Soil compaction is a common observation under mechanized farming and is one of the major problems facing modern agriculture. Soil compaction increases soil strength and decreases soil physical fertility through decreasing storage and supply of water and nutrients, which leads to additional fertilizer requirement and increasing production cost (Hamza and Anderson 2005). Numerous physical changes in soils due to compaction result in a poor response for N and P fertilizers. Soil compaction results in the soil particles coming closer resultantly decreasing soil bulk density and soil porosity. Because the points of contact between soil particles are increased, compaction also results in an increase of soil strength. In fine-textured soil, compaction reduces the available water capacity of soil, resulting in decreasing nutrient availability.

3.5 Soil Temperature

Soil temperature is one of the important environmental factors affecting plant growth and fertilizer response of crops (Mackay and Barber 1984; Pregitzer and King 2005). Temperature affects most physical processes occurring in the soil and the rate of chemical reactions increases with rise in temperature that controls nutrient availability. Soil temperature affects fertilizer efficiency by changing solubility of fertilizers, cation exchange, and ability of the plants to absorb and use nutrients (Pregitzer and King 2005; Hussain et al. 2010; Hussain and Maqsood 2011). Volatilization losses of N are related to high soil and atmospheric temperature. Soils in warm regions generally fix higher amounts of P compared to temperate regions. Soil temperature can be managed to an extent by common management practices including tillage, mulching, and irrigation. Moreover, root growth is severely affected by either too cold or hot soil temperature ultimately affecting nutrient uptake (Marschner 1995).

3.6 Soil Moisture

Soil moisture regulates nutrient movement within soil and their uptake by plants. Drought conditions can limit nutrient uptake because of decreased nutrient movement as well as decreased root growth (Marschner 1995).

Excessive moisture leads to leaching loss of added fertilizers whereas lack of moisture results in poor availability of the added fertilizer and high osmotic pressure of the soil solution due to concentration effect fertilizers (Taylor et al. 1983). Thus, efficient water management is complementary to efficient fertilizer management. Maximum efficiency of fertilizers can be obtained only in the presence of adequate soil moisture and vice versa. Mengel and Haeder (1973) demonstrated that increasing soil moisture from 10 to 28 % increased K transport by up to 175 %.

3.7 Soil pH

Soil pH is one of the major edaphic factors that regulate nutrient availability (Marschner 1995). Most plant nutrients are available at soil pH 6 to 7.5. If soil pH is lower or higher than the range, nutrient availability reduces sharply and even 1 unit pH increase or decrease can decrease/increase 100 times nutrient availability. At low pH, most micronutrients except molybdenum are available and even can be present in toxic concentrations because of their increased solubility (Tan 2011). In contrast, their availability reduces at alkaline pH particularly of Zn, Fe, Cu, and Mn.

Plant nutrient availability depends on the prevalent soil pH. In highly acidic or alkali soils, efficiency of P fertilizers is low. In such situations, efficiency of fertilizers can be increased by correcting the soil condition, using suitable amendments. Physiologically alkaline fertilizers such as calcium carbonate and the like should receive priority on acid soils and physiologically acid fertilizers, or alternatively use of acidic fertilizers such as ammonium sulphate on alkaline soils. At pH higher than 7, Ca and Mg ions, as well as the presence of carbonates of these metals result in precipitation of P fertilizers, decreasing their availability (Cole and Olsen 1959; Shen et al. 2011).

3.8 Soil Organic Matter

The organic matter in soil not only supplies different nutrient elements, but also improves physical conditions of soils, stimulates microbial activity, protects the soil from erosion, retards the fixation of nutrients, increases mobility of nutrients in soils, increases the buffering capacity, and helps in many other ways (Tan 2011; Osman 2013a, b). Potential benefits of organic matter in soil in turn increase the efficiency of applied inorganic fertilizers. However, a high amount of organic matter may not prevent P losses as a result of leaching. This may be due to the absence of Al and Fe compounds, which are mainly responsible for P retention under low pH conditions (Vance et al. 2003).

3.9 Plant Characteristics

Crop species vary in their ability to remove nutrients form soil. Furthermore, there is significant variation within cultivars of the same crop species (Aziz et al. 2006, 2011a, b, 2014; Gill et al. 2002). Numerous researchers have revealed varietal variations for K uptake in ryegrass, maize, soybean, and barley (Dunlop et al. 1979; Terman 1977; Glass and Perley 1980). Because the roots are the principal organs through which plants take up nutrients, the rooting pattern and habit have an important bearing on nutrient removal. Crops with shallow extensive fibrous roots are able to uptake a greater amount of fertilizer applied per unit area (Lynch 1995). The fertilizer needs of deep-rooted crops are generally lower than shallow-rooted crops. Munson (1985) identified five plant root factors that significantly influence nutrient uptake from soil. These include ion flux, root radius, rate of water uptake, root length, and rate of root growth.

3.10 Fertilizer Characteristics

Nutrient mobility, type of fertilizer, and the time and method of application significantly influence the FUE (Sadras and Lemaire 2014). Nitrogenous fertilizers are highly mobile and subjected to both downward and lateral mobility. In contrast, P is highly immobile (Smeck 1985). Potassium is also mobile but compared to N its mobility is lower (Nastri et al. 2000). To get maximum efficiency N and K fertilizer should be applied in frequent split doses and P as basal dressing or near the root zone (Munson 1985; Sowers et al. 1994; Awan et al. 2007). The type of fertilizer also determines the efficiency (Zaman et al. 2005). Ammonium and urea fertilizers are more efficient than nitrate fertilizers for paddy soils (Datta 1986). Water-soluble P materials are more efficient for short duration crops and in soils that are neutral to alkaline in reaction. There is also a certain amount of interaction noticed among crops and fertilizers. For example, paddy performs better when ammonium sulphate is applied as N carrier and for tobacco when potassium sulphate is applied as K carrier (Craswell et al. 1981; Vann et al. 2013).

4 Possible Ways to Improve Fertilizer Use Efficiency

Increase in FUE aims at obtaining more yield while adding a small amount of fertilizer materials. This will not only result in minimizing the production cost for a certain crop but it will also reduce the risk of environmental contamination. Hence, it improves the overall economy of a region/country. The FUE can be improved by managing soil and plant factors coupled with improvement in fertilizer materials.

4.1 Site-Specific Nutrient Management

Soil is an ultimate reservoir of plant nutrients and their availability depends upon a number of soil properties including physical, chemical, and biological (Havlin et al. 1999). As the soil system is dynamic, hence both temporal and special variability exist resulting in a huge variation in nutrient concentrations even in similar soil types. Fertilizer recommendations are general for any region or area. This may lead to over- or underapplication of applied fertilizer materials, resulting in a decreased FUE. Moreover, a plant's nutrient requirement varies with growth stages. This demands site-specific fertilization depending upon soil physicochemical properties and crop species/varieties. Fertilization according to the need of the crop is one of the management options to improve FUE and reduce the risk of environmental contamination. Precision farming technology is a valuable tool to identify and correct site-specific crop nutrient deficiencies (Roberts 2008). In addition to crop monitoring, modern technologies such as leaf color charts, chlorophyll meters, and remote sensing are useful techniques to manage nutrient requirements by crops.

4.2 Crop-Specific Nutrient Management

Crop responses to applied fertilizers vary from specie to specie; variability even exists among different cultivars of the same species. For example, cereals demand more K compared to vegetables and other crops (Greenwood et al. 1980), whereas dicotyledons require more B than monocots (Neales 1960). Thus, application of these nutrients to such crops according to their requirement will result in more efficient utilization and reduced losses to the environment. A number of studies have been reported on genotypic variation among wheat, maize, cotton, brassica, and rice cultivars for different nutrients (Kanwal et al. 2009; Maqsood et al. 2009; Aziz et al. 2011a, b, 2014). Hence, application of fertilizers to crop cultivars that are not responsive and inefficient utilizers leads towards environmental pollution. Moreover, as a plant goes through different growth stages during its life cycle, certain stages are high-demanding compared to others. Hence, FUE can be improved by applying the nutrients at the right time and in the right amount, when there is actual need for that nutrient by the growing crop. Split application of N is also one of the management options to match the nutrient requirement with the crop demand. Ortiz-Monasterio et al. (1996) found about 50 % reduction in nitrous oxide emission from irrigated wheat crop while applying only 33 % of N fertilizer at planting and the remainder after 1 month.

Nature has bestowed an excellent mechanism in plants by which certain crop species/genotypes are more efficient utilizers of applied as well as indigenous soil nutrients. This may be attributed either to more efficient nutrient uptake or its rapid assimilation during metabolic processes. Roots play an important role in this regard. However, root growth is also restricted under high nutrient concentration (Shen et al. 2012). As FUE aims at obtaining more yield with the application of less fertilizer material, therefore nutrient application should be at the optimal rate at which root growth is maximum. However, under high input systems, FUE can also be improved by maximizing root proliferation in subsurface soils either through breeding or agronomic nutrient management practices (Mi et al. 2010; Lynch 2007, 2011). More root proliferation leads to more exploration of soil nutrient reserves, hence more nutrient uptake. Farmers can achieve better FUE by growing those cultivars that are efficient utilizers of applied as well as indigenous plant nutrients.

4.3 Fertilizer Materials

Fertilizer use efficiency can also be improved by changing the morphology of the fertilizer material either by coating or by increasing the size of the granule. Fertilizers vary in nutrient solubility, availability, and recovery. Fertilizers applied to one crop may have residual effects for subsequent crops. Only less than half of the applied P may be recovered by the first crop (Sattari et al. 2012), whereas most of N fertilizers are readily available to plants and mobile in the soil system. This leads to higher losses of applied N. Coated N fertilizers with controlled release of N can ensure a continuous supply of N to plants for longer periods (Mulder et al. 2011; Ni et al. 2011a, b; Xie et al. 2011; Yang et al. 2011).

Controlled/slow-release fertilizers for improving NUE from urea have also been practiced in many parts of the world. In addition, urease inhibitors were also introduced to minimize N losses from urea. A number of inorganic and organic urease inhibitors were tried in the past (readers are referred to the review by Chien et al. 2009). However, *N*-(*n*-butyl)thiophosphorictriamide (NBTPT) was found to be most effective compared to others such as phenylphosphorodiamidate (PPDA) (Byrnes 1988; Lu et al. 1989). NBTPT addition to soil resulted in 60 % reduction in ammonia volatilization losses compared to control where no urease inhibitor was applied (Cantarella et al. 2005). In addition, some other laboratory and field studies (Chien et al. 1988; Christianson et al. 1990; Freney et al. 1995) revealed that cyclohexylphosphorictriamide (CHPT) was even more effective than NBTPT. Combined nitrate and urease inhibitors were also tried to see their impact on improving FUE (Nastri et al. 2000; Radel et al. 1992; Zaman et al. 2005). However, until now urease inhibitors can delay NH_3 losses for only 1–2 weeks in the case of surface application of urea (Chien et al. 2009). Moreover, it also depends upon soil physicochemical properties coupled with moisture and temperature. Nevertheless, coating of urea with natural biodegradable polymers and micronutrients can also reduce N losses from 30 to 67 % (Junejo et al. 2011). In addition, the concept of urea supergranules has also been reported with some advantages over the routine application of normal granules. This will act as a slow-release fertilizer.

These controlled released fertilizers only partially reduce nutrient losses and further research is required to check nutrient losses by applying the right type of fertilizer. Therefore, research efforts must be directed towards cheaper and environmentally friendly fertilizers that have minimal nutrient losses and greater FUE. A number of new fertilizer products are now available to improve fertilizer use efficiency including sulphur-coated urea, slow-release fertilizers, smart fertilizers, and nitrification inhibitors.

4.4 Integrated Nutrient Management

Integrated nutrient management (INM) (i.e., combined use of organic and inorganic sources of nutrients) is also an important key to achieve higher FUE (Yamoah et al. 2002). Organic amendments not only improve soil fertility status but also result in improvement of soil physicochemical properties such as structure and nutrient and moisture retention, as well as porosity/aeration. However, while adding organic amendments to soil, their C:N ratio and mineralization rate should also be kept in mind (Treadweell et al. 2007).

Incorporation of legumes in crop rotation is also an integral component of INM. Legumes not only improve soil nutrient reserves but also improve soil physical properties helpful in root proliferation, hence more efficient nutrient uptake. Rahman et al. (2009) observed a significant increase in N use efficiency while incorporating broadbean and hairy vetch legume crops in a rice-based cropping system. INM by using green manures, animal manures, and crop residues reduces the fertilizer application rate along with reduced emission of N_2O (Aulakh 2010), hence more FUE. Long-term studies on INM in China were conducted in multilocation field trials for rice by Zhang et al. (2011). They observed 20–30 % reduction in fertilizer use coupled with 20–80 % increase in agronomic FUE. However, success of this INM system demands a comprehensive training of the farmers. Otherwise imbalanced use of nutrients will not only waste the resources but lead towards environmental contamination.

4.5 Method of Fertilizer Application

Nutrient losses can also be minimized by following proper application methods. Conventional fertilizer application methods such as broadcasting and side dressing are less efficient compared to fertigation and foliar fertilization techniques (Rehman et al. 2012). Nevertheless, it also depends upon specific mineral nutrient, crop species, and soil properties. For example, banded application of P to crops results in more P uptake compared to broadcast application. This improved P uptake might be attributed to reduced soil contact, hence less fixation of applied P fertilizers. Sitthaphanit et al. (2009) observed reduced leaching losses of N, P, and K by split application and delaying the basal application in a tropical sandy soil. N losses from urea and other fertilizers can also be minimized by its deep placement into the soil. Deep placement of urea supergranules is one of the best management options to improve FUE in flooded rice in Bangladesh and Vietnam (Roy and Hammond 2004). However, its application is laborious and costly, hence impracticable for developed countries of the world.

Unconventional methods of fertilizer application are also in practice in many parts of the world. Nutrients are applied directly to the leaves (foliar fertilization) or to the roots (drip fertigation) where they are actually required. It also involves reduced fertilizer and labor cost. Moreover, it will result in improved water use efficiency in arid and semiarid regions of the world. Liang et al. (2014) found that optimal daily fertigation is a better approach to improve cucumber yield and FUE under greenhouse conditions. Alam et al. (2005) conducted a study on wheat crop employing different N and P application methods and found 74 % increase in P fertilizer efficiency over top-dressed N and P. Fertigation results in improved N use efficiency as more NO_3 are present in the upper soil surface and NO_3 leaching losses to the groundwater decrease (Hebbar et al. 2004; Hou et al. 2007; Hassan et al. 2010). However, there are certain limitations that should be addressed before following these practices. In the case of fertigation, fertilizer material should not be corrosive and also not react with other chemicals in water. In addition, good quality water should also be used otherwise precipitation of salts will result in clogging the entire irrigation system. Therefore, generally fertigation is practiced for vegetable and fruit plants.

Foliar feeding of nutrients to plants is also a promising management strategy to improve FUE. With micronutrients that are generally required in small quantities, their uniform application to growing plants can also be carried out by foliar application. Dixon (2003) reported that foliar application of N and P is about 7 and 20 % more efficient compared to soil application of these nutrients. Foliar application of urea resulted in 80 % recovery of applied N in wheat crop (Smith et al. 1991). Foliar application along with the bed planting method resulted in improved agronomic efficiency, that is, about 93.82 % compared to conventional methods where it was only 43.67 % (Bhuyan et al. 2012). However, foliar fertilization of plants should be done at very low rates of fertilizer material otherwise leaf burning will result in crop damage. In addition, nutrient feeding through foliar application also demands a comprehensive knowledge of crop growth stage and nutrient demand.

4.6 Balanced Fertilization

Balanced nutrition is an important key to improve FUE. The major reason for low N use efficiency in many agricultural soils of the world is either high N input or low N input. In the case of high input agricultural systems, it leads towards the contamination of natural resources. Indeed N deficiency is ubiquitous throughout the world but in addition, certain other essential elements such as P, S, K, Zn, and B are also deficient. According to an estimate about half of the world's cereal-growing soils are Zn deficient (Cakmak 2002). Boron deficiency has also been reported in more than 80 countries worldwide (Shorrocks 1997). However, in many parts of the world mostly farmers apply N coupled with a nominal quantity of P fertilizer while ignoring the use of K and other macro- and micronutrients. This imbalanced fertilization results in a wider N:P ratio of about 7:1 to 6:1 (Vitousek et al. 2009). Furthermore, a very wide N:K ratio (i.e., 1:0.23 to 1:0.36) exists throughout the world (Krauss 2004). This practice is more common in developing countries and is one the major constraints to improve nutrient utilization efficiency in the existing cropping systems. As plants need 17 essential elements for their growth and development, so overuse of only one nutrient creates a strong imbalance and results in reduced NUE by plants. A number of studies reveal that addition of S, K, P, and Zn along with N results in enhanced N recovery from the applied fertilizer source, hence more FUE (Aulakh and Malhi 2004; Gordon 2005; Salvagiotti et al. 2009; Liu et al. 2012a, b, c). Dobermann et al. (2002) observed 30–40 % increases in N recovery efficiency of rice from balanced fertilization. More efficient recovery of nutrients from applied fertilizers will lead towards reducing the burden of contaminants on the environment.

5 Moisture Conservation and Water Management

Moisture conservation in rainfed areas by mulching and deep ploughing will enhance fertilizer efficiency. Similarly management of irrigation water at critical crop stages is also important to improve fertilizer efficiency.

6 Future Challenges

6.1 Limiting Resources of Rock Phosphate

Limiting raw material for fertilizer manufacturing further increases the importance of FUE. Rock phosphate is the only raw material for most P fertilizers. According to Global Phosphorus Research Initiative, reservoirs of rock phosphate are estimated to deplete completely in the next 100 years (GPRI 2014). This demands wise use of available rock phosphate and higher FUE (Cordell et al. 2011). Moreover, the only option when rock phosphate will not be available will be managing the P cycle while adding the required P rates in the form of organic matter (Dawson and Hilton 2011). Then this organic matter must be mineralized at a rate of crop P demand. Related strategies are already known and often listed under organic farming. However, organic farming is uneconomical in most developing countries due to lower crop yields and greater expense. A great number of scientists are working to find a suitable alternative technology for the days when rock phosphate will no longer be available. Plant breeding for better P uptake and use efficiency for a P-deficient environment is being advocated and efforts are underway; however, newly developed cultivars of agronomic crops actually require greater inputs of P fertilizer as increase in yield is often related to greater fertilizer demand.

6.2 Depleting Soil Fertility

Exhausting cropping systems are depleting nutrients from the soils (Foster and Magdoff 1998) and heavy fertilizer applications can damage the environment due to losses of nutrients. Also, higher fertilizer rates decrease FUE and may result in uneconomical yield if applied more than the crop demands. Restoration, maintenance, and buildup of soil fertility status require knowledge about various soil aspects (Palm et al. 1997; Sanchez et al. 1997; Lahmar et al. 2012). Due to imbalanced application of fertilizers, soil is more depleted in micronutrients as compared to macronutrients (Fan et al. 2008). For many cropping systems, workable strategies are still not known to maintain soil fertility and produce greater yield by taking into consideration soil and environmental health.

6.3 Soil-Specific Recommendations

It is recommended that fertilizers should be applied according to crop requirement and soil characteristics (Pierce and Sadler 1997). Soil- and crop-specific fertilizer recommendations take into account soil, crop, and environmental factors for greater nutrient recovery and yields (Swinton and Lowenberg-DeBoer 1998). The right type of fertilizer applied in the right amount, with the right method, and at the right time are important considerations of FUE (Bruulsema et al. 2008). However, there is a need for developing kits for determining site-specific crop nutrient deficiencies. This will be a great breakthrough in improving FUE and reducing the risk of environmental contamination of land, air, and water resources.

Soils differ greatly in physical, chemical, and biological characteristics. Therefore, plant-available pools of nutrients in soils also vary (Hussain et al. 2011). The native status of a particular nutrient in the soil is the most important factor controlling the required rate of fertilizer. Based on this approach, scientists have formulated critical concentrations of plant-available nutrients in soils. These critical limits are (in mg kg^{-1} soil): nitrate-N (extraction with AB-DTPA) >20, P (extraction with $NaHCO_3$) >15, K (extraction with NH4OAc) >150, Zn (extraction with DTPA) >1.0, Cu (extraction with DTPA) >0.5, Fe (extraction with DTPA) >4.5, Mn (extraction with DTPA) >2.0, and B (extraction with hot water) >1.0 (Watanabe and Olsen 1965; Mahler et al. 1984; Soltanpour 1985; Quevauviller et al. 1996). Depletion of nutrients from soil solution by plant uptake is restored from various other nutrient pools in soils (Viets 1962; Barber 1995). However, soil buffering capacity is partially ignored when recommending fertilizers on the concentration of plant-available nutrients in the soil. Therefore, FUE would differ if soil buffering capacity is sufficient to supply nutrients over a longer period of time.

Only soil P and K are investigated in detail by different adsorption and release models for soils. Reports suggest recommending fertilizer rates based on adsorption isotherms: however, this is limited to P and K only (Zhengli et al. 1988; Mehadi et al. 1990; Dobermann et al. 1996). However, recommendations based on adsorption isotherms are often too complex to be understood by farmers. Moreover, there are site-to-site variations among the fields of a farm and even within a single field. There is a demand for a more farmer-friendly and dynamic system of fertilizer recommendations that consider all soil characteristics. Efforts are underway to estimate site-specific fertilizer requirements by use of advanced technology (Mueller et al. 2001; Franzen et al. 2002; Mallarino and Wittry 2004). However, the desired success is still awaited.

6.4 Biofortification, Environment, and FUE

Biofortification of edible plant parts through genetic and agronomic means is being advocated on a large scale (Bouis et al. 2011). Biofortification strategies currently focus on seven mineral elements (Fe, Zn, Cu, Ca, Mg, I, and Se) that are most commonly deficient in human diets (White and Broadley 2009). Agronomic biofortification strategies require higher rates of fertilizer application to increase food quality (Hussain et al. 2013). However, the greater the nutrient applied, the lesser will be FUE and there will more environmental hazard.

Computations for FUE include amount of fertilizer applied, amount of nutrients uptaken by plants, and yield of the crop (Jat and Gerard 2014). Environmental considerations, food quality parameters, and actual farm profits are not considered in FUE. Nevertheless, these factors play a key role in suitability and profitability of fertilization (Prasad 2008). In future, new computations of FUE are required to include these factors. Farm profit can easily be calculated. However, the most challenging task is to quantify environmental hazards of fertilization in a given soil-crop-environment and management combination. Probably, the amount of nutrient lost in the atmosphere or water bodies is more hazardous for the environment as compared to the amount of fertilizer temporarily retained in the soil.

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