Impacts and Management of Temperature and Water Stress in Crop Plants

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Abstract

Plant growth and development are affected by various abiotic stresses like drought, submergence, salinity and high and low temperature. These abiotic stresses cause average yield losses of greater than 50% in a majority of crop plants. Food production needs to be doubled by 2050 to meet the growing demands of an increasing global population. Significant damage is being caused to crops, especially through temperature and water stress associated with climate change. High- and low-temperature stresses affect crop productivity by adverse biochemical changes in plants. Similarly, drought and water stress also affect the crop's performance throughout the growing season. Understanding plant responses and molecular and physiological changes occurring during these stresses is necessary to improve current cultivars and release new cultivars with enhanced resistance to such stresses. An overview of the impacts of high- and low-temperature stress, drought and submergence in plant growth and development and the physiological and molecular responses of plants is discussed. Strategies adopted by plants to overcome these stresses through avoidance and tolerance mechanisms are also briefly discussed.

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9.1 Introduction

Plants are sessile organisms and have developed the ability to survive at extreme environmental conditions that affect their development. Adverse environmental factors can limit crop production as much as 70% (Boyer 1982). Abiotic stresses like high/low temperatures, freezing, drought and salinity cause major losses to crop productivity worldwide. These stresses in crops are of major concern since these limit plant growth, metabolism and thus productivity. Average yield loss of greater than 50% is accounted for due to these abiotic stresses in a majority of crop plants (Bray et al. 2000). Recent changes in climate have aggravated abiotic stresses in plants, and two major factors threatening crop productivity are temperature and water. Increasing concentrations of greenhouse gases like CO_2, methane, chlorofluorocarbons and nitrous oxide are gradually increasing the average ambient global temperature (Wahid et al. 2007). As per IPCC (Intergovernmental Panel of Climatic Change), average global temperature may rise 1 and 3 °C above current temperature by 2025 and 2100, respectively (Jones et al. 1999). Increase in temperature causes heat stress and very low temperatures cause chilling and freezing stress in plants. Plants undergo extensive reprogramming at cellular and molecular level to tolerate low temperatures, and this affects plant growth and productivity (Conroy et al. 1994; Yadav 2010). These extreme conditions affect growth and developmental processes of plants by altering the morphology, physiology and biochemistry of plants at the cellular and whole plant level (Seneweera et al. 2005). However, some plants have adopted survival mechanisms through avoidance and tolerance to heat and cold stresses.

Only 2% of fresh water is available for consumption (Shiklomanov 1993). The availability of natural water resources for day-to-day consumption and agricultural purposes varies with the location and the season of the year. Seasonal changes, as well as unexpected changes, in water availability create problems for sustainability in agriculture. Excess and limited availability of water causes submergence and drought, respectively. According to UNCCD, 12 million hectares in the world are lost due to drought or desertification annually. Further, excess water affects 15 million hectares or more lowland rice-growing areas in South and Southeast Asia. Both limited and excess water cause stress to plants and limit their productivity. Knowledge of the physiological and molecular responses of plants to these stresses and their tolerance mechanisms is essential for improving crop resistance and thereby increasing productivity (Fernando et al. 2016). An overview of plant response to temperature and water stresses in terms of physiological and molecular aspects, strategies adopted by plants to alleviate these stresses and biotechnological approaches to overcome such stresses is presented in this chapter.

9.2 High- and Low-Temperature Stress

Temperature above and below the optimum hinders the growth and development of crop plant and is considered as heat and cold stress, respectively (Kotak et al. 2007). Heat stress can be lethal and lead to major crop losses. Severe losses due to heat waves were observed in the USA during 1980 and 1988 and caused a total loss of 55 and 71 billion dollars, respectively (Lobell et al. 2011; Mittler et al. 2012). Heat stress affects all crop plants; in wheat, grain yield loss of 3–5% was observed when wheat was grown at one-degree increase in average temperature above 15 °C under controlled environments (Gibson and Paulsen 1999). Rice, a staple food of Asian countries, is also highly susceptible to high-temperature stress. About 3 million hectares of rice cultivation was affected by heat stress in China in 2003 causing a total loss of 5.18 million tons of yield (Peng et al. 2004). There has been a continuous increase of 0.13 °C in global average temperature per decade since 1950. An increase of 0.2 °C per decade for the next two to three decades is expected globally (Lobell et al., 2011). In Australia, by 2030, the annual mean temperature will be increased by 0.2–4 °C (Zheng et al. 2012). Low-temperature stress (LTS) also affects plant growth and crop production. Substantial loss due to LTS accounts for $2 billion each year. In some cases, cold stress may not cause yield losses; however, it may result in reduced quality. One of the major losses due to LTS was accounted for in 1995 during early frost events in the USA costing $1 billion loss in corn and soybean crop cultivation (Sanghera et al. 2011). In Australia, frost events cause major losses in wheat cultivation especially when it strikes the crops at the reproductive stage (Frederiks et al. 2012).

9.2.1 Growth Effects

Heat stress and low-temperature stress affect seed germination, photosynthesis, reproductive development and yield. It also results in oxidative stress (Hasanuzzaman et al. 2013a). In rice, seed germination is influenced by high- and low-temperature stress. Mild heat stress caused due to a slight increase in temperature causes delayed germination. However, extreme temperature stress (heat and cold) might inhibit the seed germination completely, and this is called as thermo-inhibition (Fig. 9.1; Takahashi 1961). At plant level, especially in crop plants like rice and wheat, heat stress during reproductive stages is more detrimental than during the vegetative stage (Wollenweber et al. 2003; Xie et al. 2009). Rise in temperature by 1–2 °C more than the optimum affects grain filling in crops by shortening the period of filling and so affects the yield in cereals (Hasanuzzaman et al. 2013a). In wheat, optimum temperature for anthesis and grain filling is about 12–22 °C, and any increase in temperature above this affects grain filling and grain size (Farooq et al., 2011). In rice, HTS during grain filling causes spikelet sterility and also reduces the duration of the grain-filling phase resulting in yield reduction (Fig. 9.1; Xie et al. 2009).

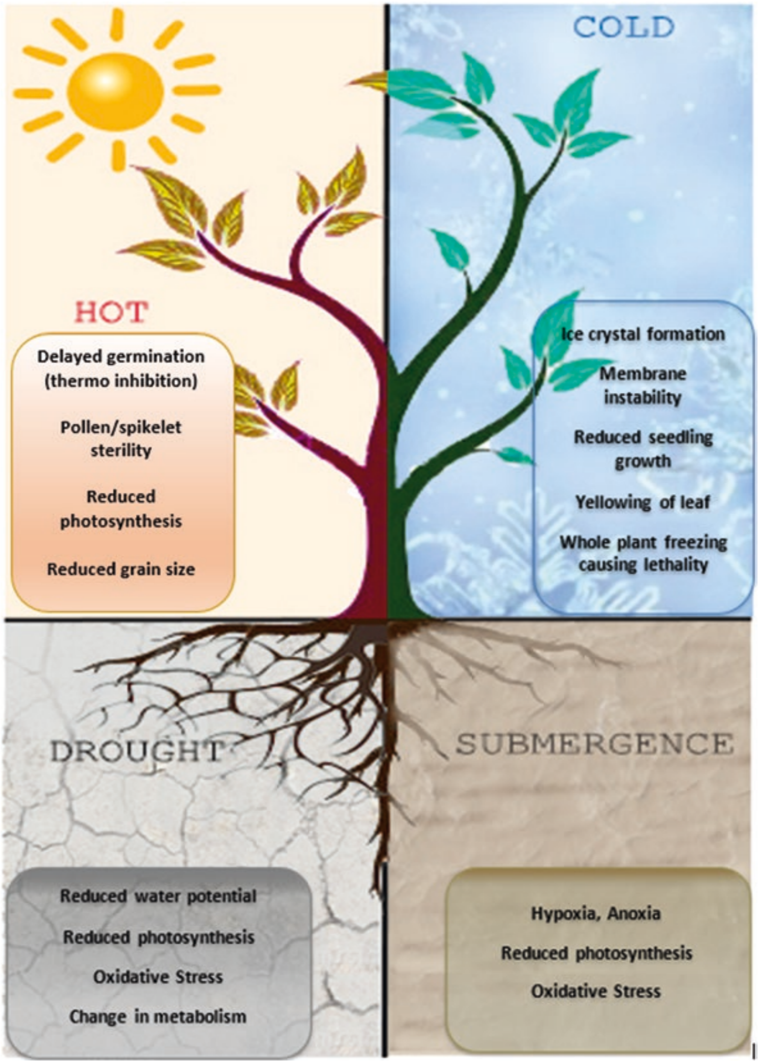

Fig. 9.1 Effects of temperature and water stress in plants. High (hot) and low (cold) temperature and excess (submergence) and scarcity of water (drought) are stresses that affect crop productivity and yield. Cellular and physiological effects of these stresses are summarised in this picture

Low-temperature stress (LTS) can be classified into two categories, freezing and chilling stress. Chilling stress is caused by exposing plants to low temperatures (0–15 °C) that injures the plant but does not form ice crystals, whereas freezing stress is caused by exposing the plants to temperatures below 0 °C that causes injury by ice crystal formation (Fig. 9.1). LTS also affects plants at different growth stages leading to reduction in growth and yield (Hasanuzzaman et al. 2013b). LTS mainly affects early stages of plant growth especially the seedling stage. Injuries caused by

LTS during seedling stages are discoloration and reduction in seedling growth, whitening and yellowing of leaf and failure to grow after transplantation (Buriro et al. 2011; Hasanuzzaman et al. 2013b).

Frost is a major low-temperature stress especially in Australia that hinders barley, wheat and legumes like field pea, fava bean, lentil and chickpea cultivation. Damage caused to agricultural crops mentioned above, post-head emergence or pod emergence, is economically significant (Frederiks et al. 2012). Radiant frost is witnessed when crops are grown in spring with optimum day temperature but experience rapid fall in temperature during nights. Consequently, rapid radiation occurs resulting in a super cooling effect that drops the plant canopy and actual plant temperatures to as low as −5 °C. This causes whole plant freezing resulting in plant death (Frederiks 2010).

9.2.2 Physiological Aspects

High-temperature stress (HTS) affects the plants at different growth stages resulting in physiological impairment and thus reduced growth. Photosynthesis is one of the physiological processes affected greatly by heat stress (Fig. 9.1). In wheat crops, excessive heat damages chlorophyll by altering the structural organisation of thylakoids thereby affecting its functionality and also by reducing the chlorophyll content (Xu et al. 1995). Similar damages of heat stress to the photosynthetic apparatus and process are observed in rice (Xie et al. 2009).

Excessive heat also decreases the photosynthetic pigments, which in turn affects photosynthesis (Cao et al. 2009). Further, excess heat induces water loss from the leaf, negatively affecting leaf water potential resulting in closure of stomata. This is one of the major phenomena affecting photosynthesis under heat stress. In *Vitis vinifera*, about 15–30% of photosynthesis reduction during heat stress was caused by stomatal closure (Fig. 9.1; Greer and Weedon 2012). HTS affects the reproductive health of crops; exposure to high temperatures during flowering affects its fertility due to impaired pollen and ovary development. HTS causes water loss in cells, which impairs cell size resulting in reduced growth in crop plants. At extreme HTS conditions, plants undergo programmed death of cells and tissues as a result of water loss and denaturation of proteins and enzymes (Hasanuzzaman et al. 2010).

LTS also causes damages in crop plants similar to HTS. LTS causes ice crystal formation in the apoplasm of cells in the leaves which results in cellular dehydration. This in turn results in stomatal closure and affects the cellular homeostasis in plants (Hasanuzzaman et al. 2013b). Cellular dehydration in roots resulting from LTS leads to osmotic stress caused by water imbalance in the cells (Chinnusamy et al. 2007; Hasanuzzaman et al. 2013b). LTS also affects photosynthesis by damaging the organisation of chlorophyll and thylakoids similar to heat stress (Fig. 9.1; Hasanuzzaman et al. 2013b). Stability and structure of the plasma membrane are affected due to cellular dehydration and chemical instability of its lipid components (Yadav 2010).

9.2.3 Plant Responses and Tolerance

HTS for short and long periods can affect morphology and physiology and induce biochemical changes in plants depending on the developmental stage, leading to reduced growth and yield. Crop plants subjected to high temperatures over long periods of time exhibit symptoms like scorching of leaves and twigs; sunburns on leaves, branches and stems; leaf senescence and abscission; shoot and root growth inhibition; fruit discoloration and damage; and reduced yield (Wahid et al. 2007). High temperature can lead to shortening of the life cycle of plants. Mild changes in temperature may induce changes in membrane properties and activate calcium channels. Calcium signalling leads to alteration in plant metabolism resulting in acclimation to mild heat stress. However, if plants are subjected to high-temperature stress for prolonged periods, they produce ROS (reactive oxygen species) inducing oxidative stress throughout the plant (Mittler et al. 2012). Harmful ROS like singlet oxygen (O^{2-}), superoxide (•O2), hydroxyl (OH^{-1}) and hydrogen peroxide (H_2O_2) are produced. These react with proteins, DNA and all the components of the cell disturbing cellular homeostasis (Asada 2006; Moller et al. 2007). Heat stress-induced oxidative stress is very damaging and causes protein degradation and membrane instability (Hasanuzzaman et al. 2013a). Excess accumulation of ROS in the plants induces programmed cell death and damages the whole plant (Qi et al. 2010).

Survival mechanisms of plant to HTS can be classified into avoidance and tolerance. Avoidance of HTS can be short term by altering the leaf orientation and membrane lipid composition or transpirational cooling, or it can be long term with morphological and phenological adaptations (Hasanuzzaman et al. 2013a). Plants also adopt escape mechanisms to HTS by reducing their life cycle through early maturation; however, this causes yield reduction (Rodríguez et al. 2005; Hasanuzzaman et al. 2013a). Ability of plants to grow, survive and produce economic yield at HTS is termed as tolerance. Tolerance of plants may also be classified as short and long term. Short-term tolerance mechanisms include morphological and anatomical changes. At molecular level, HTS induces heat stress transcription factors which in turn induce production and accumulation of HSPs (heat shock proteins) and other heat-induced transcripts as molecular chaperones to protect plant metabolism (Mittler et al. 2012). Plants produce antioxidants to counteract the damaging effects of excess ROS accumulated due to HTS. Various enzymatic and non-enzymatic ROS scavengers are synthesised, and these detoxify the plant system and prevent programmed cell death.

Temperature that causes cold stress varies from one plant to another. Optimal temperature for one plant might cause cold stress to others. However, whenever a plant experiences cold stress, it responds by showing various phenotypic and physiological symptoms. Phenotypic symptoms include stunted plant growth, bushy appearance, reduced leaf expansion, chlorosis of leaves, wilting and even necrosis at severe conditions. LTS at the time of reproductive development leads to sterility in plants (Hasanuzzaman et al. 2013b). In fruit crops, extreme cold stress induces excessive fruit drop and fruit cracking (Yang et al. 2010). At the cellular level, cold stress induces ice crystal formation resulting in dehydration of the cell. Ice crystals are lethal to cells since it damages the cell membranes. LTS also induces oxidative stress by excess ROS accumulation leading to programmed cell death (Hasanuzzaman et al. 2013b).

Plants adapt to cold stress by certain avoidance and tolerance mechanisms. One of the major effects of cold stress in plants is membrane disintegration. Cold stress in plants reduces the fluidity of membranes resulting in rigid membranes. This membrane rigidification enhances cold acclimation in plants by inducing cold-responsive genes. Similar to HTS, calcium signalling and antioxidants play an important role in tolerance to LTS in plants. Further, plants tolerate or recover from cold stress through repair mechanisms, restructuring the plasma membrane and accelerating osmolite synthesis (Yadav 2010; Hasanuzzaman et al. 2013b).

9.2.4 Management Strategies

Employing a combination of genetic improvement and cultural practices can alleviate impacts of heat and cold stress in plants. Cultivars that endure and tolerate these stresses without any economic loss in yield can be developed through genetic improvement. Cultural practices include adjusting and modifying planting time and planting density of plants to avoid these stress conditions (Wahid et al. 2007; Hasanuzzaman et al. 2013b). Other practices include external application of protectants like osmo-protectants, phytohormones, signalling molecules and trace elements that can protect during adverse conditions especially during HTS (Hasanuzzaman et al. 2013a).

Cultivars that are tolerant to high- and low-temperature stresses can be identified through proper screening methods and selection criteria through conventional breeding techniques in fields. However, other stress factors like pathogens and pests could be a hindrance in identifying resistant cultivars in the field. Glasshouse screening could be used as an alternative for field screening; nonetheless, certain factors like low genetic variation and unreliable selection criteria make it difficult to identify heat- or cold-tolerant varieties (Wahid et al. 2007; Hasanuzzaman et al. 2013b). Quantitative trait loci (QTL) associated with heat stress-tolerant traits have been identified in wheat, rice and maize (Talukder et al. 2014; Yang et al. 2002; Frova and Sari-Gorla 1994; Collins et al. 2008). These traits were associated with the reproductive stage of growth in plants (Collins et al. 2008). QTLs associated with resistance to chilling at seedling stage have been identified in crop plants like maize, sorghum, rice and tomato (Presterl et al. 2007; Lou et al. 2007; Goodstal et al. 2005; Knoll and Ejeta 2008). Loci associated with freezing tolerance at vegetative phase of plant growth have been identified across *Triticeae* species and also in *Arabidopsis* model plant (Alonso-Blanco et al. 2005; Båga et al. 2007; Collins et al. 2008). Very little is known about the QTLs for cold tolerance associated with the reproductive phase of crop plants (Collins et al. 2008).

Recent advances in biotechnology approaches have paved the way to develop high- and low -temperature-tolerant crops through genetic modification. Transgenic crops expressing heat shock proteins and heat shock transcription factors have increased heat tolerance in many crops like maize, rice, carrots and tobacco (Hasanuzzaman et al. 2013a). Manipulating the expression of small non-coding RNAs especially microRNAs could also increase heat tolerance and alleviate heat sensitivity in crop plants. Genetically modified crops expressing antifreeze proteins from winter flounder fish in wheat have shown increased frost tolerance characteristics. Antifreeze proteins bind to growing ice crystals in the cell and inhibit its growth increasing the tolerance of plants to freezing (Khanna and Daggard 2006).

9.3 Drought and Submergence Stress

Both water scarcity and excess water affect plant growth, development and production. Severity and duration of each stress determine the total production loss in agriculture. According to UNCCD, 12 million hectares in the world are lost due to drought or desertification annually. This land extent reduces 20 million tons of annual grain production for consumption (http://www.unccd.int). IPCC reported that global temperature would be raised by an average of 1.1–6.4 °C by the end of the twenty-first century which would increase the area under extreme arid lands by 1–30%. On the other hand, under the climate change context, annual rainfall patterns have changed, and excess water affects 15 million hectares of lowland rice-growing areas in South and Southeast Asia.

9.3.1 Physiological Aspects

Drought reduces water potential of the leaves by changing the cell's turgor pressure. Less water in the plant induces ABA production that leads to stomatal closure. This reduces CO_2 assimilation affecting the photosynthetic machinery in thylakoids of the mesophyll cells, which are the source of fluorescence signals. Cell peroxidation damage occurs in the drought-stressed plants with the accumulation of reactive oxygen species, namely, singlet oxygen (O^{2-}), superoxide ($\bullet O_2$), hydroxyl (OH^{-1}) and hydrogen peroxide (H_2O_2). Further, there is a reduction in the electron transport rate that creates oxidative stress reducing the photosynthetic capacity of the plants under drought stress. Changes in metabolites such as sugars, acids and carotenoids under drought stress directly affect the quality of the plant's end product (Ripoll et al. 2016).

Unpredicted waterlogging caused by heavy rains followed by poor drainage is a serious problem in a changing climate scenario. Under waterlogging conditions, soil gets saturated, and under submergence stress, the plant is partially or completely covered by the water body. In both instances, soil becomes anaerobic, and under anaerobic conditions, soil produces toxic components and emits different gases to the environment. These conditions accelerate plant death.

Diffusion of gases such as O_2, CO_2 and ethylene is reduced under submergence stress. Hypoxia and anoxia conditions under submergence stress are critical for plant growth (Fig. 9.1). Hypoxia is the low diffusion of O_2 to the roots under water through the plant canopy, which is above the water level. Anoxia is the total absence of O_2 to the root system due to complete submergence of the whole canopy (Lone et al. 2016). Reduction of O_2 diffusion under water hampers aerobic respiration. Anaerobic respiration produces the required energy for the plants at anoxia once aerobic respiration is arrested (Pradhan 2016). Fermentation enzymes are required for anaerobic respiration, and it produces different metabolites that maintains the stability of pH in the cell contents.

When photosynthesis is affected by less gas diffusion and poor light penetration, unavailability of soluble sugars decreases the activity of the glycolytic pathway. When the plant is able to survive utilising stored food reservoirs or using anaerobic respiration till the water recedes, the plant must be regrown in an aerated environment. The strong reactive oxygen species (ROS) are produced in plants under aerated environment upon de-submergence. Antioxidant mechanisms are required for the survival of the plant in the presence of ROS (Xu et al. 2010).

9.3.2 Plant Response and Tolerance

Plant response to water stress is a complex mechanism controlled by gene expression followed by biochemical metabolism through varied physiological processes. Leaf area, plant height, biomass and dry matter production are the morphological growth indices affected by drought stress. These indices and physiological traits such as photosynthetic efficiency, maximum quantum yield, photochemical and non-photochemical quenching, gas exchange measurements, stomatal conductance, relative water content and malondialdehyde (MDA) content are considered in the evaluation of drought stress of the plants (Sairam et al. 1998; Yousfi et al. 2016). Plants use different mechanisms like acceleration of life cycle; development of water absorption and retention mechanisms or organs within the plant; osmotic, metabolic and morphological adjustments; and genetic modifications to avoid, tolerate or overcome drought stress.

Under submergence stress, plants change their architecture depending on the type of flood. Complete submergence stress is the condition where plants are completely covered by floodwater for a considerable period of time. With the quiescence strategy, plant growth is arrested to conserve energy so it can be utilised once the water recedes. This strategy is important for tolerance under complete submergence stress. If the plant remains submerged for a long period, it will die upon complete depletion of food reserves. Elongation growth is a strategy used by plants to keep the canopy above the water level and is associated with tolerance under flash flooding where the water level increases suddenly but is not retained for a longer period to cover the plant canopy completely. However, if all the food resources were depleted before the canopy emerges from the water body, it would cause the death of the plants.

There is a natural multifaceted alteration in plant anatomy and metabolism to function under low O_2. The arrangement of soft tissues to provide space and a continuous gas channel for facilitation of an internal O_2 pathway from the canopy to the root system is called aerenchyma (Bailey-Serres and Voesenek 2008). Ethylene stimulates aerenchyma formation and root growth under submergence stress. Metabolic adjustment under submergence stress is driven by various plant hormones such as ethylene, gibberellin and abscisic acid. Finally, factors such as ATP production under limited O_2 diffusion, management of cytosolic pH due to the accumulation of various metabolites, effects of the reactive oxygen species produced under anaerobic conditions, the persistence of the antioxidant mechanism and aerenchyma development decide the fate of the plant under submergence stress.

9.3.3 Management Strategies

Evolution of plants under drought conditions has created drought-tolerant plants. Selection of such plant types for cultivation was practised in the early days. However, low heritability, polygenic nature of the trait, epistasis and genotype-by-environment interactions were the limitations of this type of selection. Later, selected plant materials were bred with elite lines for the production of better cultivars, but the complexity of drought tolerance mechanism hampers the breeding for drought tolerance.

QTL analysis reveals the segments of chromosomes determining the variation of the considered agronomic or physiological trait. Tightly linked markers to the prominent QTLs are used in marker-assisted selection in agriculture. The accuracy of QTL mapping and marker density of the genetic linkage map determines marker-assisted QTL efficiency (Cattivelli et al. 2008). The polygenic nature of drought tolerance, impact of a single chromosomal location and environment interaction of QTL determine the overall success of the breeding program. Finding QTLs related to yield and stress tolerance is much more promising in marker-assisted selection since the tolerance trait and its relationship with the yield would not be strong.

Many drought-tolerant genes have been identified in various studies. On the other hand, the complexity of the drought-tolerant transcriptome has also been revealed. The mechanism of drought tolerance has been studied further by leveraging the information from *Arabidopsis* a model plant to other crops by genome synteny. Metabolic engineering or overproduction of desired metabolites for the tolerance of the stress is another approach in improving plants for stress tolerance. Plant gene transformation techniques are important to introduce tolerant/resistant genes into genomes of elite breeding lines. Inoculation of plant growth-promoting bacteria is another attempt to overcome drought stress.

Natural variation in submergence tolerance can be seen within crop species including their wild, weed or landraces. Finding new genetic materials with substantial tolerance to submergence is needed to broaden gene pools of modern crops. Submergence tolerance of a crop species varies with the developmental stage, flooding intensity and duration. Finding tolerant materials according to stress level is a must in the development of submergence tolerance in plants. A strong submergence-tolerant QTL in rice, *Sub1*, is presently utilised as a marker for assisted breeding and gene transformation (Neeraja et al. 2007). *Sub1* suppresses plant elongation under submergence stress. Finding such QTLs or genes with different tolerant mechanisms is needed to fill the gaps in submergence tolerance at different growth stages under varying stress conditions in crops.

9.4 Conclusion

Abiotic stresses due to temperature and water are being amplified as a consequence of climate change. To overcome this problem and meet the global demand for food, tolerant crops must be selected or developed through appropriate technologies. Physiological aspects, mechanisms of tolerance and management strategies for better crop production must be thoroughly studied to effectively use such technologies.

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