14 Effects of Ultraviolet-B Radiation and Its Interactions with Climate Change Factors on Agricultural Crop Growth and Yield

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Abstract Crops are often exposed to multiple factors of climate change including: (1) enhanced ultraviolet-B (UV-B) radiation, (2) elevated carbon dioxide concentrations (CO_2), and (3) episodes of elevated temperatures and water stress during critical stages of crop development. Our understanding of crop responses to individual climate change stress factors has significantly advanced in recent years. However, crop responses to a combination of stress factors are less understood and need attention. In addition to direct effects on various physiological, growth, and yield traits of plants, the interaction of plants with biotic factors (particularly insects and pathogens) will play an important role in determining crop productivity. The objective of this chapter is to provide a summary of crop responses to UV-B, CO_2, temperature, drought, and a combination of multiple stresses. Exposure to above ambient UV-B radiation decreases crop productivity through negative effects on photosynthesis, growth, dry matter production, yield, and grain quality. Elevated CO_2 often improves photosynthesis, growth, and yield of most crop species. Alternatively, exposure to both above optimum temperatures and water stress significantly decreases crop productivity and quality, particularly when stress occurs during sensitive stages (reproductive phase) of crop development. The positive effects of elevated (CO_2) on photosynthesis and growth do not generally overcome the negative effects of UV-B radiation, elevated temperatures, or water stress on productivity and quality of grain crops. Crop species and cultivars within crop species vary in their responses to both individual and a combination of stress factors, suggesting a scope for genetic improvement. Further research should be focused on breeding for tolerance to multiple stresses of regional and local importance. An increased knowledge of crop responses to multiple stresses and genetics may also improve crop simulation models resulting in a better understanding, prediction and management of crops in a changing environment.

Keywords climate change, crop growth and yield, drought stress, genetic variability, multiple abiotic stresses, temperature

14.1 Introduction

The growing population of today's world (6.7 billion, U.S. Census Bureau, 2008) faces great challenges due to limited resources for the production of adequate amounts of food, fiber, feed, industrial products, and ecosystem services. As the global population increases by nearly 80 million each year, policies must be developed to ensure the needs of a future population of 8 billion by 2025 and more than 12 billion by 2050 (U.N. Population Division, 2008) are met. About 84% of this growth is expected to occur in developing countries. Since there is essentially no new arable land that can be cultivated, the increased food supply must primarily come from more intensive cultivation of existing arable land. Furthermore, with intensive agriculture, soil degradation will become a major concern. The world's water resource is also finite, and the increased demands will result in reduced availability of water for agriculture. Urban communities do not generally give high priority to the preservation of agricultural resources, such as land and water. In many highly populated countries, food and fiber needs are being met by irrigating up to 75% of the arable land and introducing high yielding cultivars of most grain crops that have higher input use efficiency thus maximizing production. In addition, the benefits humans derive from natural ecosystems, such as marketable products and goods (i.e., timber, fish, pharmaceuticals), recreational opportunities (i.e., camping, boating, hunting, hiking, fishing), maintaining biodiversity, aesthetic and spiritual experiences, and other services (i.e., erosion control, water purification, carbon sequestration, oxygen production), are being threatened by the growing human population through habitat destruction and air and water pollution. In addition to these stresses, there is a threat of global climate change due to increased greenhouse gas concentrations in the atmosphere and the depletion of the ozone layer assumedly due to anthropogenic activities.

Climate change is not a new phenomenon. The planet's climate has changed tremendously over geological time, and the changes are still occurring. However, what appears to be different is the possibility of a new driving force and the cause of the climate change. Changes that were observed over a geological time period now occur over a shorter time span, particularly since the beginning of the industrial revolution. Apparently, human activities are causing climate change. Concentrations of key anthropogenic greenhouse gases, such as carbon dioxide (CO_2), methane (CH_4), nitrous oxide (N_2O), and tropospheric ozone (O_3) have reached their highest levels ever, primarily due to the combustion of fossil fuels, agriculture, and land-use changes. Pre-industrial concentrations of CO_2, CH_4, and N_2O were about 280 ppm, 700 ppb, and 270 ppb, respectively. Ozone depleting chemicals, such as chlorofluorocarbons (CFC-11) and hydrofluorocarbons (HFC-23), did not exist during that period, and perfluoromethane was about 40 ppt. The current CO_2 concentration is about 380 ppm (increasing at the rate of 1.9 ppm/year), CH_4 is about 1745 ppb (7.0 ppb/year), and N_2O is about 314 ppb (0.8 ppb/year) (IPCC, 2007). Even if we curtail emissions today, these gases will stay in the atmosphere for a long time as the atmospheric lifetimes for these chemicals vary (5 to 200 years for CO_2, 12 years for methane, and 114 years for N_2O). These changes in the atmospheric chemistry are causing the so called "greenhouse" effect (Fig. 14.1(a)).

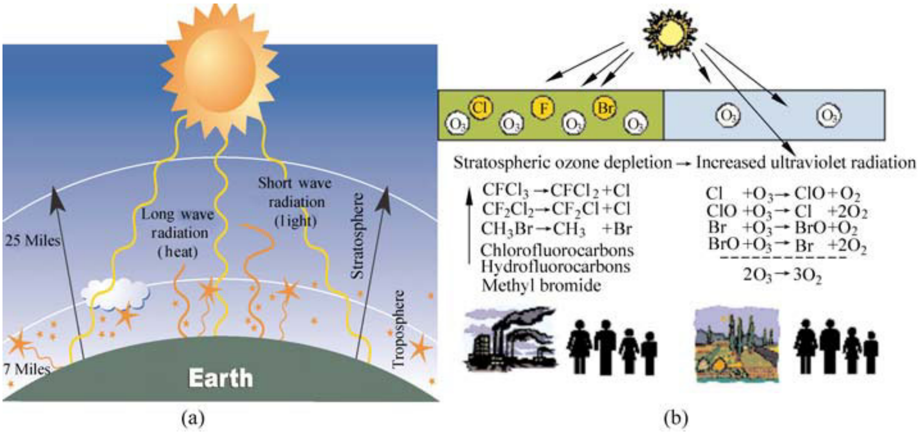

Figure 14.1 Process of global warming (a) and stratospheric ozone depletion (b). Long wave radiation is absorbed by various greenhouse gases in the atmosphere leading to increased temperatures. Anthropogenic emissions of chlorofluorocarbons (CFCs), hydrofluorocarbons, and bromocarbons released in the troposphere move up into the stratosphere. Upon exposure to radiation, atomic chlorine or bromine is released; these react with ozone and convert into oxygen, leading to depletion of ozone. Stratospheric ozone depletion leads to an increase in UV radiation reaching the earth's surface. Adapted with permission from Prasad et al. (2003b)

As the sun's energy passes through the atmosphere and warms the earth's surface, some is reflected back into the atmosphere and dissipates into space. The greenhouse effect refers to accumulation of specific gases that absorb the reflected radiation, effectively trapping heat in the lower atmosphere similar to what occurs in a glasshouse. The most important heat trapping gases are CO_2, water vapor, CH_4, N_2O, CFC-11, and ozone.

If current greenhouse gas emission rates continue, both agricultural and natural ecosystems will face enormous pressure from the stresses caused by these heat trapping gases. Past changes have presumably resulted in an increase in global temperature of about 0.6℃ over the last century. Climate models project even greater warming during the 21st century. The CO_2 concentration is projected to reach 405 ppm to 460 ppm by 2025, 445 ppm to 640 ppm by 2050, and 720 ppm to 1,020 ppm by 2100 (IPCC, 2007). The projected global mean temperature increases (above values in 1990) for those CO_2 stabilization scenarios are 0.4℃ – 1.1℃ by 2025, 0.8℃ – 2.6℃ by 2050, and 1.4℃ – 5.8℃ by 2100. Similarly, the projected mean sea level rise for these same periods is 3 cm – 14 cm, 5 cm – 32 cm, and 9 cm – 88 cm, respectively. These changes in climate were unprecedented during the last 10,000 years. It is also projected that all land areas will warm more rapidly than the global average, particularly at high northern latitudes in the cold season. Projections additionally indicate there will be more hot days, fewer cold days, cold waves, and frost days, and a reduced diurnal temperature range with higher nighttime temperatures. As the world becomes warmer, the hydrological cycle will also become more intense, resulting in more uneven and intense precipitation. This will result in increased summer drying and an associated risk of both droughts and floods. The projected climate change will have both beneficial and adverse effects on environmental as well as socioeconomic systems, but the larger and more abrupt climate changes will cause more adverse effects to be more damaging, particularly on seed-bearing plants.

In addition to the greenhouse effect, another phenomenon known as "ozone hole" is occurring. Ozone, a form of oxygen, plays two roles in the atmosphere. Near the ground, ozone is an air pollutant and a minor greenhouse gas that damages human health and the environment. In the upper atmosphere, known as the stratosphere (10 miles to 30 miles above the earth's surface), ozone forms a layer that helps protect life on earth from the ultraviolet (UV) radiation; sun's harmful rays. The term "ozone hole" refers to the thinning of this layer due to chemical reactions in the stratosphere, especially at higher latitudes, that are caused by the release of ozone-depleting chemicals known as halocarbons (Fig. 14.1(b)). The rate of change in chlorofluorocarbons (CFC) has declined due to the agreement of member countries to the guidelines proposed by the Montreal Protocol. Nonetheless, the concentrations are still high (268 ppb), and other chemicals, such as HFC-23 and perfluoromethane, are present at about 14 ppt and 80 ppt, respectively. Atmospheric concentrations of many of these gases are either decreasing or increasing in response to reduced emissions under the regulations of the Montreal Protocol and its amendments. However, the resident atmospheric times for these chemicals vary greatly (45 years for CFC-11, 260 years for HFC-23, and more than 50,000 years for perfluoromethane), and will have long-term effects on climate systems. Thus, the ozone layer within the stratosphere has thinned substantially, resulting in an increased ground-level UV radiation of about 35% from the pre-industrial period.

There are strong chemical interactions between greenhouse gases and ozone. Ozone and CFCs are minor greenhouse gases. Several gases involved in the ozone depletion chemistry are also greenhouse gases. For example, water vapor,

CH_4, and N_2O can ultimately lead to increases of stratospheric gases (such as NO_2), which can catalytically destroy ozone. It is predicted that increases in greenhouse gases could delay recovery of ozone and may even lead to increased ozone depletion late in the current century (Randeniya et al., 2002; McKenzie et al., 2003). Another chemical feedback is concerned with decreased stratospheric temperatures that could occur as a result of future global warming at the earth's surface. This will tend to slow reactions that destroy ozone at mid-latitudes and thus, may facilitate recovery of the ozone layer (Rosenfield et al., 2002). Ozone depletion at high latitudes proceeds much more rapidly through heterogeneous chemistry on the surfaces of ice and acid crystals that occur when temperatures are below a critical threshold which could be influenced by global warming and delay ozone recovery in the polar region. Several radiative feedback processes also exist (McKenzie et al., 2003). Increases in temperature can lead to changes in cloud cover, rainfall patterns, ice accumulation, and surface albedo. Similarly, radiative changes caused by stratospheric ozone depletion have offset some global warming effects, and could, in the event of future ozone recovery, exacerbate future global warming. Interactions between ozone depletion and global warming are complex. It is suggested that although current ozone depletion is dominated by chlorine and bromine (Fig. 14.1(b)) in the stratosphere, in the longer term (~100 years), the impact of climate change will dominate through the effects of changes in atmospheric dynamics and chemistry (McKenzie et al., 2003).

The main consequence of ozone depletion is increased UV radiation reaching the earth's surface. Ultraviolet radiation is an electromagnetic form of energy that comes from the sun. This energy is classified into several regions based on wavelength, which is measured in nanometers (nm). One nanometer is a millionth of a millimeter. The shorter the wavelength is, the greater the energy of the radiation. The main components of radiation in order of decreasing energy are gamma rays, X-rays, UV, visible light, infrared radiation, microwaves, and radio waves. Ultraviolet radiation is further divided into three categories based on wavelength: UV-A (between 320 nm and 400 nm); UV-B (between 280 nm and 320 nm); and UV-C (between 200 nm and 280 nm). Calculations based on relations with total ozone and total irradiance suggests that UV irradiance has increased since the early 1980s by 6% – 14% in middle and high latitudes of the northern and southern hemispheres. It is projected that every 1% decrease in ozone will increase UV exposure by 2% – 3% in the lower atmosphere.

Shorter wavelength radiation causes more damage to biological systems. UV-A is the least damaging component within the UV spectrum and reaches the earth's surface in large quantities. Both UV-B and UV-C are very harmful. Most UV-C radiation is absorbed by ozone, rarely reaching the stratosphere and never reaching the earth's surface. UV-B radiation is most likely to reach the earth's surface with increased ozone depletion. Factors, such as altitude, latitude, and time of day, influence the amount of UV-B exposure. Current global terrestrial UV-B radiation levels range between 0 and 12 kJ m^{-2} on a given day with near

Equator and mid-latitudes receiving higher doses (Total Ozone Mapping Spectrometer, 2009, http://toms. gsfc. nasa. gov/ery_uv/euv_v8. html). Small increases in solar UV-B radiation can have substantial effects on plants at both the cellular and the whole-plant levels. Relationship and plant responses to various climate change factors are illustrated in Fig. 14.2.

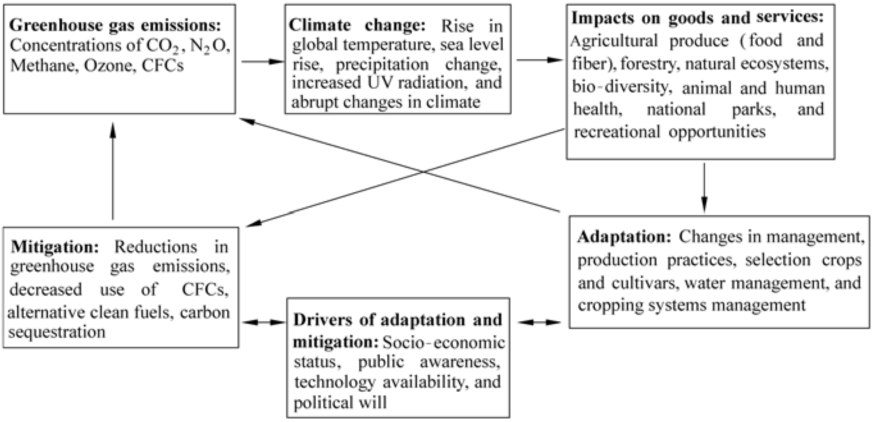

Figure 14.2 Linkages between various facets of greenhouse gas emissions, climate change, ecosystem goods and services, and drivers of adaptations and mitigation

14.2 Abiotic Stress Factors and Crop Yield

Agricultural production and productivity are highly sensitive to changes in climate and weather conditions. Therefore, changes in regional and global climate, particularly climatic variability, affect local as well as global food, fiber, and forest production (Easterling et al., 2007). Atmospheric carbon dioxide, temperature, rainfall patterns, ozone, and UV-B radiation have changed since the dawn of industrial revolution, and the scientific community expects current trends to continue into the future (Houghton et al., 2001; IPCC, 2007). Although crop productivity may benefit from rising CO_2 levels, the increased potential for abiotic stresses, such as increased incidence of drought, flooding, heat waves, and higher UV-B radiation, may challenge community dependence on local agricultural production. Hence, the overall impact of climate change on agriculture will depend on the balance among these climatic factors. These climate change factors have reduced productivity of many crops at both regional and global scales (Teramura, 1983; Lobell and Asner, 2003; Ciais et al., 2005; Lobell et al., 2008). A recent study suggests that, due to climate change, southern Africa could lose production of approximately 30% of its main crop maize (*Zea mays* L.) by 2030, and in southern Asia, production loss of many regional staples, such as rice

(*Orzya sativa* L.), millets (*Pennisetum* sp.), and maize could be up to 10% (Lobell et al., 2008). Similarly, Lobell and Asner (2003) estimated that each degree centigrade of increased temperature during an average growing season may reduce U.S. soybean (*Glycine max* L. Merril) and maize production by 17%. Studies indicate that climate change scenarios that include a combination of factors, such as heat stress, drought, and flooding, reduce crop yields more than a change in a single factor alone (Easterling et al., 2007). Therefore, it is expected that the interaction of abiotic stress factors will influence crop productivity in future climates.

The genotype (thus the genetic background) of a plant defines its range of performance and is determined by a set of heritable traits (Hall, 2001). Consequently, the phenotype produced by a particular genotype results from the interaction of these genotypic traits within the environment where the plant is grown. Therefore, crop yield is determined by genotypic effect, environmental effect, and the effect attributed to the genotype by environmental interaction. In the natural habitat, crop plants are subject to a combination of abiotic conditions that may include one or more stresses, such as heat, drought, and UV-B radiation. Interactions among these factors elicit a variety of responses in plants depending upon the intensity, duration, and timing (developmental stages in a plant species) of the stress. In most cases, abiotic stress conditions reduce crop performance and yield. One important strategy for coping with abiotic stresses is to develop new cultivars with tolerance to the abiotic stress conditions that have minimum yield loss or stable yield under multiple stress conditions. Selection of tolerant cultivars and genetic traits in a population is crucial for developing new cultivars that can adapt to a wide range of environments. This can only be accomplished by subjecting the species of interest to different abiotic stress conditions and determining responses of various growth- and yield-related traits to these stressors. Studies utilizing vegetative and reproductive parameters simultaneously under realistic growth conditions are limited. Therefore, plant processes to a combination of stress factors are not well understood (Rizhsky et al., 2004; Koti et al., 2007; Tegelberg et al., 2008).

14.3 Crop Responses to UV-B and Other Climate Change Factors

Even though UV-B represents a small fraction (0.5%) of total solar radiation, exposure to UV-B at the current and projected levels is known to elicit a variety of responses to all living organisms, including crop plants (Teramura, 1983; Runeckles and Krupa, 1994; Teramura and Sullivan, 1994; Caldwell et al., 1998; Kakani et al., 2003a). Changes in CO_2 and temperature accompanied by emission of ozone-depleting compounds, such as CFCs, CH_4, and N_2O caused by anthropogenic activities, reduces the thickness and affects distribution of the stratospheric ozone column (IPCC, 2007). The increase in UV-B radiation is closely associated with stratospheric ozone depletion as ozone absorbs the UV-B radiation portion of the solar spectrum (Long, 1991). Relative to the 1970s, the midlatitudes' O_3 column losses for the period of 2002 − 2005 were approximately 3% in the northern and 6% in the southern hemisphere (WMO, 2007). Current global distribution of mean daily doses of UV-B radiation during summer in most crop growing regions ranges from 2 to 9 kJ m^{-2} (McKenzie et al., 2007).

Previous reviews and published studies clearly demonstrate the extent of damage caused by both ambient (Teramura, 1983; Caldwell et al., 1989; Teramura and Sullivan, 1994) and elevated UV-B radiation (Teramura, 1983; Rozema et al., 1997; Krupa, 1998; Searles et al., 2001; Kakani et al., 2003a) on crop growth and yield. Damage varies widely among species and among cultivars of the same species. Teramura (1983) reported that more than 70% of 130 species were significantly affected by elevated UV-B in terms of total biomass production. In a statistical analysis of 77 crop species, mostly based on vegetative growth and a few yield parameters, Krupa (1998) reported sensitivity of more than 50% crop species, including several agriculturally important crops. In a recent review of 129 reports of 35 crop species, including cereals, legumes, oil, sugar, fiber, and tuber crops, enhanced UV-B radiation was shown to directly affect most of the crop growth (Kakani et al., 2003a). Affects included photosynthesis, production of defensive compounds (UV-B absorbing compounds and wax contents), and decreased vegetative growth which led to a myriad of secondary and tertiary effects, including altered crop growth and development. This, in turn, affected light interception which lowered canopy photosynthesis, reduced fruit production and retention, and finally yield.

14.3.1 Specific Effects of UV-B Radiation on Plants

Plants are highly sensitive to UV-B radiation because of their sessile nature. In plants, UV-B radiation damages cell membranes and all organelles within the cell, including the chloroplasts, mitochondria, and deoxyribonucleic acid (DNA) within the nucleus. Damage to these cell organelles directly or indirectly affects basic plant metabolic processes, such as photosynthesis, respiration, growth, and reproduction. Consequently, UV-B damage harms crop yield and quality. An overview of various processes affected by UV-B radiation at cellular and plant levels is presented in Tables 14.1 and 14.2. However, the effect of UV-B radiation varies with intensity and duration of irradiation and stage of plant development. In addition, sensitivity to UV-B radiation varies widely among plant species and cultivars of the same species. Studies on physical or physiological reasons for differences in tolerance to UV-B radiation among species need further attention.

Table 14.1 Effects of exposure to UV-B radiation on various physiological processes in plants. Adapted with permission from Prasad et al. (2003b)

Trait	Decreases	Increases	No Effect
DNA damage		✓	
Protein destruction		✓	
Fatty acid destruction		✓	
Photosynthesis	✓		
Photosystem Ⅰ	✓		
Photosystem Ⅱ	✓		
Rubisco	✓	✓	
Stomata closure			
Chlorophylls	✓		
Flavonoids		✓	
Waxes		✓	
Epidermal hairs		✓	
Cuticle thickness		✓	
Reproduction			
Pollen viability	✓		
Pollen tube growth	✓		
Fertilization	✓		
Cell division	✓		
Cell size			✓

Table 14.2 Effects of exposure to UV-B radiation on various growth and yield parameters in plants. Adapted with permission from Prasad et al. (2003b)

Trait	Decreases	Increases	No Effect
Photosynthesis	✓		
Stomatal conductance	✓		
Phenology			✓
Senescence		✓	
Plant height	✓		
Branching		✓	
Leaf area	✓		
Leaf growth and expansion	✓		
Leaf thickness		✓	
Specific leaf weight		✓	
Dry mater production	✓		
Flowering	✓	✓	
Fruit (grain) number	✓		
Fruit (grain) weight	✓		
Yield	✓		
Quality	✓		
Disease incidence			
Powdery mildew	✓		
Rust		✓	
Insect	✓	✓	

14.3.1.1 Genetic (DNA) and Ultra-Structural Damage

Ultraviolet radiation is efficiently absorbed by most organic substances, which causes many photochemical reactions in the living cells. The nucleus of each cell consists primarily of genetic material in the form of DNA. Nuclear DNA is inherently unstable and can be damaged by spontaneous or metabolically induced changes generated by environment. DNA is highly sensitive to UV-B radiation which can cause damage resulting in heritable mutations if not repaired and thus, can significantly influence various physiological processes. DNA is considered the primary absorbing compound in the cell in the UV-B region of the spectrum. Exposure of DNA to UV-B radiation can result in: (1) breakage of bonds in the DNA and DNA-protein cross links; (2) chromosomal breakage; (3) chromosomal aberrations; and (4) exchange and production of toxic and mutagenic photoproducts (e.g., cyclobutane pyrimidine dimmers (CPDs), 6, 4 pyrimidine- pyrimidone or 6, 4-photoproduct, thymine glycols, and pyrimidine hydrates). These changes in DNA alter transcription, replication, and recombination of genes and cause significant changes in plant metabolic and genetic processes. Proteins, membrane lipids, and other essential substances in the cell can also be altered through exposure to UV-B radiation, resulting in protein degradation and lipid peroxidation. These damages influence genetic makeup and affect protein synthesis, enzyme activities, and gene expression. All cellular life-forms possess DNA repair enzymes that recognize chemically modified bases, including those formed by UV radiation. Furthermore, cells have evolved through a variety of biochemical mechanisms to restore the integrity of the genetic material after DNA damage and retain its stability. These processes are called “DNA repair mechanisms.” There are two main mechanisms of DNA repair of CPDs and 6, 4-photoproduct, photo repair, and dark repair. In photo repair, the enzyme photolyase mediates the repair by forming a complex with the CPDs and 6, 4-photoproducts in a lesion-specific matter that is stable in the absence of light. In dark repair, the 6, 4-photoproducts are removed from the DNA by nucleotide excision of the damaged oligonucleotide, gap-filling DNA synthesis, and restore ligation in the correct pairing order (Sancar, 1994).

Exposure to UV radiation can result in changes in the ultrastructure of various cellular components in many plant species. Ultrastructural changes are generally caused by damage and dilation of the nuclear membrane. UV-B radiation causes damage to chloroplast structure through swelling of chloroplasts, rupture of the chloroplast wall, dilation of thylakoid membranes, disruption of the thylakoid structure, and disintegration of the double membrane that envelops surrounding chloroplasts accompanied by the accumulation of large starch granules (He et al., 1994). It is also known to cause swollen cisternae in the endoplasmic reticulum, damage to the mitochondria and plastids, and vesiculation of plasmalemma and tonoplasts. In addition, UV-B radiation alters cell shape and structure. These changes in ultrastructure can potentially affect various physiological processes, such as cell division, photosynthesis, respiration, and reproduction. However, plants have some defense and repair mechanisms that help minimize and deal with expected damages at the cellular level by removing or repairing damaged parts, and at the whole-plant level by producing UV-B absorbing compounds and pigments in leaves. These compounds mainly include flavonoids and anthocyanins, which are accumulated in the vacuoles of the epidermal and subepidermal cell layers.

14.3.1.2 Plant Photosynthesis

Photosynthesis is the process by which plants convert carbon dioxide and water into carbohydrate in the presence of sunlight. The photosynthetic apparatus is one of the important target sites of UV-B damage (Vu et al., 1982; 1984; Allen et al., 1997). Direct effects of enhanced UV-B radiation on photosynthesis include: (1) damage to ultrastructure of chloroplasts that are principal sites for photosynthesis; (2) impairment of light energy transfer (i.e., electron transport system of photosystem Ⅱ(PSⅡ) and to a lesser extent, photosystem Ⅰ(PSⅠ); (3) decrease in activity of Ribulose 1, 5-bisphosphate carboxylase/oxygenase (Rubisco); (4) decreased carbon dioxide fixation and oxygen evolution; and (5) decreased starch and chlorophyll content. Components affected in PSⅡ are the water-oxidizing system, light-harvesting complex, and synthesis of chlorophyll a/b-binding proteins. Exposure to UV-B radiation decreases both activity and concentration of Rubisco. UV-B inactivation of Rubisco could mainly be due to modification of the peptide chain, degradation of the protein, and/or diminished transcription of the gene. As indicated previously, almost every facet of photosynthetic machinery can be directly or indirectly damaged by exposure to UV-B radiation. However, electron transport mediated by PSⅡ appears to be the most sensitive (Fiscus and Booker, 1995). Within PSⅡ, all parts from the Mn binding sites to the plastoquinone acceptor sites on thylakoid membrane are sensitive.

In addition to the direct effects of UV-B radiation, photosynthesis may also be indirectly affected by: (1) induction of stomatal closure; (2) decreased individual leaf area and total canopy leaf area; (3) changes in leaf thickness and anatomy; and (4) changes in canopy architecture and morphology. All these changes can potentially decrease light interception and gas exchange, which results in lower canopy photosynthesis. However, the stomatal closure mechanism reduces evapo-transpiration water losses and increases water use efficiency, which leads to increased plant growth and yield.

14.3.1.3 Plant Morphology and Architecture

Although UV-B radiation constitutes a small portion of the solar spectrum, it induces a range of strong morphological effects in plants, including leaf thickness, leaf discoloration, cotyledon curling, inhibition of hypocotyl growth, stem and leaf elongation, axillary branching, and shifts in root-shoot ratio (Jansen, 2002). In most plant species, leaves exposed to UV-B radiation initially develop irregular patches (Fig. 14.3). With continued exposure to UV-B radiation, these chlorotic patches become brown necrotic spots and die (Singh et al., 2008a). The appearance of chlorotic and necrotic patches is generally attributed to decreases in leaf chlorophyll content (Zhao et al., 2003).

Elevated UV-B radiation can result in slower stem extension rates, shorter internode lengths leading to shorter plant height, decreased individual leaf size, fewer leaves leading to less leaf area, and fewer tillers and branch lengths (Kakani et al., 2003b; Reddy et al., 2003; Zhao et al., 2003). Overall, these morphological changes result in a smaller canopy. Plant architecture is modified by UV-B radiation. When exposed to UV-B radiation, both attached and detached tendrils of pea plants form spiral coils. In addition, enhanced UV-B radiation causes increased leaf epicuticular wax and stomatal index, and reductions in thickness of palisade and mesophyll tissues without altering the thinness of the epidermal layers (Kakani et al., 2003b).

(a) Control (b) Chlorotic patches (c) Necrotic patches

Figure 14.3 Typical symptoms of exposure to UV-B radiation on control leaves of cotton plants: (a) No symptoms, (b) Initial chlorotic patches, and (c) Necrotic patches after prolonged exposure. Adapted with permission from Prasad et al. (2003b)

14.3.1.4 Plant Development and Growth

Elevated UV-B radiation can delay flowering time in several different crops (Kakani et al., 2003a; Singh et al., 2008a). However, in some crops, UV-B radiation does not influence early bud or flower development, or the time to first flower (Sinclair et al., 1990). UV-B radiation does affect flower size, anther number, and pollen production, germination, and tube growth in many plant species (Kakani et al., 2003a). Cotton (*Gossypium hirsutum* L.) flowers produced on plants exposed to elevated UV-B were smaller due to reduced petal and bract size, and had fewer anthers (Kakani et al., 2003b). In general, reproductive organs of most plant species (pollen and ovules) are highly protected by sepals, petals, and ovary walls. In these plants, pollen is susceptible after it falls on the stigma. Exposure to UV-B radiation decreases pollen germination and rate of pollen tube growth by 10% – 25% in several crop species (e.g., maize, rye (*Secale cerale* L.) and tobacco (*Nicotiana tabacum* L.); Torabinejad et al., 1998). Increased UV-B radiation decreased total pollen production, pollen germination, and tube growth (Koti et al., 2004).

Consequently, it affects the fertilization process, which results in fewer seeds in sensitive plants. However, once the pollen tube penetrates the stigma surface, the walls of the style and ovary may provide some protection against UV-B radiation.

Growth is the rate of increase in weight and size of plant organs, such as leaf, stem, or root. Dry matter is the total weight of all plant organs. Exposure to UV-B radiation caused decreases in growth of leaves and stems in many plant species in both controlled environment and field studies (Kakani et al., 2003a). However, the effects of UV-B radiation on plant growth and dry matter accumulation were generally smaller under field conditions than under controlled environmental conditions (Caldwell et al., 1994; Olszyk et al., 1996). The decrease in growth of leaves, main stem, and branches is due to reduced cell division rather than decreased cell size. Reduction in plant height from exposure to UV-B is due in part to decreased levels of a growth hormone (indole acetic acid) in plants. The smaller and more compact canopy reduces the amount of UV-B intercepted by the plant, but also reduces the potential or total photosynthetic area essential for growth. The combination of these various factors results in decreased total dry matter or biomass production. In regard to exposure to UV-B radiation, the majority of crop species (60%) show a reduction in dry matter production, a moderate 24% show no change, and only 8% of crop species show an increase in dry matter production (Kakani et al., 2003a).

14.3.1.5 Plant Yield and Quality

Yield is the economic product harvested from plants (e.g., grain from wheat (*Triticum aestivum* L.), seeds from pods of soybean, roots from carrot (*Daucus carota* L.), seed and lint from cotton). Similar to changes in dry matter production, change in yield of crop species from exposure to UV-B varies with species. Some species (e.g., pea (*Pisum sativum* L.), barley (*Hordeum vulgare* L.), and mustard (*Brassica juncea* L.)) show severe reduction; others (e.g., cowpea (*Vigna unguiculata* L.), millets, and tobacco) show less or no yield reduction. The main causes of yield loss are reduced fruit (grain) number due to failure in fertilization, abortion of fruiting structures, and decreased fruit size due to reduced supply of assimilates to the growing sink (fruits). Kakani et al. (2003a) reviewed responses of various crops to UV-B radiation in both controlled environmental and field studies; almost half the studies showed that enhanced UV-B radiation decreased yield, the other half showed no UV-B effect on yield, and a few studies showed increased yields. These differential responses were due to variability in intensity of UV-B radiation. The UV-B radiation in these studies varied and ranged from $2.5-63$ kJ m^{-2} d^{-1} simulating $10\%-50\%$ of stratospheric O_3 depletion. In addition, the variable responses can also be due to differences in responses of cultivar and crop species to UV-B radiation.

Ultraviolet-B radiation also affects the quality of the economic product. For example, seed oil and protein content in soybean are reduced on exposure to UV-B radiation. Enhanced UV-B radiation decreased grain size and increased total nitrogen and storage protein (glutelin), thus affecting the taste of food products (Hidema et al., 2005). Similarly, Gao et al. (2004) investigated UV-B effects under field conditions and showed that increased UV-B not only decreased dry matter production and grain yield, but also affected grain quality by decreasing protein, sugar, and starch levels while improving lysine levels. Overall, studies conducted to date suggest that climate models predict UV-B radiation will decrease the growth, yield, and quality of crops (Hidema and Kumagai, 2006).

To date, the most comprehensive knowledge on the impact of UV-B radiation on various physiological, growth, and yield components has been developed at Mississippi State University within controlled environmental growth chambers maintained at optimum water, temperature, and nutrient conditions (Reddy et al., 2001; Reddy et al.; 2002, Reddy et al., 2003). Recently, Reddy et al. (2009) used an environmental productivity index to develop functional algorithms to accurately quantify and model impacts of UV-B radiation on the physiology, growth, development, and yield of cotton. On the basis of the critical limit, defined as 90% of optimum or the control, they showed that canopy photosynthesis and total dry weights were most sensitive with lower critical limits of 7 kJ m^{-2} d^{-1} and 7.3 kJ m^{-2} d^{-1}, respectively, compared with stem elongation (8.7 kJ m^{-2} d^{-1} UV-B) or leaf expansion (11.2 kJ m^{-2} d^{-1} UV-B). The identified critical limits and algorithms are currently being incorporated into the mechanistic cotton model GOSSYM to predict yields under present and future climate change conditions across the U.S. cotton belt (Liang et al., 2008). The evaluation and understanding of the impact of UV-B radiation on yield and yield quality of economically important crops requires further study under both field and controlled environmental conditions. The knowledge gained should be incorporated into existing crop simulation models.

14.3.1.6 Pest Damage

The impact of elevated UV-B radiation on plant species is well understood, but knowledge of the effects of UV-B on insect pests and disease-causing pathogens (fungi and bacteria) is limited. Research conducted thus far has shown both a decrease and an increase in disease and pest damage in response to increased UV-B radiation. Effects of UV-B on diseases and insects could be attributed to direct effects on their growth and indirect effects through changes in tissue characteristics and/or composition. Caldwell et al. (2003) summarized the literature and concluded that higher levels of UV-B radiation generally led to less herbivore and/or reduced insect growth compared with lower levels of UV-B. The magnitude of the effects was sizable, with potential ecosystem-level consequences for species composition, organic matter decomposition, and nutrient cycling. Solar UV-B can affect insect herbivores through reduced growth, survivorship, and fecundity (Lindroth et al., 2000) through changes in leaf characteristics (appearance and composition). Insects can perceive UV-B (Mazza et al., 2002), modify their behavior to avoid UV-B radiation, and protect themselves by regulating their cuticular pigmentation to screen damaging wavelengths (Gunn, 1998). Studies demonstrated that thrips consumed less leaf tissue and Lepidopeteran larvae had lower survivorship in laboratory assay when fed on leaves grown under near-ambient solar UV-B compared with leaves from UV-B excluded plots (Mazza et al., 1999; Zavala et al., 2001). The lower larvae survival was attributed to higher levels of soluble phenolics and lower lignin content in the foliage exposed to UV-B radiation. Similarly, bioassay studies suggested that adult specimens of leaf beetles tend to preferentially feed on plants not exposed to UV-B if given the opportunity to choose between UV-B exposed and unexposed plant materials (Ballare et al., 1996). However, the impact of UV-B radiation on mechanisms of other behavior of adult insects, such as oviposition and breeding, that are more relevant under natural conditions are not well understood and need investigation.

Ultraviolet-B radiation changes the chemistry, morphology, and physiology of plants. This can directly influence pest and disease incidence. For example, UV-B can affect leaf nitrogen content, available carbohydrate, and fiber (Zavala et al., 2001) indirectly influencing insect growth and survival. Plants exposed to UV-B can also stimulate production of secondary metabolites, i.e., phenolics and jasmonic acid (Mazza et al., 2000; Izaguirre et al., 2003; Izaguirre et al., 2007) which can influence insect incidence or behavior by acting as either a deterrent or attractant (Harborne, 1988). Some insects protect themselves from UV-B radiation by feeding on the underside of the leaves where UV-B penetration is lower (Paul et al., 1997) and avoiding areas of plants where defensive chemicals accumulate (McCloud et al., 1992). UV-B radiation effects on insect herbivores can also have consequences on parasitoids by affecting host quality (Soler et al., 2005) which leads to decreased survival and growth of parasitoid larvae (Holton et al., 2003).

Plant pathogen and disease incidence, as well as intensity, are also influenced by exposure to UV-B radiation (Raviv and Antignus, 2004). The effect of UV-B on plant pathogens can occur either through direct effects on various stages of pathogen development, such as spore germination, germ tube extension (Paul et al., 1997; Fourtouni et al., 1998), and sporulation (Ensminger, 1993) or indirectly by influencing host-plant resistance by damaging cells, decreasing plant growth and morphology (decreasing leaf and cuticle thickness), or modifying gene expression (Caldwell et al., 2003). However, it is very difficult to differentiate the effects of UV-B radiation on the host from those on the pathogen itself under field conditions. Stimulated compounds in plants that are localized in epidermis or mesophyll can also function as phytoalexins or antifungal compounds (Keller et al., 2003). Most studies on the effect of UV-B on fungi have focused on reproductive development. Fungal propagules showed high sensitivity (Rotem and Aust, 1991), but some exhibited enhanced sporulation in response to UV-B radiation. However, sensitivity of fungi to UV-B is not always reflected in a reduced infection of the plant (Raviv and Antignus, 2004). In fact, the spread of several disease-causing fungi can be decreased by filtering out UV-B radiation

(Fourtouni et al., 1998). In contrast, several pathogenic fungi (e.g., wheat leaf blotch causing fungi (*Septoria tritici*)) exhibit reduced infection under UV-B (Paul et al., 1997). In general, increasing disease severity primarily involves modification of host plant tissues, whereas decreased severity appears to involve either host plant changes or direct UV-B damage to the pathogen (Caldwell et al., 2003). Despite linkages between plants and herbivores, limited information is available on impacts of UV-B on host plant-insect interactions. A more definite understanding of the effects of UV-B on diseases and insects is needed to accurately predict consequences of ozone depletion on plant ecosystems.

14.3.2 Strategies for Protection against UV-B Radiation

Plants have evolved through several mechanisms by which they protect themselves from the damaging effects of UV-B radiation (Table 14.3).

Table 14.3 Protective mechanisms against damage by UV-B radiation in plants. Adapted with permission from Prasad et al. (2003b)

Repair mechanisms
• DNA repair: photo-reactivation enzymes (photolyase); excision repair by removing damaged part of DNA; bypass damaged DNA and fill gaps later from sister duplex.
Defense mechanisms
• Increase reflectance to avoid entry of UV-B radiation through cuticle wax, leaf hairs, and trichomes. • Increase absorption of UV-B radiation at epidermal cells by production of pigments, such as flavonoids, carotenoid, and anthocyanins. • Production of antioxidant enzymes (e.g., superoxide dismutase, ascorbate peroxidase, glutathione reductase) and compounds (ascorbates, alpha-tocopherol, and polyamines) that protect against oxidative stress caused by UV-B exposure.

14.3.2.1 Repair Mechanisms

Plants have constantly been exposed to sunlight, including UV radiation before formation of the ozone layer. In the process of evolution, certain plants developed a tolerance to solar UV-B radiation that limits the amount of DNA damage they suffer. All cellular life-forms possess DNA repair enzymes that recognize chemically modified bases, including those formed because of UV radiation. Furthermore, cells have evolved through a variety of biochemical mechanisms to restore the integrity of the genetic material after DNA damage and thus retain its stability. These processes, called “DNA repair mechanisms,” include photo-reactivation, excision repair (nucleotide and base excision repair), and post-replication repair. Photoreactivation mainly involves photolyase, an enzyme responsible for the direct splitting of cyclobutane pyrimidine dimers. Excision repair is done by nicking the damaged part of DNA, removing the bases in the damaged strand, and synthesis of the gap. In post-replication repair, DNA damage is bypassed during DNA replication and the resulting gaps are filled in later using the information from the sister duplex. Such DNA repair mechanisms are observed in both nuclear and chloroplast DNA. However, different plant species and varieties within a species vary in their ability to repair the damage caused by UV-B.

14.3.2.2 Defense Mechanisms

Plants are exposed to UV-B radiation as it passes through the epidermal layers to reach the sensitive sites. Therefore, the surface structure, physiology, and composition of the epidermal layer play an important role in protecting (shielding) cells from UV-B radiation. The important surface characteristics of the epidermal layer, which reduces penetration of UV-B radiation, include protective structures, such as trichomes and wax coating. These structures have the capacity to attenuate, absorb, and reflect UV-B radiation because of their optimal structure and presence of chemical compounds.

Studies have also shown that UV-B radiation leads to oxidative stress in plant systems as observed in many other abiotic (temperature and light) and biotic (insects and diseases) stress conditions. Therefore, as a result of UV-B exposure, plants increase production of flavonoids and antioxidant enzymes (e.g., superoxide dismutase, ascorbate peroxidase, and glutathione reductase) that provide defense against UV-B radiation. Other chemicals, such as alpha tocopherol (vitamin E), peroxidases, ascorbates, beta carotene, and polyamines, provide protective functions against UV-B damage.

Flavonoids are produced and mainly deposited in epidermal and mesophyll layers and leaf hairs. The presence and distribution of flavonoids at different locations can provide an efficient screen to UV-B radiation. Flavonoids are very effective in screening (absorbing) UV-B radiation and reducing damage to sensitive cell organs (i.e., DNA, chloroplasts, and mitochondria). In addition, anthocyanins and carotenoids could potentially screen UV radiation, particularly in flowers, and provide protection to pollen grains. These compounds attenuate the damaging solar UV-B radiation, but they transmit photosynthetically active radiation through the epidermis. Thus, these compounds do not directly influence photosynthesis and other physiological processes.

UV-B-mediated alterations in plant growth and yield are dependent upon species sensitivity and combined responses to other abiotic and biotic stresses (Teramura and Sullivan, 1994). The inconsistencies may be explained by either genotypic differences in UV-B sensitivity, different environmental conditions under which plants were grown, and/or the intensity of UV-B (Musil et al., 2002; Kakani et al., 2003a). A bulk of these studies conducted in growth chambers, greenhouses, or the field use different types of exposure systems that may be responsible for interpreting the results as intraspecific differential sensitivity of crop species (Runeckles and Krupa, 1994).

14.3.3 Crop Response to Atmospheric CO_2 Concentration

The projected increase in atmospheric CO_2 is expected to enhance growth and production of agricultural terrestrial plants (Easterling et al., 2007). Studies have also shown that the effects of elevated CO_2 on plant growth and yield may depend on photosynthetic pathway, plant species, growth stage, and management practices, such as water and nitrogen applications (Jablonski et al., 2002; Kimball et al., 2002; Ainsworth and Long, 2005). Crops with C_3 photosynthetic pathway respond markedly to increasing CO_2 concentrations compared to C_4 crops. Common C_3 crops are small grain cereals (wheat, rice, barley, oat (*Avena sativa* L.), and rye); grain legume or pulses (soybean, peanut (*Arachis hypogaea* L.), various beans (*Phaseolus* sp.) and peas), root and tuber crops (potato (*Solanum tuberosum* L.), cassava (*Manihot esculenta* L.), sugar beet (*Beta vulgaris* L.), and yams (*Dioscorea* sp.), and most oil, fruit, nut, vegetable, and fiber crops. Common C_4 crops are maize, sugarcane (*Saccharum officinarum* L.), sorghum (*Sorghum bicolor* L. Moench), millet, and many tropical and subtropical zone (warm-climate) grass species. Elevated CO_2 generally increases both above- and belowground biomass, volume and length of roots, and biomass allocation to roots (increased root-shoot ratio). Root and tuber crops tend to have a greater yield response to elevated CO_2 than seed or forage crops. Increased photosynthesis also favors symbiotic nitrogen fixation in legumes. Since legumes can supply nitrogen via symbiotic nitrogen fixation, legumes (both seed and forage) respond relatively more to increased CO_2 than non-legumes. Seed yields generally increase in a nonlinear fashion in response to increased CO_2; however, this increase in not as much as photosynthesis because part of the fixed carbon goes to increased vegetative biomass. Averaged across several species and under unstressed conditions, analysis shows that, compared with the current CO_2, crop yields increased at 550 ppm, CO_2 was $10\%-12\%$ for C_3 crops and $0\%-10\%$ for C_4 crops (Ainsworth et al., 2004; Gifford, 2004; Long et al., 2004). However, in a recent analysis of the FACE (free-air-carbon-dioxide enrichment) experimental results, Long et al. (2005, 2006) argued that crop responses to elevated CO_2 might be lower than previously thought because of overestimation of responses using crop models. Others have suggested that these new analyses are in fact consistent with previous findings from both FACE and other experimental settings (Tubiello et al., 2007). It is recognized that the models may overestimate the actual field-level responses because of many limiting factors including disease and insects, weeds, soil, water, and nutrient quality, which are neither well understood at large scales nor well implemented into the models (Easterling et al., 2007). In addition, the increase of CO_2 is subjected to a considerable interaction with other climatic factors; therefore, the rising CO_2 can not be assumed to be a single factor because of the associated changes in the temperature and other climatic factors (Giorgi et al., 1998; Prasad et al., 2002; Prasad et al., 2003a, b; Prasad et al., 2005; Zoltán, 2005) that directly affect crop growth and development. The beneficial affects of elevated CO_2 on seed yields are decreased for several crops under elevated temperatures (Prasad et al., 2002; Prasad et al., 2003a; Prasad et al., 2006a).

14.3.4 Crop Response to Temperature

The inferences from global circulation model simulations indicate that earth's mean surface air temperature warming for a doubling of atmospheric CO_2 is expected to increase by 2℃ – 4.5℃ (IPCC, 2007). Additionally, it is projected that heat waves will be more intense, more frequent and longer lasting in future warmer climates (Meehl and Tebaldi, 2004). Daily minimum temperatures (nighttime temperature) are projected to increase faster than daily maximum temperature (daytime), leading to decreases in diurnal temperature (IPCC, 2007). For example, in summer 2003, Europe experienced an extreme climate anomaly that caused July temperatures to increase 6℃ above the long-term mean and resulted in an approximate 30% reduction in terrestrial gross productivity across Europe (Ciais et al., 2005). Day/night temperatures greater than 36°/30℃ commonly occur during a crop's life cycle in most of the world's tropical growing regions where daytime temperatures can occasionally reach up to 45℃ (Warrag and Hall, 1983, Ismail and Hall, 1998; Hall, 2004a; National Climate Data Center, 2008). The projected global temperature increase will subject these locations to an even higher temperature regime, particularly for night temperatures (IPCC, 2007).

Temperature is the most important abiotic factor that determines plant adaptation to different climatic zones and seasons of the year. Most annual crops can be described as being adapted to either the cool season or warm season (Hall, 2001; Cutforth et al., 2007) depending on their temperature range of survival ($T_{\mathrm{max}} - T_{\mathrm{min}}$; Reddy and Kakani, 2007). Temperature also plays an important role in determining the sowing date of a crop species based on seed germination and survival of the seedlings. The minimum threshold for seed germination differs among crop species (e.g., soybean 10℃, cowpea 18℃, upland cotton 16℃, and maize 14℃; Ismail and Hall, 1997; Hall, 2001; Cutforth et al., 2007). Similarly, optimum temperatures depend upon the developmental stage of the plant and species. The optimum temperature for peanut growth and development is between 25℃ and 30℃ (Williams and Boote, 1995), whereas the optimum temperature for pollen germination and tube growth ranges between 30℃ and 34℃ (Kakani et al., 2002). The cardinal temperatures for growth and development of a crop species are also process dependant (Reddy et al., 1997a; Reddy and Kakani, 2007; Reddy et al., 2007a). A temperature stress could be anything below and/or above the optimum which influences the functionality and success of the biochemical pathway. This may reduce efficiency of the particular phase of development, resulting in a loss of economic yield (Singh et al., 2008b). Studies on cowpea and common bean have shown that heat stress during floral bud development can reduce fruit set because of damage to the pollen mother cells, resulting in poor anther dehiscence and reduced pollen number and viability (Warrag and Hall, 1983; Warrag and Hall, 1984; Gross and Kigel, 1994). Peanut (Prasad et al., 1999) and sorghum (Prasad et al., 2008) plants were more sensitive to high-temperature stress during microsporogenesis (just prior to flowering) and at flowering. High-temperature stress during pre-flowering stages mainly influences viability of male or female gametes, whereas at flowering, high-temperature stress decreases pollen dehiscence, germination, and tube growth, resulting in decreased fruit set and grain numbers. A negative association between increased daily mean temperature and reduction in yield has been reported in many crops (Ismail and Hall, 1998; Walton et al., 1999). Lobell and Asner (2003) projected an approximate 17% yield reduction in corn and soybean for each degree centigrade increase in average growing season temperature above the optimum in the U.S.. Most grain crops (i.e., peanuts, rice, wheat, soybean, and maize) are already being grown above optimum growth temperature; further increases in temperature due to climate change or increased frequencies of high-temperature stress during sensitive periods of reproduction will decrease crop yields (Reddy et al., 1997b; Lobell and Asner, 2003; Prasad et al., 2003a; Boote et al., 2005; Prasad et al., 2006a; Prasad et al., 2009).

14.3.5 Crop Response to Drought

Climate change is predicted to bring regional-scale precipitation extremes, causing both flooding and drought in certain areas (Giorgi et al., 1998). Most model simulations predict decreased precipitation by the end of the 21st century in subtropical regions (IPCC, 2007). Increased precipitation extremes are also likely in major agricultural production areas, e.g., southern and eastern Asia, eastern Australia, and northern Europe (Christensen et al., 2007). The 2003 summer drought in Europe caused a severe reduction in corn yield in eastern Europe (Ciais et al., 2005) and in forest biomass productivity in southern Europe (Gobron et al., 2005).

Water shortage is one of the most important factors limiting crop production worldwide due to geographic limited availability of irrigation water or the occurrence of drought mainly caused by reduced rainfall. Demand for drought-tolerant genotypes will increase due to diminishing water resources and alteration in precipitation patterns under climate change scenarios (Longenberger et al., 2006; Christensen et al., 2007). Understanding the detrimental effects of drought on plant processes and identifying the tolerance mechanisms will help breeders to develop tolerant genotypes.

Drought stress induces several changes in various physiological, biochemical, and molecular components of photosynthesis. Drought can influence photosynthesis through either pathway regulation by stomatal closure and decreasing flow of CO_2 into mesophyll tissue or by directly impairing metabolic activities. The main metabolic changes are declines in regeneration of Ribulose bisphosphate (RuBP) and Rubisco protein content, decreased Rubisco activity, impairment of ATP synthesis and photophosphorylation, and decreased inorganic phosphorus. Effects of drought on whole plant processes are manifold and can influence germination, emergence, leaf, root, tillers, stem development and growth, dry matter production, floral initiation, panicle exertion, pollination, fertilization, seed growth, seed yield, and seed quality. For most crop plants seed is the starting point of the growth cycle. Seeds begin biochemical changes shortly after imbibing water. Water uptake and imbibition of water by seed are dependent upon the soil water availability. Drought delays imbibition and thus can lead to decreased germination rates and total germination percentage. Leaf expansion is one of the growth processes most sensitive to drought (Alves and Setter, 2004; Reddy et al., 2009). This sensitivity is expressed in terms of smaller cells and reductions in the number of cells produced by leaf meristems (Randall and Sinclair, 1988; Tardieu et al., 2000). Drought stress can also influence total leaf area through its effect on the initiation of new leaves, which decreases under drought stress. Drought and heat stress alter the initiation and duration of developmental phases. In most cases, the length of time from floral initiation to anthesis is decreased by moderate drought and/or temperature stress, but is increased by severe stress. Drought stress during panicle development inhibits the conversion of vegetative to reproductive phase, and plants remain vegetative until this stress is relieved. Panicle initiation in sorghum was delayed by as many as 2 to 25 days and flowering by 1 to 59 days under drought stress, with more severe effects when drought was imposed at both early and late stages of panicle development (Craufurd et al., 1993). Drought stress inhibits pollen development and causes sterility. It also shortens the spike development duration (period during which potential kernel or seed numbers are determined) and the grain filling duration (during which the grain or seed weight is determined). Drought stress during later stages of panicle or flower development decreases seed numbers and can also increase the duration from seed set to full seed growth. Drought affects yield by limiting seed numbers caused by either influencing the amount of dry matter produced by the time of flowering (this is particularly true for determinate plant types), or by directly influencing pollen or ovule function which leads o a decreased seed set. Secondarily, drought influences seed filling by limiting the assimilate supply, leading to smaller seed size and lower yields.

Past difficulties have been associated with the identification of physiological traits that could be used as indicators of drought tolerance (Longenberger et al., 2006). However, various plant characteristics such as water use efficiency (Condon et al., 2002), root characteristics (Basal et al., 2003), canopy temperature (Patel et al., 2001), leaf water potential and leaf relative water content (Chiulele and Agenbag, 2004), and stomatal conductance (Bota et al., 2001; Flexas et al., 2002; Medrano et al., 2002) have been used as possible indicators to assess drought tolerance in crop species. Understanding the mechanisms of drought tolerance in crop species, particularly those adapted to dry conditions, will help plant breeders improve agronomic performance of these species by incorporating the superior traits into new species or cultivars (Clavel et al., 2005).

14.3.6 Crop Response to Multiple Abiotic Stress Factors

In natural habitats, plants are routinely subjected to a combination of abiotic factors. Under climate change scenarios, plants will be exposed to CO_2, UV-B radiation, temperature, and water stress simultaneously and their performance can be assessed only when grown under these multiple abiotic stress conditions. Many recent studies suggest that temperature and precipitation changes in future decades will modify, and often limit, the direct effect of CO_2 enrichment on plants (Easterling et al., 2007). For instance, high temperature during flowering may lower positive CO_2 effects by reducing reproductive traits such as grain number, size, and quality in several crops (Reddy et al., 1997b; Prasad et al., 2002; Prasad et al., 2003a,b; Baker, 2004; Prasad et al., 2006a; Caldwell et al., 2005). Prasad et al. (2006a) showed that adverse effects of high temperature on reproductive processes (seed set and harvest index) of sorghum were more severe at elevated CO_2 than at ambient CO_2. Similarly, for rice (Matsui et al., 1997) and red kidney bean (Prasad et al., 2002), the ceiling temperature for a seed set was 2°C cooler for plants grown at elevated CO_2 than at ambient CO_2. Increased temperatures may also reduce CO_2 effects indirectly by increasing water demand. Rainfed wheat grown at 450 ppm CO_2 demonstrated yield increases with temperature increases of up to 0.8°C, but declines with temperature increases beyond this point (Xiao et al., 2005). Future CO_2 levels may favor C_3 over C_4 plants (Ziska, 2003; Ainsworth et al., 2004; Gifford, 2004; Long et al., 2004); however, the opposite is also expected because of coupled increases in temperature, UV-B radiation, and drought (Reddy et al., 1997b; Xiao et al., 2005; Koti et al., 2007).

Interactive studies on a combination of elevated CO_2 and UV-B radiation have shown counteractive effects (i.e., responses in opposite directions). The positive effects of elevated CO_2 on plant photosynthesis, growth, and yield were apparent under ambient (normal) UV-B radiation. Under enhanced UV-B radiation, the stimulated effects of elevated CO_2 were decreased. In cotton, elevated CO_2 significantly increased photosynthesis, growth, and dry matter production under no UV-B or near-ambient UV-B conditions. These responses to CO_2 were reflected in significantly higher concentrations of carbohydrates in leaves (Zhao et al., 2003). However, the detrimental effects of high UV-B on cotton photosynthesis and growth, particularly on reproductive growth, could not be alleviated by elevated CO_2. This suggests that breeding for UV-B radiation-tolerant cultivars is important in future climates with elevated CO_2. Apart from plant growth and related responses like photosynthesis, the attractiveness of plant foliage to insect herbivores may vary under combinations of elevated CO_2 and enhanced UV-B (Caldwell et al., 2003). Lavola et al. (1998) found that insects preferred plants grown with enhanced

UV-B, and the combination of high CO_2 and enhanced UV-B increased the tendency of the insects to consume more foliage.

Sullivan and Teramura (1990) studied the combined effects of enhanced UV-B radiation and drought. Both drought and UV-B radiation altered biochemical and photochemical processes of photosynthesis and independently elicited similar reductions in growth. However, no additive affects were observed on photosynthesis, growth, or yield. Their results suggested that UV-B radiation may significantly affect soybean growth and photosynthesis primarily when water is readily available and that these effects may be obscured by drought when growth and yield are already reduced. In cowpea, for example, the combination of enhanced UV-B and drought stress elicited beneficial effects on morphological and growth characteristics (Balakumar et al., 1993).

Plant response to enhanced UV-B radiation might also be influenced by nitrogen fertilization. Hunt and McNeil (1998) reported that when plants received more nitrogen, their growth was more depressed by exposure to enhanced UV-B, whereas nitrogen-deficient plants were not responsive to UV-B. Similarly, the response of elevated CO_2 is achieved only when plants are sufficiently supplied with nitrogen. Moreover, the requirement of nitrogen under elevated CO_2 may be greater because of increased growth and biomass production. Interactive effects of elevated CO_2 and potassium (K) supply on cotton showed that elevated CO_2 significantly increased photosynthesis, leaf area, and biomass production of K sufficient plants, but did not affect K concentration (Reddy and Zhao, 2005). There were significant interactive effects of CO_2 and K on leaf area, canopy photosynthesis, and biomass accumulation and partitioning. The stimulation of physiological and growth parameters observed because of elevated CO_2 was lost under severe K deficiency. Interactive effects of climate change factors and soil fertility have received far less attention and need investigation. As several climate change factors can directly influence crop growth and yields, crops grown in future climate would require changes in fertilizer management practices.

Ultraviolet radiation also interacts with temperature stress (both low and high temperatures). Temperature above and below optimum can negatively influence crop growth and yield, and interaction among factors can alter limits of temperature tolerance. Beerling et al. (2001) reported that frost sensitivity of subarctic plant species was enhanced under elevated UV-B. They also showed that elevated CO_2 led to an increase in frost sensitivity of these species and if both elevated CO_2 and enhanced UV-B were imposed, there was a further increase in frost sensitivity. At high temperatures, some synergistic effects of enhanced UV-B and the elevated temperature were observed (Caldwell et al., 2003). In some tropical legumes, enhanced UV-B reduced growth of the plants at moderate temperatures (20℃ – 30℃); but at 40℃, chloroplasts in leaves were modified and thus masked the UV-B depressions of growth (Kulandaivelu and Nedunchezhian, 1993; Nedunchezhian and Kulandaivelu, 1996). Recent studies on cotton showed that of various growth and developmental processes, square and boll retention were most sensitive to high temperature and UV-B radiation (Reddy et al., 2004). Positive interactions were found on the number of main stem nodes, total leaf area, and total fruiting sites. Leaf photosynthesis increased with higher temperatures, but was reduced only by extreme UV-B radiation at high temperatures. The interaction between temperature and UV-B was additive on boll retention causing severe boll loss. Reddy et al. (2004) concluded that in current and future climates, severe yield losses would occur in the presence of high temperatures and UV-B radiation. Both these environmental factors stress plants by reducing reproductive mechanisms as well as vegetative growth.

Drought and high-temperature stress often occur simultaneously, but they can have very different effects on various physiological, growth, developmental, and yield processes. Few studies that examined the impact of combined effects of drought and high-temperature stress suggested that this combination produced a significantly higher detrimental effect on crop growth and productivity compared with each stress applied individually (Craufurd and Peacock, 1993; Savin and Nicolas, 1996). In addition, combinations of drought and heat stress were found to alter physiological processes, such as photosynthesis, accumulation of lipids, and transcript expression (Jagtap et al., 1998; Jian and Huang, 2001; Rizhsky et al., 2004). The interactive or combined effects of drought and high-temperature stress on reproductive processes of crop plants have not been well defined or quantified for any crop species and require further investigation. There might be differences in the response of reproductive function to these stresses. For example, in corn, both drought and heat stress have a direct influence on seed set or seed formation (Westgate, 1994). However, the cause is a result of effects on different processes. Heat stress decreases pollen viability, whereas drought stress (as measured for low leaf water potential) inhibits pistillate flower development and function.

Experiments designed to explore the interaction among these factors are useful for determining the potential effect of these abiotic stresses on crop plants (Caldwell et al., 2007). In a modeling approach, Runeckles and Krupa (1994) suggested that there may be no interaction between these stress factors as a whole, or to certain plant processes, and that the major variable will override the plant response. Otherwise, there may be an additive effect or greater-than-additive effect when the plant response is greater than the sum of responses to the individual factors. Additionally, there is a possibility of a less-than-additive interaction; for example, if CO_2 and/or temperature would stimulate more plant dry matter production and repair processes in UV-B sensitive plants (as shown in sunflower (*Helianthus annuus* L.) and maize seedlings in one of the earliest interactive studies involving CO_2, temperature), and UV-B radiation (Mark and Tevini, 1997).

In a recent study, Tegelberg et al. (2008) reported no significant interaction between elevated CO_2, temperature, and UV-B for the activity of defensive enzymes, growth-regulating polyamines, photosynthetic pigments, and soluble protein in silver birch (*Betula pendula* L. Roth). In contrast, there were significant interactions between these abiotic stresses for most of the vegetative and reproductive parameters in soybean (Koti et al., 2005; Koti et al., 2007). However, studies that simultaneously evaluate both vegetative growth and yield attributes under multiple stress conditions are limited. In a recent study, Singh (2008) demonstrated that vegetative and reproductive processes in cowpea respond differently under multiple abiotic stress conditions, including UV-B radiation. Therefore, given the changing climate, it will be useful to study the relative response of vegetative and reproductive plant attributes for important grain and legume crops.

The interaction between abiotic stresses can drastically alter the response mechanisms in plants. This interaction may cause either a positive or negative effect, or can even counteract (neutralize) the effects of individual stresses depending upon the species. Elevated temperatures alleviated the damaging effects of UV-B radiation on various growth parameters in sunflower and corn (Mark and Tevini, 1997), whereas high temperatures in combination with UV-B resulted in an increased reduction in the growth of soybean (Koti et al., 2007). The response of plants to multiple abiotic stresses is unique and should be treated as a new state of abiotic stress rather than a combination of two or more stress factors (Mittler, 2006). One abiotic stress factor evokes a chain of complex metabolic processes in plants in the presence of other stress factors. Developing new crop genotypes of a species with enhanced tolerance to a given stress factor may fail to withstand in the presence of another abiotic stress. Therefore, plant breeders must consider the variable effects of possible climate change when developing breeding programs or transgenic plants for abiotic stress tolerance (Hall and Ziska, 2000; Mittler, 2006).

14.4 Abiotic Stress Tolerance and Cultivar Screening Tools

There is a large variation in tolerance or susceptibility to abiotic stresses, particularly to different climate change factors including UV-B radiation (Reddy et al., 2005; Singh et al., 2008a), high temperature stress (Craufurd et al., 2003; Prasad et al., 2006b; Ristic et al., 2008), and water stress (Foulkes et al., 2002; Upadhyaya, 2005; Bakheit, 2008; Singh, 2008). This variation can provide an opportunity for genetic improvement of plant species through either traditional plant breeding techniques (selection and crossing) or modern molecular biology techniques, such as plant transformation. Screening wide germplasm from various locations and origins including native wild relatives of crop plants and landraces for single and multiple abiotic climate change factors may prove useful for identifying tolerant traits and in developing climate-ready species or cultivars for a given region.

The available genotypic variability of a species offers an opportunity for breeders to design and develop specific plant types to suit different agro-ecological environments. Effectiveness of selection for a trait depends on the magnitude of genetic and nongenetic causes in the expression of phenotypic differences among the genotypes in a population and is expressed as heritability of the trait (Thiaw and Hall, 2004). A thorough understanding of the physiological basis of differences in stress tolerance could be used to select or create new cultivars of crops that have increased productivity under such conditions (Wentworth et al., 2006). The genetic association of a trait with a higher level of physiological and/or developmental attributes facilitates adaptation of a crop to a stress condition and has proven useful for breeding purposes and developing improved lines of a crop species (Singh and Sharma, 1996). Several screening methods, such as cell membrane thermostability in soybean (Martineau et al., 1979; Blum et al., 2001) and cowpea (Ismail and Hall, 1999), in vitro pollen germination in canola (Singh et al., 2008b), cotton (Kakani et al., 2005), peppers (*Capsicum spp.*; Reddy and Kakani, 2007), and soybean (Koti et al., 2004; Salem et al., 2007), chlorophyll fluorescence in *Arabidopsis* (Barbagallo et al., 2003), photosynthesis and stomatal conductance in cotton (Lu et al., 1998), and intrinsic water use efficiency and associated gas exchange parameters in almond (*Prunus dulcis* L.), wheat, and cowpea (Brodribb, 1996; Condon et al., 2002; Singh, 2008), have been used at field and laboratory scales to identify tolerant traits and genotypes to abiotic stresses.

Abiotic stresses adversely affect various cellular functions, but photosynthesis is particularly sensitive to heat and drought stress (Berry and Bjorkman, 1980; Brodribb, 1996; Haldimann and Feller, 2005). Fluorescence parameters have been shown to relate directly to the photosynthetic rates of leaves (Genty et al., 1990; Edwards and Baker, 1993) and have been widely used to study leaf photosynthetic performance (Maxwell and Johnson, 2000). Consequently, any small perturbation in photosynthetic metabolism significantly modifies the fluorescence characteristics of plants. The sensitivity of chlorophyll fluorescence to the stress-induced perturbation in plant metabolism can potentially make it useful for screening genotypes with differential responses to abiotic factors (Brodribb, 1996; Barbagallo et al., 2003). Previous studies suggest significant changes in the photochemical activities of cowpea leaves subjected to heat (Costa et al., 2003; Costa et al., 2004), UV-B (Premkumar and Kulandaivelu, 1996; Lingakumar et al., 1999), and drought conditions (Lopez et al., 1987; Souza et al., 2004).

Hall (2004b) proposed a yield component model that can be incorporated for selection of most legumes, including cowpea cultivars in the high-temperature-limited production zones. Four yield components (number of flowers per unit area, number of pods per flower, number of seeds per pod, and weight of individual seeds) that contribute to yield reduction were recognized. In a simple screening approach for heat tolerance, Ismail and Hall (1999) found an association between reproductive-stage heat tolerance and higher cell membrane thermostability measured as electrolyte leakage from leaves subjected to high-temperature treatment. In an extremely hot field environment, negative correlations were observed between grain yield and electrolyte leakage ($r = -0.79$, $n = 9$), and pod set and electrolyte leakage ($r = -0.89$, $n = 9$) among nine cowpea breeding lines.

A similar approach could also be used to assess variable differences among species and cultivars of the same species under UV-B radiation.

An increased concern in regard to abiotic stress effects on crop plants has prompted screening for tolerance in crop populations (Hall, 2001). Many crops have been screened by using various abiotic stress response indices derived from the different stages of plant growth in response to single or multiple abiotic stresses (Dai et al., 1994; Saile-Mark and Tevini, 1997; Koti et al., 2004; Hubbard and Wu, 2005). Several crops, including rice (Dai et al., 1994), wheat (Yuan et al., 2000), bean (Saile-Mark and Tevini, 1997), and corn (Hubbard and Wu, 2005), have been screened by using several UV-B and drought response indices derived from plant growth responses under UV-B or drought conditions. In addition, multivariate analyses, such as principal component analyses and factor analysis, have been used for efficiently characterizing the stress responsiveness of a population under study and the associated plant attributes (Hofmann et al., 2001; Kaspar et al., 2004; Singh et al., 2008a).

Simultaneous occurrences of different abiotic stresses are common in natural plant habitats, which greatly modify the individual stress effect. This modification in the degree of response mechanisms could have been caused because of co-activation of different response pathways by simultaneous exposure of plants to different abiotic stresses leading to synergistic or antagonistic effects (Mittler, 2006). Developing a crop plant with enhanced tolerance to a stress combination, including UV-B radiation by either traditional breeding or genetic engineering, requires an understanding of the complex cross-communication between different signaling pathways and their direct or indirect effects on plant growth and metabolism (Hall, 2004a; Mittler, 2006).

Hall and Ziska (2000) recommended that plant breeders should consider possible climate change when developing a breeding strategy. Grain yield in legumes, such as cowpea, can be enhanced by selection of greater reproductive sinks under high temperatures, which will minimize the feedback effect that down regulates the photosynthetic mechanisms (Ahmed et al., 1993; Hall and Allen, 1993). However, yield has less importance in a trait-based breeding program particularly for high-temperature and drought tolerance. The yield reduction caused by abiotic stresses is a consequence of several first-order effects, such as photosynthetic performance (photosynthesis and fluorescence reduced water use efficiency), morphogenesis (differentiation and developmental rate), and production of defense compounds (phenolic compounds, and free amino acids and waxes) affecting overall vegetative growth and dry matter production. Therefore, survival capacity and maintenance of normal metabolic activity in the presence of stress conditions are key features for sustaining higher yields and should be considered an important component of breeding programs.

Molecular genetic mapping of the plant genome has facilitated identification of biomarkers that are closely linked to known resistance genes such that their isolation is clearly feasible in the future (Easterling et al., 2007). Temperature and drought stress resistance are especially relevant to climate change. Earlier studies have demonstrated genetic modifications to major crop species (e.g., maize and soybean) that increased their water deficit tolerance (Drennen et al., 1993; Kishor et al., 1995; Cheikh et al., 2000), although this may not extend to a wider range of crop plants. Little is known about how the desired traits achieved by genetic modification will perform under multiple abiotic conditions that commonly occur in the natural environment. The genomic approach offers new germplasm and understanding, but the emergent nature of yield from physiological processes demands that all components contributing to the yield be considered. It is important to understand the interactions of various regulatory pathways within plants, and between plants and environments, to understand key links between gene activity and crop yield (Sinclair and Purcell, 2005). Biotechnology is not expected to replace conventional agronomic breeding (Easterling et al., 2007); however, it will be a crucial adjunct to conventional breeding because both will be needed to meet future environmental challenges, including climate change (Cheikh et al., 2000; FAO, 2004).

14.5 Climate Change and Aerobiology and Public Health

In recent years, concerns regarding possible links among climate, plant biology, aerobiology, and public health (Ziska et al., 2008) have increased. Atmospheric CO_2, the main input needed for photosynthesis, stimulates plant growth; however, the rate of stimulation depends on the species. Plants with an indeterminate growth habit will benefit immensely because additional carbon can increase the production of branches/tillers and result in more nodes/fruiting sites on all branches, thus adding more potential for flowers to produce additional pollen (Reddy and Hodges, 2000; Ziska and Caulfield, 2000; Jablonski et al., 2002; Kimball et al., 2002; Long et al., 2005; Long et al., 2006; Easterling et al., 2007). In addition, plants grown in elevated CO_2 can also stimulate earlier flowering and sustained growth due to additional carbon, which will lead to a longer flowering period and pollen production range. Higher temperatures, on the other hand, will increase the rate of development, and in most cases promote early flowering and also a greater number of flowers and pollen if the change in temperature is small. If the change in temperature is large, flower and pollen vitality (production, viability and germination) will be curtailed regardless of other factors such as elevated CO_2. Other climate change factors, such as elevated UV-B, normally suppress flower and pollen production. However, the effects vary depending on the species and cultivars within a species (Teramura, 1983; Caldwell et al., 1989; Teramura and Sullivan, 1994; Rozema et al., 1997; Krupa, 1998; Searles et al., 2001; Kakani et al., 2003a).

The influence of multiple climatic variables (e.g., UV-B radiation, CO_2, and temperature) is limited, and a definite conclusion regarding the combined effects of these variables on plant pollen is harder to assess at this time. Studies conducted across natural gradients in climatic factors from rural to urban areas indicate that increasing levels and temporal shifts in aeroallergen production and allergenicity are linked to rising temperatures and/or CO_2 (Ziska et al., 2003; Ziska and George, 2004; Mohan et al., 2006; Rogers et al., 2006; Ziska et al., 2008). However, quantity and seasonality of pollen production depend on the plant response to environmental conditions. As previously indicated, several climate change factors influence pollen production of not only crop plants, but also several weed species (Ziska and Caulfield, 2000; Ziska et al., 2003) and allergenic pollen-producing tree species (Emberlin et al., 2002; Wan et al., 2002). Allergenic tree pollen from birch showed earlier spring floral initiation and pollen release in response to spring warming (Emberlin et al., 2002). Similarly, a simulated increase of summer temperature (+4°C) increased growth and re-growth following cutting, with an 85% increase in overall pollen production (Wan et al., 2002). Research on loblolly pine (*Pinus taeda* L.) also showed that elevated CO_2 resulted in early pollen production from younger trees and greater seasonal pollen production (LaDeau and Clark, 2006). Recent research also suggested that algernicity associated with poison ivy will increase with rising CO_2 (Mohan et al., 2006). As described in the previous section, climate change factors can also influence fungal spore production, which can influence allergen production. Increased exposure to allergic fungal spores can also influence human diseases, such as asthma (Dales et al., 2004). The linkage between aeroallergen production and alergenicity and the incidence of asthma intensity and incidence needs further investigation.

14.6 Concluding Remarks

Increased UV-B radiation and its interaction with other climate change factors, such as temperature, water stress, and elevated CO_2, can influence various physiological, growth, and yield traits of plants. In addition to direct effects on crop plants, these factors can also influence the interaction of plants with biotic factors (particularly with insect pests and plant pathogens). A comprehensive understanding of these interactions will be critical for evaluating the impact of climate change and climate variability on crop production and its long-term impact on crop ecology. Crop species and cultivars within species vary in their responses to both individual and a combination of stresses, suggesting a scope for genetic improvement. Thus, research should be more focused on breeding for tolerance to multiple stresses of regional or local importance. Sufficient care should be taken while evaluating and imposing stress treatments both in controlled environment and field conditions, particularly with respect to distribution of wavelength in the UV range for UV-B stress, diurnal differences and patterns between day and night temperatures for heat stress, time and intensity for moisture stress, and also acclimation response of plants to stressed environments. Experimentalists (molecular biologists and crop physiologists) should also consider light regimes that mimic filed-level solar radiation regimes while studying effects of stress factors on plants. The method of the imposition of stress could influence the quantitative response of any trait. As our knowledge of crop responses to multiple environmental stresses increases, it might be important to incorporate these algorithms, including genetic responses, into existing crop simulation models to develop better predictions of crop production and available management options in future climates.

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References

Ahmed FE, Hall AE, and Madore MA (1993) Interactive effects of high temperature and elevated carbon dioxide concentration on cowpea (*Vigna unguiculata* (L.) Walp.). Plant Cell Environ. 16: 835 – 842

Ainsworth EA and Long SP (2005) What have we learned from 15 years of free-air CO_2 enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy properties and plant production to rising CO_2. New Phytol. 165: 351 – 372

Ainsworth EA, Rogers A, Nelson R, and Long SP (2004) Testing the "source-sink" hypothesis of down-regulation of photosynthesis in elevated (CO_2) in the field with single gene substitutions in *Glycine max*. Agric. For. Meteorol. 122: 85 – 94

Allen DJ, Mckee IF, Farage PK, and Baker NR (1997) Analysis of limitations to CO_2 assimilation on exposure of leaves of two *Brassica napus* cultivars to UV-B. Plant Cell Environ. 20: 633 – 640

Alves AAC and Setter TL (2004) Response of cassava leaf area expansion to water deficit: Cell proliferation, cell expansion and delayed development. Ann. Bot. 94: 605 – 613

Baker JT (2004) Yield responses of southern U.S. rice cultivars to CO_2 and temperature. Agric. For. Meteorol. 122: 129 – 137

Bakheit BR (2008) Variability and correlations in grain sorghum genotypes (*Sorghum bicolor* (L.) Moench) under drought conditions at different stages of growth. J. Agron. Crop Sci. 165: 355 – 360

Balakumar T, Vincent VHB, and Paliwal K (1993) On the interaction of UV-B radiation (280 nm – 315 nm) with water stress in crop plants. Physiol. Plant. 87: 217 – 222

Ballare CL, Scopel AL, Stapleton AE, and Yanovsky MJ (1996) Solar ultraviolet-B radiation affects seedling emergence, DNA integrity, plant morphology, growth rate, and attractiveness to herbivore insects in *Datura ferox*. Plant Physiol. 112: 161 – 170

Barbagallo RP, Oxborough K, Pallett KE, and Baker NR (2003) Rapid, noninvasive screening for perturbations of metabolism and plant growth using chlorophyll fluorescence imaging. Plant Physiol. 132: 485

Basal H, Bebeli P, Smith CW, and Thaxton P (2003) Root growth parameters of converted race stocks of upland cotton and two BC_2F_2 populations. Crop Sci. 43: 1983 – 1988

Beerling DJ, Terry AC, Mitchell PL, Callaghan TV, Jones DG, and Lee JA (2001) Time to chill: effects of simulated global change on leaf ice nucleation temperature and subarctic vegetation. Am. J. Bot. 88: 628 – 633

Berry J and Bjorkman O (1980) Photosynthetic response and adaptation to temperature in higher plants. Ann. Rev. Plant Physiol. 31: 491 – 543

Blum A, Klueva N, and Nguyen HT (2001) Wheat cellular thermotolerance is related to yield under heat stress. Euphytica 117: 117 – 123

Boote KJ, Allen Jr LH, Prasad PVV, Baker JT, Gesch RW, Synder AM, Pan D, and Thomas JMG (2005) Elevated temperature and CO_2 impacts on pollination, reproductive growth and yield of several globally important crops. J. Agric. Meteorol. 60: 469 – 474

Bota J, Flexas J, and Medrano H (2001) Genetic variability of photosynthesis and water use in Balearic grapevine cultivars. Ann. Appl. Biol. 138: 353 – 361

Brodribb T (1996) Dynamics of changing intercellular CO_2 concentration (C_i) during drought and determination of minimum functional C_i. Plant Physiol. 111: 179 – 185

Caldwell CR, Britz SJ, and Mirecki RM (2005) Effect of temperature, elevated carbon dioxide, and drought during seed development on the isoflavone content of dwarf soybean (*Glycine max* (L.) Merrill) grown in controlled environments. J. Agric. Food Chem. 53: 1125 – 1129

Caldwell MM, Teramura AH, and Tevini M (1989) The changing solar ultraviolet climate and the ecological consequences for higher plants. Trends Ecol. Evol. 4: 363 – 367

Caldwell MM, Flint SD, and Searles PS (1994) Spectral balance and UV-B sensitivity of soybean: a field experiment. Plant Cell Environ. 17: 267 – 276

Caldwell MM, Teramura AH, Tevini M, Bornman JF, Björn LO, and Kulandaivelu G (1998) Effects of increased solar ultraviolet radiation on terrestrial ecosystems. J. Photochem. Photobiol. B: Biol. 46: 40 – 52

Caldwell MM, Ballare CL, Bornman JF, Flint SD, Bjorn LO, Teramura AH, Kulandaivelu G, and Tevini M (2003) Terrestrial ecosystems, increased solar ultraviolet radiation and interactions with other climate change factors. Photochem. Photobiol. Sci. 2: 29 – 38

Caldwell MM, Bornman JF, Ballaré CL, Flint SD, and Kulandaivelu G (2007) Terrestrial ecosystems, increased solar ultraviolet radiation, and interactions with other climate change factors. Photochem. Photobiol. Sci. 6: 252 – 266

Cheikh N, Miller PW, and Kishore G (2000) Role of biotechnology in crop productivity in a changing environment. In: Reddy KR, Hodges HF (eds) Climate Change and Global Crop Productivity. CAP International, Oxon, UK, pp.425 – 436

Chiulele RM and Agenbag GA (2004) Plant water relations and proline accumulation on two cowpea (*Vigna unguiculata* (L.) Walp.) cultivars as a response to water stress. S. Afr. J. Plant and Soil 21: 109 – 113

Christensen JH, Hewitson B, Busuioc A, Chen A, Gao X, Held I, Jones R, Kolli RK, Kwon WT, Laprise R, Rueda VM, Mearns L, Menendez CG, Raisanen J, Rinke A, Sarr A and Whetton P. (2007) Regional climate projections. In: Solomon S, Qin D, Manning M, Marquis M, Averyt K, Tignor MMB, Miller HL and Chen Z (eds) Climate Change 2007: Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK, pp.847－940

Ciais P, Reichstein M, Viovy N, Granier A, Ogee J, Allard V, Aubinet M, Buchmann N, Bernhofer C, Carrara A, Chevallier F, De Noblet N, Friend AD, Friedlingstein P, Grunwald T, Heinesch B, Keronen P, Knohl A, Krinner G, Loustau D, Manca G, Matteucci G, Miglietta F, Ourcival JM, Papale D, Pilegaard K, Rambal S, Seufert G, Soussana JF, Sanz MJ, Schulze ED, Vesala T, and Valentini R (2005) Europe-wide reduction in primary productivity caused by the heat and drought in 2003. Nature 437: 529－533

Clavel D, Drame NK, Roy-Macauley H, Braconnier S, and Laffray D (2005) Analysis of early responses to drought associated with field drought adaptation in four Sahelian groundnut (*Arachis hypogaea* L.) cultivars. Environ. Exp. Bot. 54: 219－230

Condon AG, Richards RA, Rebetzke GJ, and Farquhar GD (2002) Improving intrinsic water-use efficiency and crop yield. Crop Sci. 42: 122－131

Costa ES, Bressan-Smith R, Oliveira JG, and Campostrini E (2003) Chlorophyll a fluorescence analysis in response to excitation irradiance in bean plants (*Phaseolus vulgaris* L. and *Vigna unguiculata* L. Walp) submitted to high temperature stress. Photosynthetica 41: 77－82

Costa JW, Hasenfratz-Sauder MP, Pham-Thi AT, Lima MDS, Dizengremel P, Jolivet Y, and de Melo DF (2004) Identification in *Vigna unguiculata* (L.) Walp. of two cDNAs encoding mitochondrial alternative oxidase orthologous to soybean alternative oxidase genes 2a and 2b. Plant Sci. 167: 233－239

Craufurd PQ and Peacock JM (1993) Effect of heat and drought stress on sorghum. Exp. Agr. 29: 77－86

Craufurd PQ, Flower DJ, and Peacock JM (1993) Effect of heat and drought stress on sorghum. I. Panicle development and leaf appearance. Exp. Agr. 29: 61－76

Craufurd PQ, Prasad PVV, Kakani VG, Wheeler TR, and Nigam SN (2003) Heat tolerance in groundnut. Field Crop Res. 80: 63－77

Cutforth HW, McGinn SM, McPhee KE, and Miller PR (2007) Adaptation of pulse crops to the changing climate of the Northern Great Plains. Agron. J. 99: 1684－1699

Dai Q, Peng S, Chavez AQ, and Vergara BS (1994) Intraspecific response of 188 rice cultivars to enhanced UV-B radiation. Environ. Exp. Bot. 34: 433－442

Dales RE, Cakmak S, Judek S, Dann T, Coates F, Brook JR, and Burnett RT (2004) Influence of outdoor aeroallergens on hospitalization for asthma in Canada. J. Allergy Clin. Immunol. 113: 303－306

Drennen PM, Smith M, Goldsworthy D, and van Staten J (1993) The occurrence of trahaolose in the leaves of the desiccation-tolerant angiosperm *Myronthamnus flabellifoliius* Welw. J. Plant Physiol. 142: 493－496

Easterling WE, Aggarwal PK, Batima P, Brander KM, Erda L, Howden SM, Kirilenko A, Morton J, Soussana JF, Schmidhuber J, and Tubiello FN (2007) Food, fibre and forest products. In: Parry ML, Canziani OF, Palutikof JP, van der Linden PJ, Hanson CE (eds) Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group Ⅱ to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK, pp.273－313

Edwards GE and Baker NR (1993) Can CO_2 assimilation in maize leaves be predicted accurately from chlorophyll fluorescence analysis? Photosynthesis Res. 37: 89－102

Emberlin J, Detandt M, Gehrig R, Jaeger S, Nolard N, and Rantio-Lehtimaki A (2002) Responses in the start of *Betula* (birch) pollen seasons to recent changes in spring temperatures across Europe. Int. J. Biometeorol. 47: 113－115

Ensminger PA (1993) Control of development in plants and fungi by far-UV radiation. Physiol. Plant. 88: 501－508

FAO (2004) The state of food and agriculture 2003－2004. Agricultural Biotechnology: Meeting the Needs of the Poor, Food and Agriculture Organization of the United Nations, Rome, Italy, p.208

Fiscus EL and Booker FL (1995) Is increased UV-B a threat to crop photosynthesis and productivity? Photosyn. Res. 43: 81－92

Flexas J, Bota J, Escalona JM, Sampol B, and Medrano H (2002) Effects of drought on photosynthesis in grapevines under field conditions: An evaluation of stomatal and mesophyll limitations. Funct. Plant Biol. 29: 461－471

Foulkes MJ, Scott RK, and Bradley RS (2002) The ability of wheat cultivars to withstand drought in UK conditions: Formation of grain yield. J. Agr. Sci. 138: 153－169

Fourtouni A, Manetas Y, and Christias C (1998) Effects of UV-B radiation on growth, pigmentation and spore production in the phytopathogenic fungus *Alternaria solani*. Can. J. Bot. 76: 2093－2099

Gao W, Zheng Y, Slusser JR, Heisler GM, Grant RH, Xu J, and He D (2004) Effects of supplementary ultraviolet-B radiation on maize yield and qualities: A field experiment. Photochem. Photobiol. 80: 127－131

Genty B, Briantais JM, and Baker NR (1990) Relative quantum efficiencies of the two photosystems of leaves in photorespiratory and not photorespiratory conditions. Plant Physiol. Biochem. 28: 1－10

Gifford RM (2004) The CO_2 fertilizing effect does it occur in the real world? New Phytol. 163: 221－225

Giorgi R, Meehl GA, Kattneberg A, Grassl H, Mitchell JFB, Stouffer RJ, Tokioka T, Weaver AJ, and Wigley TML (1998) Simulation of regional climate change with global coupled climate models and regional modeling techniques. In: Watson RT, Zinyowera MC, Moss RH (eds) The Regional Impacts of Climate Change: An Assessment of Vulnerability. Cambridge University Press, New York, NY, pp.427－437

Gobron N, Pinty B, Melin F, Taberner M, Verstraete MM, Belward A, Lavergne T, and Widlowski JL (2005) The state of vegetation in Europe following the 2003 drought. Int. J. Remote Sens. 26: 2013－2020

Gross Y and Kigel J (1994) Differential sensitivity to high temperature of stages in the reproductive development in common bean (*Phaseolus vulgaris* L.). Field Crops Res. 36: 201－212

Gunn A (1998) The determination of larval phase coloration in the African armyworm *Spodoptera exempta* and its consequences for thermoregulation and protection from UV light. Entomol. Exp. Appl. 86: 125－133

Haldimann P and Feller U (2005) Growth at moderately elevated temperature alters the physiological response of the photosynthetic apparatus to heat stress in pea (*Pisum sativum* L.) leaves. Plant Cell Environ. 28: 302－317

Hall AE (2001) Crop response to environment. CRC Press, New York, NY, p.248

Hall AE (2004a) Breeding for adaptation to drought and heat in cowpea. Eur. J. Agron. 21: 447－454

Hall AE (2004b) Comparative ecophysiology of cowpea, common bean, and peanut. In: Henry TN, Abraham B (eds) Physiology and Biotechnology Integration for Plant Breeding. Marcel Dekker, New York, NY, pp.271－385

Hall AE and Allen LH (1993) Designing cultivars for climatic conditions of the next century. In: Buxton DR, Shibles R, Forsberg RA, Blad BL, Asay KH, Paulsen GM, Wilson RF (eds) International Crop Science I. Madison: Crop Sciences Society of America, WI, pp.291-297

Hall AE and Ziska LH (2000) Crop breeding strategies for the 21st century. In: Reddy KR, Hodges HF (eds) Climate Change and Global Crop Productivity. CAB International, Oxon, UK, pp.407－423

Harborne JB (1988) The flavanoids. Advances in research since 1980. Chapman and Hall, New York, NY, p.676

He J, Huang LK, and Whitecross MI (1994) Chloroplast ultrastructure changes in *Pisum sativum* associated with supplementary ultraviolet (UV-B) radiation. Plant Cell Envrion. 17: 771－775

Hidema J and Kumagai T (2006) Sensitivity of rice to ultraviolet-B radiation. Ann. Bot. 97: 933－942

Hidema J, Zhang WH, Yamamoto M, Sato T, and Kumagai T (2005) Changes in grain size and grain storage protein of rice (*Oryza sativa* L.) in response to elevated UV-B radiation under outdoor conditions. J. Radiation Res. 46: 143－149

Hofmann R, Campbell B, Fountain D, Jordan BR, Greer DH, Hunt D, and Hunt C (2001) Multivariate analysis of intraspecific responses to UV-B radiation in white clover (*Trifolium repense* L.). Plant Cell Environ. 24: 917－927

Holton MK, Lindroth RL, and Nordheim EV (2003) Foliar quality influence tree-herbivore-parasitoid interactions: Effects of elevated CO_2, O_3, and plant genotype. Oecologia 137: 233－244

Houghton JT, Ding Y, Griggs DJ, Noguer M, van der Linden PJ, Dai X, Maskell K, and Johnson CA (2001) Climate Change 2001: The Scientific Basis. Contribution of Working Group to Third Assessment Report to the Intergovernmental Panel on Climate Change (IPCC). Cambridge University Press, Cambridge, UK, p.892

Hubbard KG and Wu H (2005) Modification of a crop-specific drought index for simulating corn yield in wet years. Agron. J. 97: 1478－1484

Hunt JE and McNeil DL (1998) Nitrogen status affects UV-B sensitivity of cucumber. Aust. J. Plant Physiol. 25: 79－86

IPCC (2007) Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK and New York, NY, p.996

Ismail AM and Hall AE (1997) Chilling tolerance during emergence of cowpea associated with a dehydrin and slow electrolyte leakage. Crop Sci. 37: 1270

Ismail AM and Hall AE (1998) Positive and potential negative effects of heat-tolerance genes in cowpea. Crop Sci. 38: 381－390

Ismail AM and Hall AE (1999) Reproductive-stage heat tolerance, leaf membrane thermostability and plant morphology in cowpea. Crop Sci. 39: 1762－1768

Izaguirre MM, Scopel AL, Baldwin IT, and Ballare CL (2003) Convergent responses to stress: Solar ultraviolet-B radiation and *Manduca sexta* herbivory elicit overlapping transcriptional responses in field-grown plants of *Nicotiana longiflora*. Plant Physiol. 132: 1755－1767

Izaguirre MM, Mazza CA, Svotos A, Baldwin IT, and Ballare CL (2007) Solar ultraviolet-B radiation and insect herbivory trigger partially overlapping phenolic responses in *Nicotiana attenuate* and *Nicotiana longiflora*. Ann. Bot. 99: 103－109

Jablonski LM, Wang X, and Curtis PS (2002) Plant reproduction under elevated CO_2 conditions: A meta-analysis of reports on 79 crop and wild species. New Phytol. 156: 9－26

Jagtap V, Bhargava S, Streb P, and Feierabend J (1998) Comparative effect of water, heat and light stresses on photosynthetic reactions in *Sorghum bicolor* (L.) Moench. J. Exp. Bot. 49: 1715－1721

Jansen MAK (2002) Ultraviolet-B radiation effects on plants: Induction or morphogenic responses. Physiol. Plant. 116: 423－429

Jian Y and Huang B (2001) Drought and heat stress injury to two cool-season turf grass in relation to antioxidant and lipid peroxidation. Crop Sci. 41: 436－442

Kakani VG, Prasad PVV, Craufurd PQ, and Wheeler TR (2002) Response of *in vitro* pollen germination and pollen tube growth of groundnut (*Arachis hypogaea* L.) genotypes to temperature. Plant Cell Environ. 25: 1651－1661

Kakani VG, Reddy KR, Zhao D, and Sailaja K (2003a) Field crop responses to ultraviolet-B radiation: A review. Agric. For. Meteorol. 120:191－218

Kakani VG, Reddy KR, Zhao D, and Mohammed AR (2003b) Ultraviolet-B radiation effects on cotton (*Gossypium hirsutum* L.) morphology and anatomy. Ann. Bot. 817－826

Kakani VG, Reddy KR, Koti S, Wallace TP, Prasad PVV, Reddy VR, and Zhao D (2005) Differences in *in vitro* pollen germination and pollen tube growth of cotton cultivars in response to high temperature. Ann. Bot. 96: 59－67

Kaspar TC, Pulido DJ, Fenton TE, Colvin TS, Karlen DL, Jaynes DB, and Meek DW (2004) Relationship of corn and soybean yield to soil and terrain properties. Agron. J. 96: 700－709

Keller M, Rogiers SY, and Schulz HR (2003) Nitrogen and ultraviolet radiation modifies grapevines susceptibility to powdery mildew. Vitis 42: 87－94

Kimball BA, Kobayashi K, and Bindi M (2002) Responses of agricultural crops to free-air CO_2 enrichment. Adv. Agron. 77: 293－368

Kishor PBK, Hong Z, Miao G, Hu C, and Verma D (1995) Over expression of Δ^1-pyrroline-5-carboxylase synthase increases proline production and confers osmotolerance in transgenic plants. J. Plant Physiol. 108: 1387－1394

Koti S, Reddy KR, Kakani VG, Zhao D, and Reddy VR (2004) Soybean (*Glycine max*) pollen germination characteristics flower and pollen morphology in response to enhanced ultraviolet-B radiation. Ann. Bot. 94: 855－864

Koti S, Reddy KR, Reddy VR, Kakani VG, and Zhao DL (2005) Interactive effects of carbon dioxide, temperature, and ultraviolet-B radiation on soybean (*Glycine max* L.) flower and pollen morphology, pollen production, germination, and tube lengths. J. Exp. Bot. 56: 725－736

Koti S, Reddy KR, Kakani VG, Zhao D, and Gao W (2007) Effects of carbon dioxide, temperature and ultraviolet-B radiation and their interactions on soybean (*Glycine max* L.) growth and development. Environ. Exp. Bot. 60: 1－10

Krupa SV (1998) Elevated UV-B radiation and crop. In: Krupa SV, Kickert RN, Jäger HJ (eds) Elevated Ultraviolet (UV)-B Radiation and Agriculture. Springer-Verlag, Heidelberg and Landes Bioscience, Georgetown, TX, pp.105－131

Kulandaivelu G and Nedunchezhian N (1993) Synergistic effects of ultraviolet-B enhanced radiation and growth temperature on ribulose 1, 5-bisphosphate carboxylase and $^{14}CO_2$ fixation in *Vigna sinensis* L. Photosynthetica 29: 377－383

LaDeau SL and Clark JS (2006) Pollen production by *Pinus taeda* growing in elevated CO_2. Funct. Ecol. 10: 1365－1371

Lavola A, Tiitto RJ, Roininen H, and Aphalo P (1998) Host-plant preference of an insect herbivore mediated by UV-B and CO_2 in relation to plant secondary metabolites. Biochem. Syst. Ecol. 26: 1－12

Liang X, Xu M, Gao W, Reddy KR, Kunkel K, and Schmoldt DL (2008) Physical modeling of U.S. cotton yields and climate stresses during 1979－2005. J. Geo. Res., Atmospheres (in press)

Lindroth RL, Hofmann RW, Campell BD, McNabb WC, and Hunt DY (2000) Population differences in *Trifolium repens* L-response to ultraviolet-B radiation: Foliar chemistry and consequences for two lepidopteran herbivores. Oecologia 122: 20－28

Lingakumar K, Amudha P, and Kulandaivelu G (1999) Exclusion of solar UV-B (280 nm－315 nm) radiation on vegetative growth and photosynthetic activities in *Vigna unguiculata* L. Plant Sci. 148: 97－103

Lobell DB and Asner GP (2003) Climate and management contributions to recent trends in U.S. agricultural yields. Science 299: 1032

Lobell DB, Burke MB, Tebaldi C, Mastrandrea MD, Falcon WP, and Naylor RL (2008) Prioritizing climate change adaptation needs for food security in 2030. Science 319: 607－610

Long SP (1991) Modification of the response of photosynthetic productivity to rising temperature by atmospheric CO_2 concentrations: Has its importance been underestimated? Plant Cell Environ. 14: 729－739

Long SP, Ainsworth EA, Rogers A, and Ort DR (2004) Rising atmospheric carbon dioxide: Plants FACE the future. Annu. Rev. Plant Biol. 55: 591－628

Long SP, Ainsworth EA, Leakey ADB, and Morgan PB (2005) Global food insecurity. Treatment of major food crops with elevated carbon dioxide or ozone under large-scale fully open-air conditions suggests recent models may have overestimated future yields. Philos. Trans. R. Soc. Lond., Ser. B: Biol. Sci. 360: 2011－2020

Long SP, Ainsworth EA, Leakey ADB, Nosberger J, and Ort DR (2006) Food for thought: Lower-than-expected crop yield stimulation with rising CO_2 concentrations. Science 312: 1918－1921

Longenberger PS, Smith CW, Thaxton PS, and McMichael BL (2006) Development of a screening method for drought tolerance in cotton seedlings. Crop Science 46: 2104－2110

Lopez FB, Setter TL, and McDavid CR (1987) Carbon dioxide and light responses of photosynthesis in cowpea and pigeonpea during water deficit and recovery. Plant Physiol. 85: 990－995

Lu Z, Percy RG, Qualset CO, and Zeiger E (1998) Stomatal conductance predicts yields in irrigated pima cotton and bread wheat grown at high temperatures. J. Exp. Bot. 49: 453－460

Mark U and Tevini M (1997) Effects of solar ultraviolet-B radiation, temperature and CO_2 on growth and physiology of sunflower and maize seedlings. Plant Ecol. 128: 224－234

Martineau JR, Williams JH, and Specht JE (1979) Tolerance in soybean. Ⅱ. Evaluation of segregating populations for membrane thermostability. Crop Sci. 19: 79－81

Matsui T, Namuco OS, Ziska LH, and Horie T (1997) Effects of high temperature and CO_2 concentration on spikelet sterility of indica rice. Field Crop. Res. 51: 213－219

Maxwell K and Johnson GN (2000) Chlorophyll fluorescence: A practical guide. J. Exp. Bot. 51: 659－668

Mazza CA, Zavala J, Scopel AL, and Ballare CL (1999) Perception of solar UVB radiation by phytophagous insects: Behavioral responses and ecosystem implications. Proc. Natl. Acad. Sci. USA. 96: 980－985

Mazza CA, Boccalandro HE, Giordano CV, Battista D, Scopel AL, and Ballare CL (2000) Functional significance and induction by solar radiation of ultraviolet—absorbing sunscreens in field-grown soybean crops. Plant Physiol. 122: 117－125

Mazza CA, Izaguirre MM, Zavala J, Scopel AL, and Ballare CL (2002) Insect perception of ambient ultraviolet-B radiation. Ecol. Lett. 5: 722－726

McCloud ES, Berenbaum MR, and Tuveson RW (1992) Furanocoumarin content and phototoxicity of rough lemon (*Citrus jambhiri*) foliage exposed to enhanced ultraviolet-B (UVB) radiation. J. Chem. Ecol. 18: 1125－1137

McKenzie RL, Bjorn LO, Bais A, and Ilyasd M (2003) Changes in biologically active ultraviolet radiation reaching the Earth's surface. Photochem. Photobiol. Sci. 2: 5－15

McKenzie RL, Aucamp PJ, Bais AF, Björn LO, and Ilyas M (2007) Changes in biologically active ultraviolet radiation reaching the Earth's surface. Photochem. Photobiol. Sci. 6: 218－231

Medrano H, Escalona JM, Bota J, Gulias J, and Flexas J (2002) Regulation of photosynthesis of C_3 plants in response to progressive drought: Stomatal conductance as a reference parameter. Ann. Bot. 89: 895－905

Meehl TGA and Tebaldi C (2004) More intense, more frequent, and longer lasting heat waves in the 21st century. Science 305: 994－997

Mittler R (2006) Abiotic stress, the field environment and stress combination. Trends Plant Sci. 11: 15－19

Mohan JE, Ziska LH, Thomas RB, Sicher RC, George K, Clark JS, and Schlesinger WH (2006) Biomass and toxicity responses of poison ivy (*Toxicodendron radicans*) to elevated atmospheric CO_2. Proc. Natl. Acad. Sci.103: 9086－9089

Musil CF, Björn LO, Scourfield MWJ, and Bodeker GE (2002) How substantial are ultraviolet-B supplementation inaccuracies in experimental square-wave delivery systems? Environ. Exp. Bot. 47: 25－38

National Climate Data Center. http://www.ncdc.noaa.gov/oa/ncdc.html

Nedunchezhian N and Kulandaivelu G (1996) Effect of ultraviolet-B enhanced radiation and temperature on growth and photochemical activities in *Vigna unguiculata*. Biol. Plant. 38: 205－214

Olszyk D, Dai QJ, Teng P, Leung H, Luo Y, and Peng SB (1996) UV-B effects on crops: Response of irrigated rice ecosystem. J. Plant Physiol. 148: 26－34

Patel NR, Mehta AN, and Shekh AM (2001) Canopy temperature and water stress quantification in rainfed pigeonpea (*Cajanus cajan* (L.) Millsp.). Agric. For. Meteorol. 109: 223－232

Paul ND, Rasanayagam S, Moody SA, Hatcher PE, and Ayres PG (1997) The role of interactions between trophic levels in determining the effects of UV-B on terrestrial ecosystems. Plant Ecol. 128: 296－308

Prasad PVV, Craufurd PQ, and Summerfield RJ (1999) Sensitivity of peanuts to timing of heat stress during reproductive development. Crop Sci. 39: 1352－1357

Prasad PVV, Boote KJ, Allen Jr LH, and Thomas JMG (2002) Effects of elevated temperature and carbon dioxide on seed-set and yield of kidney bean (*Phaseolus vulgaris* L.). Global Change Biol. 8: 710－721

Prasad PVV, Boote KJ, Allen Jr LH, and Thomas JMG (2003a) Super-optimal temperatures are detrimental to reproductive processes and yield of peanut under both ambient and elevated carbon dioxide. Global Change Biol. 9: 1775－1787

Prasad PVV, Kakani VG, and Reddy KR (2003b) Plants and environment: Ozone depletion. In: Thomas B, Murthy DJ, Murray BG (eds) Encyclopedia of Applied Plant Sciences. Elsevier, London, UK, pp.749－756

Prasad PVV, Allen LH, and Boote KJ (2005) Crop responses to elevated carbon dioxide and interaction with temperature: Grain legumes. In: Tuba Z (ed) Ecological Responses and Adaptations of Crops to Rising Carbon Dioxide. Harworth Press, USA, pp.113－155

Prasad PVV, Boote KJ, and Allen Jr. LH (2006a) Adverse high temperature effects on pollen viability, seed-set, seed yield and harvest index of grain sorghum (*Sorghum bicolor* (L.) Moench) are more severe at elevated carbon dioxide due to higher tissue temperatures. Agric. Forest Meteorol. 139: 237－251

Prasad PVV, Boote KJ, Allen Jr LH, Sheehy JE, and Thomas JMG (2006b) Species, ecotype and cultivar differences in spikelet fertility and harvest index of rice in response to high temperature stress. Field Crop Res. 95: 398－411

Prasad PVV, Pisipati SR, Mutava RN, and Tuinstra MR (2008) Sensitivity of grain sorghum to high temperature stress during reproductive development. Crop Sci. 48: 1911－1917

Prasad PVV, Staggenborg SA, and Ristic Z (2009) Impacts of drought and/or heat stress on physiological, developmental, growth and yield processes of crop plants. In: Ahuja LH, Reddy VR, Saseendran SA and Yu Q (eds) Responses of Crops to Limited Water: Understanding and Modeling Water Stress Effects on Plant Growth Processes. Advances in Agricultural Modeling Series 1. ASA-CSSA, Madison, WI. pp.301－355

Premkumar A and Kulandaivelu G (1996) Influence of ultraviolet-B enhanced solar radiation on growth and photosynthesis of potassium deficient cowpea seedlings. Photosynthetica 32: 521－528

Randall HC and Sinclair TR (1988) Sensitivity of soybean leaf development to water deficits. Plant Cell Environ 11: 835－839

Randeniya LK, Vohralik PF, and Plumb IC (2002) Stratospheric ozone depletion at northern and mid latitudes in the 21st century: The importance of future concentrations of greenhouse gases nitrous oxide and methane. Geophys. Res. Lett. 29: 101－104

Raviv M and Antignus Y (2004) UV radiation effects on pathogens and insect pests of greenhouse-grown crops. Photochem. Photobiol. 79: 219－226

Reddy KR and Hodges HF (2000) Climate Change and Global Crop Productivity. CAB International, Oxon, UK, p.448

Reddy KR and Zhao D (2005) Interactive effects of elevated CO_2 and potassium deficiency on photosynthesis, growth and biomass partitioning of cotton. Field Crop Res. 94: 201－213

Reddy KR and Kakani VG (2007) Screening *Capsicum* species of different origins for high temperature tolerance by *in vitro* pollen germination and pollen tube length. Sci. Hortic. 112: 130－135

Reddy KR, Hodges HF, and McKinion JM (1997a) Crop modeling and applications: A cotton example. Adv. Agron. 59: 225－290

Reddy KR, Hodges HF, and McKinion JM (1997b) A comparison of scenarios for the effect of global climate change on cotton growth and yield. Aust. J. Plant Physiol. 24: 707－713

Reddy KR, Read JJ, Baker JT, McKinion JM, Tarpley L, Hodges HF, and Reddy VR (2001) Soil-Plant-Atmosphere-Research (SPAR) facility—A tool for plant research and modeling. Biotronics 30: 27－50

Reddy KR, Kakani VG, McKinion JM, and Baker DN (2002) Applications of a cotton simulation model, GOSSYM, for crop management, economic and policy decisions. In: Ahuja LR, Ma L and Howell TA (eds) Agricultural System Models in Field Research and Technology Transfer. CRC Press, LLC, Boca Raton, FL, pp.33－73

Reddy KR, Kakani VG, Zhao D, Mohammed AR, and Gao W (2003) Cotton responses to ultraviolet-B radiation: Experimentation and algorithm development. Agric. For. Meteorol. 120: 249－265

Reddy KR, Kakani VG, Zhao D, Koti S, and Gao W (2004) Interactive effects of ultraviolet-B radiation and temperature on cotton physiology, growth, development and hyperspectral reflectance. Photochem. Photobiol. 79: 416－427

Reddy KR, Koti S, Kakani VG, Zhao D, and Gao W (2005) Genotypic variation of soybean and cotton crops in their response to UV-B radiation for vegetative growth and physiology. In: Bernhard G, Slusser JR, Herman JR, Gao W (eds) Ultraviolet Ground- and Space-based Measurements, Models, and Effects. Proc. SPIE, pp.156－168

Reddy KR, Kakani VG, and Hodges HF (2009) Exploring the use of environmental productivity index concept for crop production and modeling. In: Ahuja LH, Reddy VR, Saseendran SA and Yu Q (eds) Recent Advances in Understanding and Modeling of Water Stress Effects on Plant Growth Processes, Crop Science Society of America, Madison, WI. pp.387－410

Ristic ZR, Bukovnik U, Momcilovic I, Fu JM, and Prasad PVV (2008) Heat-induced accumulation of chloroplast protein synthesis elongation factor, EF-Tu, in winter wheat. J. Plant Physiol. 165: 192－202

Rizhsky L, Liang H, Shuman J, Shulaev V, Davletova S, and Mittler R (2004) When defense pathways collide. The response of *Arabidopsis* to a combination of drought and heat stress. Plant Physiol. 134: 1683－1696

Rogers CA, Wayne PM, Macklin EA, Muilenberg ML, Wagner CJ, Epstein PR, and Bazzaz FA (2006) Interaction of the onset of spring and elevated atmospheric CO_2 on ragweed (*Ambrosia artemisiifolia* L.) pollen production. Environ. Health Perspect. 114: 865－869

Rosenfield JE, Douglass AR, and Considine DB (2002) The impact of increasing carbon dioxide on ozone recovery. J. Geophys. Res. 107: 4049

Rotem J and Aust HJ (1991) The effect of ultraviolet and solar radiation and temperature on survival of fungal propagules. J. Phytopathol. 133: 76－84

Rozema J, van de Staaij J, Björn LO, and Caldwell M (1997) UV-B as an environmental factor in plant life: Stress and regulation. Trends Ecol. Evol. 12: 22－28

Runeckles VC and Krupa SV (1994) The impact of UV-B radiation and ozone on terrestrial vegetation. Environ. Pollut. 83: 191－213

Saile-Mark M and Tevini M (1997) Effects of solar UV-B radiation on growth, flowering and yield of central and southern European bush bean cultivars (*Phaseolus vulgaris* L.). Plant Ecol. 128: 115－125

Salem MA, Kakani VG, Koti S, and Reddy KR (2007) Pollen-based screening of soybean genotypes for high temperatures. Crop Sci. 47: 219－231

Sancar A (1994) Structure and function of DNA photolyase. Biochemistry 33: 2－9

Savin R and Nicolas ME (1996) Effect of short episodes of drought and high temperature on grain growth and starch accumulation of two malting barley cultivars. Aust. J. Plant Physiol. 23: 201－210

Searles PS, Flint SD, and Caldwell MM (2001) A meta-analysis of plant field studies simulating stratospheric ozone depletion. Oecologia 127: 1－10

Sinclair TR and Purcell LC (2005) Is a physiological perspective relevant in a ‘genocentric’ age? J. Exp. Bot. 56: 2777－2782

Sinclair TR, N’Diaye O, and Briggs RH (1990) Growth and yield of field-grown soybean in response to enhanced exposure to ultraviolet-B radiation. J. Environ. Qual. 19: 478－481

Singh BB and Sharma B (1996) Restructuring cowpea for higher yield. Indian J. Genet. Plant Breed. 56: 389－405

Singh SK (2008) Developing screening tools for abiotic stresses using cowpea (*Vigna unguiculata* (L.) Walp.) as a model crop. Ph.D. Dissertation, Mississippi State University, MS

Singh SK, Surabhi GK, Gao W, and Reddy KR (2008a) Assessing genotypic variability of cowpea (*Vigna unguiculata* (L.) Walp.) to current and projected ultraviolet-B radiation. J. Photochem. Photobiol. B: Biology 93: 71－81

Singh SK, Kakani VG, Brand D, Baldwin B, and Reddy KR (2008b) Assessment of cold and heat tolerance of winter-grown canola (*Brassica napus* L.) cultivars by pollen-based parameters. J. Agron. Crop Sci. 194: 225－236

Soler R, Bezemer TM, Van der Putten WH, Vet LEM, and Harvey JA (2005) Root herbivore effects on above-ground herbivore, parasitoid and hyperparasitoid performance via changes in plant quality. J. Anim. Ecol. 74: 1121－1130

Souza RP, Machado EC, Silva JAB, Lagôa AMMA, and Silveira JAG (2004) Photosynthetic gas exchange, chlorophyll fluorescence and some associated metabolic changes in cowpea (*Vigna unguiculata*) during water stress and recovery. Environ. Exp. Bot. 51: 45－56

Sullivan JH and Teramura AH (1990) Field study of the interaction between solar ultraviolet-B radiation and drought on photosynthesis and growth in soybean. Plant Physiol. 92: 141－146

Tardieu F, Reymond M, Hamard P, Granier C, and Muller B (2000) Spatial distribution of expansion rate, cell division rate and cell size in maize leaves: A synthesis of the effects of soil water status, evaporative demand and temperature. J. Exp. Bot. 51: 1505－1514

Tegelberg R, Julkunen-Tiitto R, Vartiainen M, Paunonen R, Rousi M, and Kellomäki S (2008) Exposures to elevated CO_2, elevated temperature and enhanced UV-B radiation modify activities of polyphenol oxidase and guaiacol peroxidase and concentrations of chlorophylls, polyamines and soluble proteins in the leaves of *Betula pendula* seedlings. Environ. Exp. Bot. 62: 308－315

Teramura AH (1983) Effects of ultraviolet-B radiation on the growth and yield of crop plants. Physiol. Plant. 58: 415－427

Teramura AH and Sullivan JH (1994) Effects of UV-B radiation on photosynthesis and growth of terrestrial plants. Photosynthesis Res. 39: 463－437

Thiaw S and Hall AE (2004) Comparison of selection for either leaf-electrolyte-leakage or pod set in enhancing heat tolerance and grain yield of cowpea. Field Crops Res. 86: 239－253

Total Ozone Mapping Spectrometer (TOMS) (2009) Atmosphere Chemistry and Dyna mics Brach (Online). Available at http://toms. gsfc.nasa. gov/ery_uv/euv_v8. html (verified 3 June 2009)

Torabinejad J, Caldwell MM, Flint SD, Durham S (1998) Susceptibility of pollen to UV-B radiation assay of 34 taxa. Am. J. Bot. 85: 360－369

Tubiello FN, Amthor JS, Boote KJ, Donatelli M, Easterling W, Fischer G, Gifford RM, Howden M, Reilly J, and Rosenzweig C (2007) Crop response to elevated CO_2 and world food supply: A comment on "Food for Thought..." by Long et al., Science 312: 1918－1921, 2006. Eur. J. Agron. 26: 215－223

U.N. Population Division (2008) Webpage http://www.un.org/esa/population/unpop.htm

U.S. Census Bureau, (2008) U.S. and World Population Clocks—POPClocks. http://www.census.gov/main/www/popclock.html

Upadhyaya HD (2005) Variability for drought resistance related traits in the mini core collection of peanut. Crop Sci. 45: 1432－1440

Vu CV, Allen LH, and Garrard LA (1982) Effects of UV-B radiation (280 nm－320 nm) on photosynthetic constituents and processes in expanding leaves of soybean (*Glycine max* (L.) Merr.). Environ. Exp. Bot. 22: 465－473

Vu CV, Allen LH, and Garrard LA (1984) Effect of UV-B radiation (280 nm－320 nm) on ribulose-1, 5-bisphosphate carboxylase in pea and soybean. Environ. Exp. Bot. 24: 131－143

Walton GH, Si P, and Bowde B (1999) Environmental impact on canola yield and oil. In: Wratten N, Salisbury PA (eds) Proceedings of the 10th International Rapeseed Congress (CD-ROM). The Regional Institute Ltd, Canberra, Australia

Wan S, Yuan T, Bowdish S, Wallace L, Russell SD, and Luo Y (2002) Response of an allergenic species *Ambrosia psilostachya* (Asteraceae), to experimental warming and clipping: Implications for public health. Am. J. Bot. 89: 1843－1846

Warrag MOA and Hall AE (1983) Reproductive responses of cowpea to heat stress: Genotypic differences in tolerance to heat at flowering. Crop Sci. 23: 1088－1092

Warrag MOA and Hall AE (1984) Reproductive responses of cowpea (*Vigna unguiculata* (L.) Walp.) to heat stress. Ⅱ. Responses to night air temperature. Field Crops Res. 8: 17－33

Wentworth M, Murchie EH, Gray JE, Villegas D, Pastenes C, Pinto M, and Horton P (2006) Differential adaptation of two varieties of common bean to abiotic stress: Ⅱ. Acclimation of photosynthesis. J. Exp. Bot. 57: 699－709

Westgate ME (1994) Water status and development of the maize endosperm and embryo during drought. Crop Sci. 34: 76－83

Williams JH and Boote KJ (1995) Physiology and modeling predicting the unpredictable legume. In: Patte HE, Stalker HT (eds) Advances in peanut science. APRES, Stillwater, OK, pp.301－335

WMO (2007) Scientific Assessment of Ozone Depletion: 2006. Global Ozone Research and Monitoring Project 50. Geneva, Switzerland

Xiao G, Liu W, Xu Q, Sun Z, and Wang J (2005) Effects of temperature increase and elevated CO_2 concentration, with supplemental irrigation, on the yield of rain-fed spring wheat in a semiarid region of China. Agric. Water Manage. 74: 243－255

Yuan L, Yanqun Z, Haiyan C, Jianjun C, Jilong Y, and Zhide H (2000) Intraspecific responses in crop growth and yield of 20 wheat cultivars to enhanced ultraviolet-B radiation under field conditions. Field Crops Res. 67: 25－33

Zavala JA, Scopel AL, and Ballare CL (2001) Effect of ambient UV-B radiation on soybean crops: Impact on leaf herbivory by *Anticarsia gemmatalis*. Plant Ecol. 156: 121－130

Zhao D, Reddy KR, Kakani VG, Reed J, and Sullivan J (2003) Growth and physiological responses of cotton (*Gossypium hirsutum* L.) to elevated carbon dioxide and ultraviolet-B radiation under controlled environment conditions. Plant Cell Environ. 26: 771－782

Ziska LH (2003) Evaluation of yield loss in field sorghum from a C_3 and C_4 weed with increasing CO_2. Weed Sci. 51: 914－918

Ziska LH and Caulfield FA (2000) Rising CO_2 and pollen production of common ragweed, a known allergy-inducing species: Implications for public health. Aust. J. Plant Physiol. 27: 893－898

Ziska LH and George K (2004) Rising carbon dioxide and invasive, noxious plants: Potential threats and consequences. World Resource Rev. 16: 427－447

Ziska LH, Gebhand DE, Frenz DA, Faulkner S, Singer BD, and Straka JG (2003) Cities as harbingers of climate change: Common ragweed, urbanization, and public health. J. Allergy Cli. Immunol. 111: 290－295

Ziska LH, Epstein PR, and Rogers CR (2008) Climate change, aerobiology, and public health in the northeastern United States. Mitig. Adapt. Glob. Change 13: 607－613

Zoltán T (2005) Is the long-term elevated air CO_2 environment beneficial for plants, crops and vegetation? In: Tuba Z (ed) Ecological Responses and Adaptations of Crops to Rising Atmospheric Carbon Dioxide. Haworth Press, Inc., New York, NY, pp.1－6