

Impacts of Drought and/or Heat Stress on Physiological, Developmental, Growth, and Yield Processes of Crop Plants

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Abstract

Drought and heat stress are among the two most important environmental factors influencing crop growth, development, and yield processes. A comprehensive understanding of the impact of drought and heat stress will be critical in evaluating the impact of climate change and climate variability on crop production. Both drought and heat stress influence an array of processes including physiological, growth, developmental, yield, and quality of crop. The objective of this review is to provide an overview of the influences of these two stresses on the above processes independently and in combination. Our review suggests a clear need of information on interactive effects of stresses particularly of drought and heat stress which mostly occur in combination. Both short- and long-term stresses can significantly influence growth and yield processes when stress occurs at sensitive stages. Crops are generally more sensitive to drought and/or heat stress during reproductive stages of development, which mainly influences seed numbers. Some of the important traits associated with drought- and/or heat-stress tolerance are indicated and discussed. The impacts of drought and heat stress are often different, and tolerance mechanisms may also be different. There is a wide range of crop modeling approaches (simple empirical models and more mechanistic models) that try to quantify the impact of stresses on growth, development, and yield and yield quality traits. These crop models should have the capability to quantify the impact of both short- and long-term stress events on growth, development, and yield processes. Modeling growth, development, sink-source relation, grain yield, and grain quality of crops can improve understanding of physiological and genetic nature of tolerance which can lead to increased grain yield and quality of crops. Improved models can enhance our capacity to predict crop performance in future climates and also to identify traits that can potentially be improved or exploited to obtain higher and more stable crop yields under stressed environments.



David Drexler

Drought and high temperature (heat) stress are considered to be the two major environmental factors limiting crop growth and yield. These two stresses induce many biochemical, molecular, and physiological changes and responses that influence various cellular and whole-plant processes that affect crop yield and quality. The impacts of environmental stress, particularly those of drought and heat, have been studied independently. However, under field conditions, both of these stresses often occur in combination. The interactive effects of various stresses on crop plants have received far less attention. Simultaneous occurrence of multiple stresses increases the deleterious effect, such that the effect considerably exceeds the simple additive effects of the action alone (cross-synergism). Similarly, a plant subjected to a single stress can be capable of increasing its resistance to subsequent or other stress (cross-adaptation). Crop performance in terms of growth, development, biomass accumulation, and yield depends on the crop's ability to withstand, acclimate, or recover from the stress. Both stress tolerance and recovery often involve a complex network of molecular and biochemical processes that integrate together to achieve a specific response of the whole crop. Molecular and metabolic responses of plants to a combination of drought and heat stress are unique and cannot be directly extrapolated from the response of plants to each of these different stresses applied individually (Mittler, 2006). There exists a strong relationship between the plant water status and temperature, thus making it very hard to separate the contributions of heat and drought stress under field conditions. These aspects are even more important when we consider future climate change scenarios where seasonal changes in temperature and drought and occurrences of extreme weather events are highly expected.

Changes in concentrations of carbon dioxide and other greenhouse gases have caused global surface air temperatures to rise by about 0.8°C over the last century (IPCC, 2007). It has been suggested that variability in temperature extremes and water deficit events will be more critical in future climates. This was obvious from the 2003 summer heat wave in Europe that resulted in extreme temperature episodes (up to 5°C above normal temperatures) which were sustained throughout summer period (Rennenberg et al., 2006). While understanding processes at molecular and cellular level is important, it is even more important to integrate

these processes at whole-plant level. In the following sections, we will provide fundamental knowledge of drought and/or heat stress impacts on significant processes and on agricultural productivity. In addition, some of the important practical traits useful for determination of tolerance will be discussed. For this review, the term *drought stress* is assumed when leaf water contents are lower than optimum turgor; and for the term *heat stress*, it is assumed that temperatures are above the optimum and stressful for that particular process, growth stage, or plant species.

Impact of Drought and/or Heat Stress on Physiological, Growth, and Developmental Processes

Drought (water stress) and heat stress (increases in above-optimum air temperatures) often occur simultaneously, but they can have very different effects on various physiological, growth, developmental, and yield processes. Although drought and heat stresses have been extensively studied independently, relatively little is known about how their combination affects crop productivity. The few studies that examined the impact of the combined effects of drought and heat stress suggested that the combination of drought and heat stress had a significantly higher detrimental effect on growth and productivity of crops than when each stress was applied individually (Craufurd and Peacock, 1993; Savin and Nicolas, 1996). In addition, the combination of drought and heat stress was 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 impact of drought and heat stress in combination or isolation on important physiological, growth, developmental, and yield processes are described in the following sections. We acknowledge that responses of crop or plant species to drought and/or heat stress are highly variable. Therefore, the effects are discussed in a more generalized fashion, and sufficient care should be taken while making specific conclusions regarding a particular crop or variety within a crop species which can differ in its responses. In addition, it should also be considered that drought and heat stress impacts on these various processes and traits depend on the intensity, rate of increase, duration of stress, and stage of crop development.

Physiological Processes

Photosynthesis and Respiration

Drought stress induces several changes in various physiological, biochemical, and molecular components of photosynthesis. Drought can influence photosyn-

thesis either through pathway regulation by stomatal closure and decreasing flow of CO_2 into mesophyll tissue (Chaves, 1991; Chaves et al., 2003; Ort et al., 1994; Flexas et al., 2004) or by directly impairing metabolic activities (Farquhar et al., 1989). The main metabolic changes are declines in regeneration of ribulose biphosphate (RuBP) and ribulose 1,5-bisphosphate carboxylase/oxygenase (Rubisco) protein content (Bota et al., 2004), decreased Rubisco activity (Parry et al., 2002), impairment of ATP synthesis, and photophosphorylation or decreased inorganic phosphorus. In general, during the initial onset of drought stress, decreased conductance through stomata is the primary cause of decline in photosynthesis (Cornic, 2000). At later stages with increasing severity, drought stress causes tissue dehydration, leading to metabolic impairment. In contrast, there is evidence in some species that nonstomatal inhibition (metabolic activities) may occur first, causing a temporary increase in internal CO_2 concentration (C_i), which causes stomata to close (Briggs et al., 1986). Drought stress has been shown to cause increases in C_i (Siddique et al., 1999; Kicheva et al., 1994). Recent studies suggest that both diffusive limitation through stomatal closure and nonstomatal limitation (such as oxidative damage to chloroplast) are responsible for decline in photosynthesis under drought stress (Zhou et al., 2007).

The processes involved in photosynthesis are much more tolerant to heat stress and are mostly stable in the temperature range of up to 30 to 35°C, depending on crop species. However, very high temperatures (>40°C) can negatively affect photosynthesis. The response of photosynthesis to heat stress is related to temperature dependence of Rubisco to the two substrates, carbon dioxide and oxygen. At high temperatures, the solubility of oxygen is decreased to a lesser extent than CO_2 , resulting in increased photorespiration and lower photosynthesis (Lea and Leegood, 1999). In addition, the activation and activity of Rubisco are also decreased at high temperatures (Prasad et al., 2004). Heat stress primarily deactivates Rubisco by inhibiting the enzyme Rubisco activase (Crafts-Brandner and Salvucci, 2000). The mechanism responsible for inactivation of Rubisco under heat stress is related to inability of activase to overcome the inherently faster rates of Rubisco inactivation (Salvucci and Crafts-Brandner, 2004).

The photosynthesis apparatus, photosystem II (PSII), plays a key role in the response of leaf photosynthesis to environmental stresses. Photosystem II is relatively more tolerant to drought stress than heat stress (Havaux, 1992). Drought stress resulting in relative water content (RWC) and leaf water potential of 40% and -4 MPa, respectively, did not affect PSII functioning in dark- and light-adapted leaves (Havaux, 1992). In contrast, PSII is most sensitive to heat stress. There are two main factors which make the PSII electron transport most sensitive to heat stress. First, the fluidity of thylakoid membranes increases at high

temperatures; this leads to dislodging of PSII light harvesting complexes from thylakoid membrane. Second, the PSII integrity is dependent on electron dynamics. Therefore, if heat stress disrupts metabolic processes that either deliver or accept electrons from PSII, then the PSII is likely to dislodge from the thylakoid membrane. Havaux (1992) investigated the impact of drought, heat, and strong light applied separately and in combination on PSII activity and found that drought stress enhances the resistance of PSII to heat and light stress. Although Rubisco activation was more closely correlated with photosynthesis than the maximum quantum yield of photochemistry of PSII, both processes could be acclimated to heat stress by gradually increasing the leaf temperatures (Law and Crafts-Brandner 1999). The inhibition of PSII electron transport under heat stress is often indicated by sharp increase in basal level of chlorophyll fluorescence that corresponds to photosynthetic inhibition. Use of chlorophyll fluorescence measurements have been shown to be useful in quantifying the impact of drought and heat stress on plants (Oukarroum et al., 2007; Ristic et al., 2007).

The regulation of respiration under drought or heat stress conditions is relatively less understood. It is important to understand these responses, as photosynthesis is temporally (only during daytime) and spatially (only in green tissues) restricted, while respiration occurs continuously and in all organs. Mitochondrial respiration plays a pivotal role in determining the growth and survival of plants (Gifford, 2003). Despite the importance of respiration, studies examining the impact of drought stress on respiration are limited (Ribas-Carbo et al., 2005).

Temperature is one of the most important environmental parameters influencing mitochondrial respiration. Respiration exponentially increases with increasing temperatures from 0 to 35 or 40°C, reaching plateau at 40 to 50°C. At temperature above 50°C, respiration decreases because of damage to respiratory mechanism. Drought stress can result in decreases in leaf and root respiration in the short term (Byrle et al., 2001). Temperature quotient (Q_{10} , the relative change in a process with a 10°C temperature increase) for both root and leaf respiration also decreases with increasing temperatures. However, under field conditions, the relationship between temperature and root respiration is often complicated because of the occurrence of increased soil temperature with drought. In a greenhouse study under ambient and constant soil temperatures, root respiration rates decreased under drought stress conditions (Byrle et al., 2001). In addition, it was also observed that drought-induced decreases in root respiration were greater in warmer soils than in cooler soils.

The responses of respiration to drought and/or heat stress can vary among crop species and also with age of the organs as shown by different Q_{10} values (Paulsen, 1994). Mitochondria are very stable to heat stress and their activity

increases over most of the range in which plants are grown. However, heat stress is more destructive to mitochondrial activity than to chloroplast activity in some crop species and may injure plants by disrupting growth and maintenance respiration (Paulsen, 1994). Increased respiratory losses by seeds (grains or kernels) can offset the increased influx of assimilate and can account for greater yield losses under heat stress (Wardlaw et al., 1980). Thus, increasing the efficiency of respiration and its resistance to heat stress could improve tolerance to growth and yield.

The thermal effects of photosynthesis and respiration are related to membrane function and membrane integrity. In general, heat stress influences membrane fluidity, induces membrane leakiness, and influences the integrity of protein and membranes. Thylakoid membranes are especially sensitive to drought and heat stress; hence, disturbances in photosynthesis are among the first indicators of drought and heat stress. Under drought stress, photosynthesis decreases before the decrease of respiration, resulting in decrease in the ratio of photosynthesis and respiration and also increase in photorespiration. This often suggests that drought can cause starvation and lead to plant death. However, plants are more likely to suffer greater damage to shoots from the metabolic effects of drought rather than from lack of carbohydrates.

Overall, both drought and heat stress decrease CO₂ uptake either by stomatal regulation (as in case of drought stress) or internal resistance to CO₂ diffusion, both favoring oxygenase activity, leading to increased photorespiration and decreased photosynthesis. Photosynthesis is relatively more tolerant to heat stress compared with drought stress. This differential sensitivity of photosynthesis and respiration to drought and heat stress suggests differential interaction effects. The combination of both drought and heat stress may therefore be additive or multiplicative. The limited transpirational cooling under drought stress can exacerbate the effects of already higher air temperatures (Hale and Orcutt, 1987). Some studies suggest that drought stress influences the thermal tolerance of photosynthesis (Havaux, 1992; Lu and Zhang, 1999). In contrast, some studies have reported that drought greatly exacerbates the effects of heat stress on plant growth and photosynthesis (Xu and Zhou, 2005, 2006).

Physiological characterization of plants subjected to a combination of drought and heat stress has several unique aspects such as combining high respiration with low photosynthesis, closed stomata, and high leaf temperatures (Mittler, 2006). Mittler (2006) emphasized the importance of the combination of stresses and indicated that transcript profiling studies of plants subjected to a combination of drought and heat stresses reveal a unique response involving >770 transcripts that are not altered by drought or/and heat stress. Profiling

experiments further illustrate that acclimation responses of plants to drought or heat stress are different and that only a small overlap in transcript expression was found between the two responses (Mittler, 2006). Transcript changes in metabolite accumulation were highly specific during combinations of stresses (Rizhsky et al., 2002). These studies were conducted under controlled environmental conditions and in a non-crop species (*Arabidopsis*) under very low light conditions. Therefore, further studies are required to understand the interactions of drought and heat stress on photosynthesis and respiration for field crops to improve our knowledge and improve crop models.

Most of the existing mechanistic crop models use biochemical aspects (such as Rubisco kinetics) to estimate photosynthesis. However, these models have the ability to capture the diurnal changes in photosynthesis and respiration and seasonal changes in response to senescence and thus shed light on aspects which are less understood and need attention. Stomatal conductance changes diurnally in response to factors such as leaf water potential and carbohydrate contents, which can influence rate of leaf photosynthesis and respiration. Both heat and drought stress can influence these diurnal patterns as well as seasonal patterns associated with senescence. Plant physiological responses to the interacting effects of various abiotic and biotic stresses encountered in the natural environmental conditions should be understood and incorporated into the models. Currently, we do not have a clear understanding of the response of these processes, and further attention is needed.

Whole-Plant Responses

There has been significant progress in understanding the effects of drought and/or heat stress on various processes occurring at cellular level, particularly those related to carbon assimilation and cell growth, but the effects at whole-plant or crop level and its components are still not well understood. This is due mainly to complications associated with imposition of drought and/or heat stress in field conditions and interactions with other edaphic, biotic, and abiotic environments. The effects of drought and heat stress on whole-plant processes are manifold and can influence germination, emergence, leaf, root, tiller and stem development and growth, dry matter production, floral initiation, panicle exertion, pollination, fertilization, seed growth, seed yield, and seed quality. However, it is important to understand that sometimes the negative effects during one phase or trait can be compensated by recovery and excess growth of other organ or trait. For example, lower emergence can often be compensated by increased tillering or branching, or greater seed numbers can be hindered by partially filled seeds, or poor grain

yield can be compensated by increased grain quality (where post harvest quality is more important than total yield).

For most crop plants, the 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 is dependent on the soil water availability. Drought delays imbibition and thus can lead to decreased germination rates and total germination percentage. The rate of germination or seedling emergence can be calculated as the reciprocal of time to complete germination or emergence; this commonly has a linear response to temperature (Roberts, 1988), as do other developmental events such as leaf appearance and flowering (Roberts and Summerfield, 1987). At suboptimal constant temperatures, there is a positive linear relation between rates of development (e.g., seed germination rate and flowering) from the base temperature (T_b), at which the rate is zero, to the optimal temperature (T_o) at which development occurs most rapidly. At supraoptimal temperatures, there is a negative linear relation between the optimal temperature and the ceiling temperature (T_c), when the development rate is again zero (Roberts, 1988). At constant soil moisture conditions, percentage seed germination increases with increasing temperature above T_b , reaching maximum at T_o and decreasing at supraoptimal temperatures. Increasing temperature between base and optimum temperatures increase not only the rate of germination but also total percentage germination, but temperatures above optimum temperature decreases total percentage germination (Prasad et al., 2006c). Unlike temperature response, response to drought does not follow a bell shaped curve; rather, as soil dries (drought progresses), most of the growth and developmental events respond negatively until the developmental or growth processes cease completely.

Growth Processes

Cell division and cell growth are the two primary processes involved in plant growth. In general, cell division is considered to be less sensitive to drought when compared with cell enlargement or growth. However, both cell expansion and cell division can be influenced by relatively mild drought stress, even before photosynthesis or respiration is affected. Maintenance of cell turgor plays an important role in cell growth. Leaf area expansion is often limited under drought stress, such that the expansion and development of the transpiration surface is drastically decreased. Leaf expansion is among the most sensitive growth processes to drought (Alves and Setter, 2004). 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). Alves and Setter (2004) showed that both cell expansion and production of cells contributed to a loss in leaf area depending

on the developmental stage at which the leaf was stressed. In leaves that were no longer engaged in cell division, diminished cell expansion affected leaf area by reducing mature cell size, whereas, in younger leaves, inhibition of cell division resulted in fewer cells per leaf (Alves and Setter, 2004). Both cell division and cell expansion were able to recover fully when stress occurred at early phases of leaf development, but in leaves at the final phase of either cell division or cell expansion, these processes did not resume long enough to generate full size leaves (Alves and Setter, 2004). The general effects of mild drought on leaves are a reduction in leaf numbers, rate of expansion, and final leaf size. Under severe stress, the rate of leaf elongation decreases and leaf growth can cease. Drought stress can also influence total leaf area through its effect on initiation of new leaves, which is decreased under drought stress. Continued drought stress can accelerate leaf senescence (de Souza et al., 1997) and lead to death of leaf tissue, resulting in leaf drop, particularly old and mature leaves. Rewatering plants after a relatively short period of stress (3–5 d) does not completely eliminate the effects of drought on the senescence process (Brevedan and Egli, 2003). Decreased leaf senescence under drought stress is often termed as a tolerance mechanism, particularly to post flowering drought that occurs during grain-filling stages. In contrast, loss of leaf area can serve as a drought-avoidance mechanism as reduction in leaf area can help limit further water loss.

In contrast to drought, heat stress can stimulate cell division and cell elongation rates. Temperature has the most influence on the leaf appearance rate; thus, the concept of thermal time is most commonly used. High temperatures generally increase leaf appearance rates. Leaf-elongation rates increase at high temperatures, while decreasing leaf-elongation duration (Bos et al., 2000). The impact of heat stress on leaf area expansion and dynamics are relatively less understood and need attention. Heat stress resulted in significant increases in leaf numbers, particularly when reproductive development was arrested without any decrease in leaf photosynthetic rates (Prasad et al., 2006a). The importance of the leaf development and duration of crop growth is reflected in the amount of solar radiation that can be intercepted and used to accumulate crop biomass (Sinclair, 1994).

Comparing the effects of drought and heat stress on leaf elongation, it was shown that within the leaf, drought decreased relative elongation rates at all the positions of leaf by nearly similar extent, except in the zone closest to the leaf insertion point, causing reduction in length of the zone of elongation (Tardieu et al., 2000). In contrast, temperature stress affected relative elongation rates at all positions by a similar extent; consequently, the length of zone with tissue elongation was not affected by temperature. Because of differential processes and mechanisms influencing the leaf expansion, the combination of drought and heat

stress was additive (Salah and Tardieu, 1997; Tardieu et al., 2000). This clearly suggests that developmental and regulatory systems underlying cell division play a larger role in stress response either independently or when these stresses occur in combination. As early stages of development and leaf area expansion largely determine the rate of crop growth, a better understanding of these processes under various combinations of environmental conditions is very crucial for modeling the dry matter production and thus yield.

Recent studies have shown very strong correlations between leaf elongation rates and various physiological components (Welcker et al., 2007) that can be indicative of drought and/or heat stress. These relations include (i) positive correlation between the leaf elongation rates and leaf temperatures, (ii) strong linear negative correlations between leaf elongation rates and vapor pressure deficit (difference between saturated vapor pressure at leaf temperature and ambient vapor pressure), and (iii) a strong negative linear relations between leaf elongation rates and predawn leaf water potential. In other words, the response of leaf elongation rate to meristem temperature, evaporative demand, and soil water status were all linear and highly repeatable and thus could be modeled. If these relations are further confirmed with crops or populations, these could have profound consequences both for the modeling of genotype \times environment interactions and for designing the drought tolerant cultivars (Welcker et al., 2007).

Drought and heat stress often decrease stem growth and plant height. When plants experience drought stress, stem diameter shrinks in response to changes in internal water status (Simonneau et al., 1993). Changes in stem diameter were well correlated with predawn leaf water potential under prolonged drought (Katerji et al., 1994). Yatapanage and So (2001) used stem diameter data to predict leaf water potential in sorghum [*Sorghum bicolor* (L.) Moench] and showed promising results. Severe heat stress decreases stem growth resulting in decreased plant height (Prasad et al., 2006a). Root growth is very sensitive to water and heat stresses. Heat stress often decreases root growth, and it has been shown that root growth has a very narrow optimum temperature range when compared with other growth processes (Porter and Gawith, 1999). Heat stress reduced root number as well as root length and root diameter. Root growth is also decreased when heat stress occurs during reproductive development, mainly because of decreased carbon partitioning to roots (Batts et al., 1998). In contrast, the response of root growth to drought can be variable; under moderate moisture stress, root growth can be greater because of increased partitioning of carbohydrates to roots, whereas, severe drought often limits root growth, more so when it is associated with increased soil temperatures.

Developmental Processes

By the intensity and duration of stress, drought and heat stress not only influence the transition of one developmental stage to other but also the duration of the developmental stage. Development is mostly described as a function of temperature, suggesting it to be a major driving force, except where it is also influenced by photoperiod (daylength) or vernalization requirement. Both developmental rate of individual organs such as leaves and the progress of the entire plant through various ontogenetic stages are quantitatively dependent on temperatures (Sinclair, 1994). For example, warmer temperature stimulates more rapid development of leaf canopy and also causes the overall crop development rate to increase so that the crop growing season is shortened. To a large extent for most crops, temperature defines a limited season for crop development and growth. The higher the temperature the faster is the development and thus the shorter is the duration of the growth phase. Most of these are well described by a linear relationship between temperature and rate of development from base temperature to optimum temperature, above which the rate of development can decrease again (typical bell shaped curve). Development of floral structures begins later during the vegetative phase, and flowering marks the termination of vegetative growth for most of the crops that have determinate growing habit. Indeterminate plants undergo reproductive and vegetative growth simultaneously. Reproductive development begins with floral initiation, i.e., conversion of vegetative meristems to floral initials.

Drought and heat stress alter the initiation and duration of developmental phases. In most cases, the length of time from floral initiation (panicle initiation) to anthesis (panicle exertion) 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 the stress is relieved. Panicle initiation in sorghum was delayed by as many as 2 to 25 d and flowering by 1 to 59 d under drought stress, with more severe effects when drought was imposed both at early and late stage of panicle development (Craufurd et al., 1993). Drought and heat stress can delay the panicle initiation but also can cause the cessation of panicle development at any stages between panicle initiation and flowering. Severe drought or heat stress inhibits panicle exertion and also delays flowering (Cruz and O'Toole, 1984; Prasad et al., 2006a). Once panicle initiation has occurred, the rate of development is primarily a function of temperature, particularly when water and nutrients are not limited. Drought stress or heat stress during flowering and anthesis can lead to failure of fertilization because of decreasing pollen or ovule function. Drought stress or heat stress inhibits pollen development and causes

sterility. Drought and/or heat stress 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 are 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. Similar responses were also observed under heat stress, where the time from flowering to seed-set was increased under heat stress (Wheeler et al., 2000; Prasad et al., 1999a). Long duration of spikelet development and high spike weight at anthesis was positively correlated with final grain yield in wheat under drought and heat stress conditions (Wardlaw et al., 1989; Bindraban et al., 1998). For cereal crops, longer periods of vegetative and reproductive development are often necessary to improve reproductive potential (number of productive tillers and kernels) and also leaves and tillers to provide assimilate supply during the grain filling. Studies have also shown that decreased leaf area due to drought before anthesis is correlated with reductions in the number of kernels per spike (Frederick and Camberato, 1995).

Grain- or seed-filling duration is the time from seed-set to physiological maturity. For most crop species, particularly those where there is a physical restriction for growth of seeds as in case of rice, *Oryza sativa* L., (which has fixed pericarp) and legumes such as peanut, *Arachis hypogaea* L., or soybean, *Glycine max* (L.) Merr., (which has fixed locule size for development of the seed), yield capacity is mainly a function of seed numbers per unit area and seed-filling duration. Both drought (Frederick et al., 1991; de Souza et al., 1997) and heat stress (Hellewell et al., 1996; Prasad et al., 2006a) decreases the seed-filling duration, leading to smaller seed size. Drought following flowering is known to have little effect on seed-filling rates, but seed-filling duration is shortened leading to small seed size or seed yield (Wardlaw and Willenbrink, 2000). The impact of heat stress on seed-filling rates and seed-filling duration are similar to that of drought. However, there may be a slight increase in seed-filling rate but a large decrease in seed-filling duration under heat stress. The increase in seed-filling rate does not compensate for loss of duration, thus resulting in smaller seed size and seed yields (Shipler and Blum, 1986; Tashiro and Wardlaw, 1989).

Drought stress can impose source limitation on grain filling, whereas heat stress probably has more direct influence by limiting grain-filling duration. Where water and nutrient were not limited, a change in source-sink balance by lower seed numbers did not greatly influence the decrease in seed size associated with heat stress (Wardlaw et al., 1980), suggesting that the response to heat stress is not governed by overall availability of photosynthates. Studies on interaction effects between drought and heat stress during grain filling showed that

reducing kernel (seed) number did not alter the effect of heat stress following anthesis on dry weight of remaining seeds at maturity, but reducing the number of seed did result in a greater dry weight of the remaining seeds in drought stressed plants. The relationship between the response to drought and seed number was confounded by a reduction in the extent of drought stress associated with seed removal. Data on the effect of drought stress on seed dry weight at maturity of plants with either full complement or reduced seed numbers, and subjected to low or high temperature following anthesis, indicate that the effect of drought on seed weight may be reduced, in both absolute and relative terms, rather than enhanced, at higher temperature. It is suggested that where heat stress and drought occur concurrently after anthesis, there may be a degree of drought escape associated with heat stress because of the reduction in the duration of seed filling, even though the rate of water use may be enhanced by heat stress.

Under drought stress, the duration of grain filling may be controlled by the increased rate of leaf senescence, which in turn may be regulated by the N status of the plant (de Souza et al., 1997). Drought stress during grain filling generally decreases N accumulation of new plant tissues. This is particularly so because root growth generally decreases during the seed-filling period, contributing to decreased N uptake. Therefore, the accumulation of N in the seed during the linear seed-filling period can be met either by direct uptake of N or from remobilization of N from vegetative tissues (stems, leaves, or petioles). If the rate of N deposition in the seed is not directly reduced by drought, even greater portions of seed N would be contributed by remobilized N from leaves, which would partially explain why drought stress during seed filling accelerates leaf senescence and shortens the duration of seed filling (Frederick and Camberato, 1995). There is also evidence that a decrease in the seed-filling duration under drought conditions can often be compensated by increased seed-filling rate, particularly when there is access to carbohydrates either directly from the leaf photosynthesis or from those prestored in stems or leaves. The mechanisms of enhanced utilization of prestored carbohydrates are not well understood (Yang and Zhang, 2006). Many processes are likely to be involved, including storage, carbohydrate hydrolysis, phloem loading, long-distance translocation, and phloem unloading into the seed. Altered hormonal balance in the seeds by drought stress during seed filling, especially a decrease in gibberellic acid and an increase in abscisic acid (ABA), enhances the remobilization of prestored carbohydrates to seed (Yang et al., 2001). The utilization and/or remobilization of stored reserves from leaves or stems may be strongly tied to the enzymes related to carbohydrate metabolism. Acid invertase activity plays an important role in assimilate utilization (Zinselmeier et al., 2000), and drought (Zinselmeier et al., 1995) and heat stress

(Cheikh and Jones, 1995) decreases acid invertase activity that could influence seed growth. However, the exact mechanisms responsible for decreased expression of invertase activity under drought and/or heat stress are unclear.

One possible solution for maintaining the duration of seed filling and seed size under conditions of high demand from increased numbers of seeds is the stay-green trait (delayed senescence). The stay-green trait is found in several crops (e.g., modern corn, *Zea mays* L., hybrids). Some of the modern corn hybrids remain green and retain chlorophyll until physiological maturity, whereas the leaves of lower yielding old corn hybrids senesce before physiological maturity. The stay-green trait has also been observed in other crops such as sorghum (Tuinstra et al., 1996). The impacts of this trait on drought and/or heat tolerance are discussed in a later section.

Reproductive Processes

The success of reproduction is determined largely by the environmental conditions prevailing during the growth season (Boyer and Westgate, 2004). Among the various environmental factors, drought and heat stress have direct and major influence on reproduction. Reproduction is highly phasic, with each phase showing susceptibility to drought and heat stress. Early reproductive processes particularly those of micro- and megasporogenesis, pollen and stigma viability, anthesis, pollination, pollen tube growth, fertilization, and early embryo development are all highly susceptible to drought and/or heat stress. Failure of any of these processes decreases fertilization or increases early embryo abortion, leading to lower number of seeds or grains, thus limiting crop yield.

The physiological mechanisms controlling reproductive failure or abortion under drought and heat stress are not well understood. This is a major bottleneck for developing process-based mechanistic models. It is important to understand that whether these processes under stress conditions are controlled by changes in carbon and/or nitrogen, or the stress factors have direct influence on the reproductive processes. In addition, crop developmental stages are differentially sensitive to stress conditions. Stress just before anthesis and at anthesis caused significant increase in floral abortion and lower seed numbers in peanut (Prasad et al., 1999a), wheat, *Triticum aestivum* L., (Saini and Aspinall, 1981), rice (O'Toole, 1982; Matsui et al., 2001), and maize (Claassen and Shaw 1970). Most of the reproductive abortion in legumes occurs after fertilization during the early stages of embryo development. Drought stress during early stages of embryo development increased the rate of abortion (Westgate and Peterson, 1993). It is important to know if the abortion is caused directly by decreased water potential in the floral tissues (pollen or ovary) or is a result of decreased carbohydrate or nitrogen flux

supply, or if it is related to whole-plant signaling system involving hormones (particularly ABA). The response of floral parts might be different than those of developing embryos because of additional connections (e.g., placenta or chalaza) involved to link the embryo inside the ear or pod. Under drought stress, even though the leaf water potential was decreased, the embryos did not respond in similar fashion and had normal water potentials (Westgate et al., 1996). Drought imposed at flowering can also decrease photosynthetic rates and thus decrease the amount of photosynthates allocated to floral organs, causing increased abortion (Raper and Kramer, 1987). However, the demand for photosynthates by the small embryo is low, particularly during the very early stages of development, and the sink strength of these is much lower than in other tissues (such as vegetative tissues) to experience shortage of photosynthates. This strongly suggests that additional signaling systems must be involved to link the developmental responses which can result in early embryo abortion.

The plant hormone ABA signals drought stress. Increased concentrations of ABA in the root is observed under drought stress and may help maintain root growth and increase root hydraulic conductivity, which can lead to increase in water uptake and postpone development of water stress. Studies indicate that a stress induced hormone, ABA, plays an important role in signal transduction of stress from the whole plant (places where drought stress is sensed) to the remote plant parts such as developing embryos (where stress is not sensed) leading to sterility or abortion. ABA is transported in the xylem from roots to shoots, where it can cause stomatal closure, decrease leaf expansion and thus preventing the dehydration of leaf tissues. ABA can be produced abundantly in leaves under drought stress conditions and can be easily translocated into seeds (embryo), and it can influence embryo development. ABA has also been shown to be involved in mobilization of reserves under drought stress conditions. Studies with exogenous application of ABA suggest that mitotic and meiotic processes and developing seeds under full water conditions, showed similar responses to those of drought stress and led to lower seed-set and seed development (Mambelli and Setter, 1998; Myers et al., 1990).

Exposure to heat stress during flowering results in pollen sterility and loss of seed-set in legumes (groundnut; Prasad et al., 2000b; dry bean, *Phaseolus vulgaris* L., Prasad et al., 2002; cowpea, *Vigna unguiculata* (L.) Walp.; Ahmed et al., 1992; soybean; Salem et al., 2007) and cereals (rice; Satake and Yoshida, 1978; Jagadish et al., 2007; wheat, Saini et al., 1983). Lower seed-set under heat stress can be caused either by poor anther dehiscence, hence low numbers of germinating pollen grains on the stigma (Matsui et al., 2000; Prasad et al., 2006b; Jagadish et al., 2007) or because of decreased pollen viability (Prasad et al., 2000b, 2002,

2006a, 2006b) or ovule function (Gross and Kigel, 1994). However, in some crops [e.g., corn, sorghum, and millet, *Pennisetum glaucum* (L.) R. Br.] which produce large amounts of pollen grains, the ability of pollen to germinate or growth of pollen tube inside the style are more sensitive to environmental stresses. In species producing large amounts of pollen grains, loss of pollen viability under heat or drought stress would only decrease seed-set if the amount of pollen was also limited and/or if anther dehiscence was influenced by stress. Both microsporogenesis (pollen development) and megasporogenesis (stigma development) are injured under heat stress, resulting in lower seed-set (Cross et al., 2003; Young et al., 2004). Pollen is known to be relatively more sensitive to heat stress conditions. The mechanisms responsible for pollen sterility, lower seed-set or early embryo abortion under heat stress are not clear and need further investigation. There are several hypotheses that are proposed as possible mechanisms responsible to decreased pollen viability under drought and heat stress, some of which include: (i) developmental abnormalities in anthers leading to dislocation of microspores prematurely (Saini et al., 1984); (ii) dysfunction of tapetal cells because of abnormal vacuolization (Lalonde et al., 1997); (iii) premature degeneration of tapetal cells and lack of endothelial development (Ahmed et al., 1992); (iv) altered carbohydrate accumulation and metabolism (Jain et al., 2007; Saini, 1997); and (v) oxygen starvation in the developing microspores which could lead to loss of gametophyte viability.

Studies on maize have suggested that heat stress effects are associated with disruption of cellular and nuclear integrity, particularly in the cells in the periphery of the endosperm and it has been suggested that cytokinins may be responsible for these mediations (Jones and Setter, 2000). Heat stressed plants had no detectable levels of cytokinin, leading to seed abortion (i.e., cessation of dry matter accumulation before initiation of rapid starch deposition in the endosperm) or cease starch deposition prematurely (Cheikh and Jones, 1994). The decreased cytokinin pool under heat stress may be a result of decreased synthesis, conjugation to less active forms, or metabolism to inactive forms. Cheikh and Jones (1994) found that enzyme cytokinin oxidase (CKO) is relatively heat stable, and its activity increases under heat stress. This suggests that decline in endogenous cytokinin levels under stress was mainly caused by increased stimulation of cytokinin metabolism.

Recent studies suggest that there is a quantitative response to heat stress (temperature) between fertility and tissue temperature for both rice (Jagadish et al., 2007) and peanut (Prasad et al., 1999b) above a particular threshold temperature. There was a strong negative linear relation between pollen production and cumulative temperature $>34^{\circ}\text{C}$ in peanut (Fig. 11-1; Prasad et al., 1999b) and

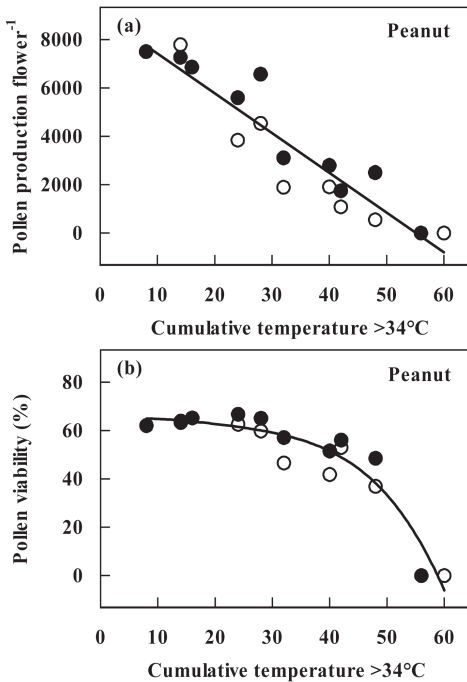


Fig. 11-1. Relationship between accumulated hourly temperature and (a) pollen production and (b) pollen viability in peanut. Redrawn with permission from Prasad et al. (1999b).

between spikelet fertility and cumulative temperature >33°C in rice (Fig. 11-2; Jagadish et al., 2007). Pollen germination and rate of pollen tube growth were also highly sensitive to heat stress (Prasad et al., 2000b; Kakani et al., 2002). A modified bilinear model best described the response of pollen germination and pollen tube growth to temperature in peanut (Kakani et al., 2002), cotton, *Gossypium* spp., (Kakani et al., 2005), and soybean (Salem et al., 2007). Such quantitative responses of pollen production, spikelet fertility, and response of pollen germination and pollen tube growth suggest a method to model the temperature responses and the interactions between the temperature and duration of heat stress on reproductive processes at more mechanistic way, where necessary. Short periods of heat stress can also influence pollen viability, seed-set, and grain growth (Prasad et al., 2000b; Stone and Nicolas, 1998). Exposure to as short as 1 h to temperature >37°C during flowering decreases seed-set (Matsui et al., 2000). Similarly exposure to temperature >33°C for first half of the day (6 h after anthesis) was enough to decrease pollen viability and thus seed-set in peanut (Fig. 11-3; Prasad et al., 2000b) and yield (Prasad et al., 2000a). As such, short durations of temperature stress can cause sterility; the timing of the episode of the high temperature relative to peak flowering will be very critical to quantify the impact of heat stress

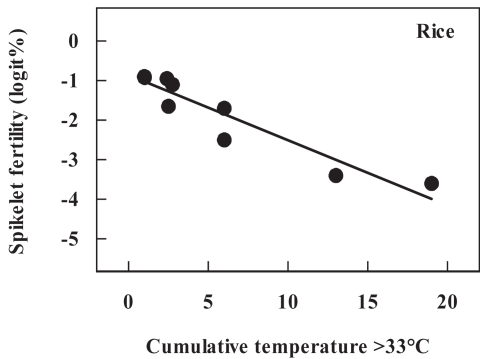


Fig. 11-2. Relationship between accumulated hourly temperature and spikelet fertility in rice. Redrawn with permission from Jagadish et al. (2007).

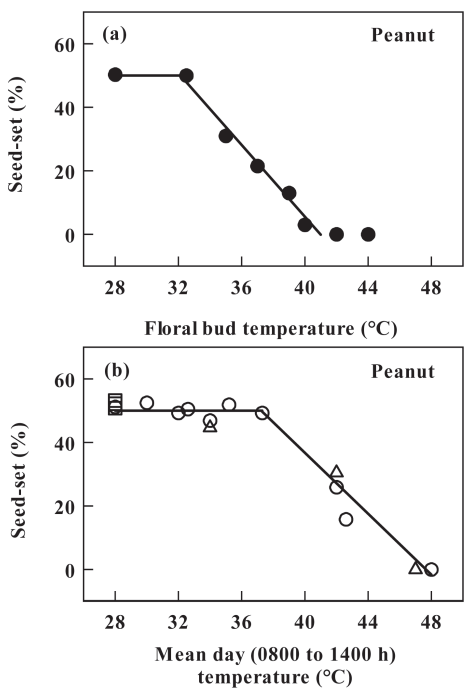


Fig. 11-3. Loss in seed-set (%) in peanut (a) when exposed to heat stress at flowering and (b) when exposed to heat stress during first 6 h (0800–1400 h) of the day. Redrawn with permission from Prasad et al. (2000b).

particularly to evaluate the phenotype and also for modeling the impact of heat stress (Wheeler et al., 2000).

The response of these reproductive processes at the whole-plant level may differ on the basis of the determinate or indeterminate nature of crop. Indeterminate crops (peanut, cowpea, pea, canola, *Brassica napus* L., and dry bean) undergo floral initiation over a longer period of time and floral development and events coinciding during nonstress or lower stress periods can compensate for inhibited development during the periods of higher stress. Increased reproductive abortion

at one stage can be compensated by increased seed-set at another stage of development or later flush of flowers, which may escape stress. Similarly decrease in seed-set and numbers can also sometimes be compensated by adjustment in seed yield. In contrast, determinate crops undergo floral initiation over a very short period of time and stress during this period can severely influence reproductive development (e.g., rice, wheat, barley, *Hordeum vulgare* L., and corn). Some plants can produce additional late tillers which can compensate for loss from the main tillers. However, the reproductive potential of late tillers is generally much smaller than those of main tillers.

Drought stress later during the reproductive development (after fertilization) decreases seed size rather than seed number. Seed size is the final component of yield. Seed size is largely dependent on the availability of photosynthetic reserves that are either currently available or those that can be moved from other parts into the grains. Seed size is mainly decreased by the reductions in assimilate and nitrogen supplies either through decreased photosynthetic rates or because of decrease in photosynthetic leaf area observed under drought stress. In addition, drought can also directly shorten the seed-filling duration, resulting in smaller seed size and yield. Some studies suggest faster grain filling and enhanced mobilization of stored carbohydrates can minimize the effects of drought on yield (Zhang et al., 1998). Drought and heat stress can negatively influence leaf area production and also green leaf area duration, thus decreasing the available photosynthates to seeds, ultimately influencing grain size and yield. High temperature can also directly influence the seed-filling rate or seed-filling duration, influencing the seed size and yield (Prasad et al., 2006a; Zhang et al., 1998) without negatively influencing the leaf photosynthesis and total leaf area. In contrast to temperature, seed growth was shown to be relatively insensitive to direct drought stress in soybean (Egli, 1994). Decreased leaf water potential did not influence individual seed growth rates either on a long-term or short-term basis because it did not affect seed water status (Westgate et al., 1989; Westgate and Grant, 1989). This is because of lack of vascular connection between the embryo and the mother plant. If drought stress inhibited photosynthesis or availability of photosynthesis as indicated earlier, it would decrease individual seed growth rates (Westgate et al., 1989). Genotypes selected for rapid ear growth under well watered conditions were shown to maintain relatively higher seed-set under drought conditions at flowering (Bolanos and Edmeades, 1996).

The interactive or combined effects of drought and heat stress on reproductive processes of crop plants have not been well defined and quantified for any crop species and needs investigation. There might be differences in response of reproductive function to these stresses. For example in corn, both drought

and heat stress have direct influence on seed-set or seed formation (Westgate, 1994). However, the cause is a result of effects on different processes. Heat stress decreased pollen viability, whereas drought stress (as measured low leaf water potential) inhibits pistillate flower development and function.

At present, crop models simulate seed-set (seed numbers) on the basis of carbon and nitrogen demand and/or availability. However, as discussed above reproductive processes that result in the seed-set themselves can be influenced by heat and drought stress. Incorporating these factors into the existing models would be challenging, and new approaches need to be developed. One possible approach would be to model potential sinks and rate of sink additions as a function of temperature and drought stress. The retention of those sinks and their growth can be modeled on the basis of carbon and nitrogen demand and supply as a function of stress factor. Some of these approaches are already being used in few models such as GOSSYM (McKinion et al., 1998) and CROPGRO (Boote et al., 1998).

Partitioning, Yield, and Yield Components

Under mild drought stress, pattern of resource allocation generally favors root growth rather than shoot growth. Severe stress conditions often decrease root growth. Timing of drought stress also has great influence on partitioning of carbohydrates and nitrogen. If drought stress occurs during early vegetative growth stages, there is a shift of partitioning toward roots rather than shoots, increasing the root-to-shoot ratio. This increase is due mainly to decreased shoot weight rather than increased root weight. Root mass rarely increases under stress, whereas root length and root volume often increase in response to mild stress. If drought stress occurs during the reproductive phase, there is no influence on the root-to-shoot ratio, but flowering and seed-set are decreased. If drought stress occurs after flowering, there is generally increased partitioning of resources toward seed filling.

Yield is mainly a function of various components which can broadly be divided into the number of plants (germination), dry matter production (growth, tillers, potential reproductive sites), seed numbers (reproductive processes and seed-set), and seed size (product of seed-filling rate and seed-filling duration). Drought mainly influences yield by limiting seed numbers 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 to decreased seed-set. Secondly, drought influences seed filling mainly by limiting the assimilate supply, leading to smaller seed size and lower yields. In contrast, heat stress mainly influences yields through seed numbers (Fig. 11–4; Wheeler et al., 1996) by influencing pollen or ovule function resulting

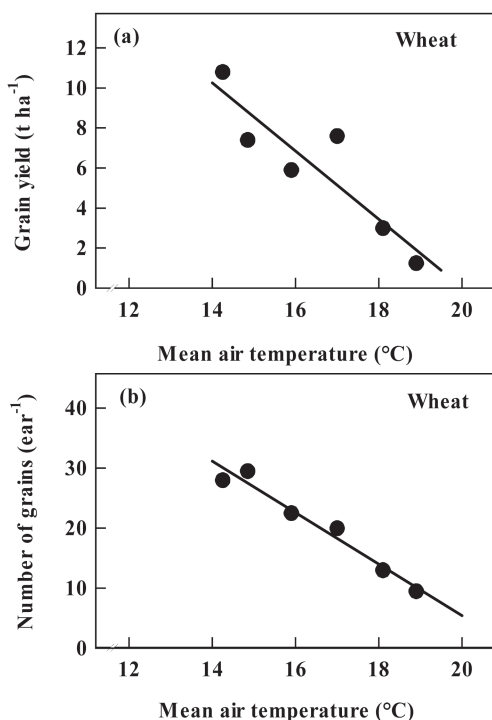


Fig. 11-4. Influence of mean temperatures from anthesis to harvest maturity on (a) grain yield and (b) number of grains per ear of a winter wheat cultivar. Redrawn with permission from Wheeler et al. (1996).

in lower seed-set. Heat stress directly influences seed-filling duration, leading to smaller seed size and lower yields. There might be compensation mechanisms for some of these traits such as increased seed size, which may compensate for lower seed numbers; however, these responses may vary depending on crop species. The crops such as indeterminate soybean, wheat, rice, and barley, where there is the ability to branch and tiller, which allows substantial reproductive compensation through seed numbers (Sadras, 2007). However, in species such as corn and sunflower (*Helianthus annuus* L.), where selection for one or few inflorescence may morphologically limit the seed numbers, there is increased variability in seed size. For example, in wheat there is often a very strong relation between the vegetative growth and seed numbers, provided there is no direct influence of drought or heat stress on reproductive processes (such as pollen and ovule function or panicle exertion). Similarly, there is a strong relationship between seed numbers and yield when compared with seed-size and yield. Recent review has provided some highlight into evolutionary trade-off between seed size and seed number in crop plants and concluded that seed size is generally more conservative than seed number (Sadras, 2007). Such greater changes and variability in yield components seeks greater physiological understanding and analysis of these processes, and even more under stress environments.

Resource-based crop simulation models use partitioning of dry matter as an important component of yield. Grain yield is generally simulated by assuming that the fraction of total above ground dry weight partitioned to grain (harvest index) is fairly constant. However, more recently stress response harvest indexes have also been used for more accurate prediction. Resource-based crop simulation often achieve significant accuracy in estimation of grain yield through appropriate resource allocation and also using stress responsive harvest index approaches (Meinke et al., 1997; Stockle et al., 2003). However, under stress conditions such as heat stress where the total dry matter is not reduced in proportion to yield because of the impact of several developmental events and other processes as described above, yield should be predicted as a function of seed numbers and seed size. It is important to consider the purpose of the model while determining to use a simple model or a more mechanistic model. Harvest index will give sufficient accuracy of grain yield in nonstressed environments. When harvest index is stable, the accuracy of yield predictions is entirely a function of the simulated rate of crop dry matter accumulation, and determination of grain sink size is not important. In contrast, the determination of kernel number (seed-set) is important when harvest index declines below normal range (for e.g., <0.48 for corn), particularly under high-stress conditions. The complexity of model selection or development is based on the purpose of the model. The recent development in gene-based crop simulation models can allow integration of individual traits, and such yield compensating mechanisms may mechanistically capture these effects at the crop level (Hammer et al., 2004; Hooogenboom et al., 2004; Messina et al., 2006). However, a combination of both resource capture and genetic and mechanistic approaches in crop models can provide increased understanding on physiological, genetic, and agronomic consideration in current and future climates.

Seed Quality

There are three important aspects of seed quality: (i) size of individual seed, (ii) composition or nutritional quality of seed, and (iii) ability of seed to germinate and grow. Growth environment plays an important role on all three aspects of seed quality. The impacts of drought and heat stress on seed size have been discussed in the earlier section. Drought and heat stress can have a profound impact on seed quality of cereals and legumes, mainly because of their impact on nutrient uptake, assimilate supply, partitioning, and remobilization of nutrients. This section will be explained with reference to wheat (cereal) and soybean (legume) where most of the literature is concentrated. Examples from other crops will be mentioned as necessary. The impacts on nutritional quality are mainly discussed in term of starch and protein (cereals) and oil and protein (legumes) contents.

The major characteristics that influence the suitability of grain for processing not only include grain size but also its homogeneity, fracture properties, specific weight and starch, protein and nonstarch polysaccharide contents, and sedimentation volume (which correlate with bread making quality) all of which can be influenced by both genotypes and environment (Gooding et al., 2002; Coles et al., 1997). As discussed earlier, both drought and heat stress reduces carbohydrate accumulation, which can influence protein concentration, by allowing more N concentration per unit of starch accumulated in the grain (Stone and Nicolas, 1998). Total protein content under heat stress may be decreased because of greater decreases in grain yield than protein accumulation (Stone and Nicolas, 1998). Heat stress during grain filling can increase protein concentration; it significantly decreases the functionality of the protein (Corbellini et al., 1997), which is important for the end-use quality. Heat stress also decreases the duration of protein accumulation, and therefore the amount accumulated, but does not affect the rate of protein accumulation. Although drought stress during flowering and grain filling often increase protein concentration and viscosity (Dubetz and Bole 1973), it decreases flour extraction, flour volume, loaf volume, and loaf score during baking (Randall and Moss, 1990; Gaines et al., 1997). Similarly, heat stress causes significant reductions in flour yield and mixing time (Gibson et al., 1998) and loaf volume (Blumenthal et al., 1991). Heat stress during grain filling also results in poor dough quality by decreasing aggregation property because of a reduction in the high molecular weight glutenins and an increase in gliadin accumulation, which decrease dough strength (Blumenthal et al., 1993; Stone et al., 1997; Randall and Moss, 1990).

Heat stress during post flowering stages decreases starch deposition, causes a reduction in starch granule size, deformed starch granules, and reduced amyloplast numbers (Jenner, 1994; Shi et al., 1994). Short-term exposure to heat stress (1 d at 35°C in wheat) also decreased activity of soluble starch synthase (SSS), but further increase in duration of stress did not impose any additional impact (Hawker and Jenner, 1993). Studies also conferred that temperature differences in starch synthase efficiency were correlated with difference in the temperature sensitivity of grain filling. There is often an inverse relationship between grain protein content or product quality traits and grain yield (Gooding et al., 2002; Dabaeke et al., 1996; Feil, 1997; Guttieri et al., 2000). Grain yields were, to a greater extent, more decisive for the protein and starch yields than the content (Erekul and Kohn, 2006). Little is known about the mechanisms during grain development that results in such changes in composition and nutritional quality (Toole et al., 2007).

Daniel and Triboi (2002) quantified and compared the impact of heat and drought stress on protein aggregation during grain development in wheat. They used a modeling approach in which rate and duration of protein accumulation were calculated as a function of thermal time. These studies showed that effects of temperature and drought on grain weight and on the quality of N in the grain were similar. Heat stress decreased the duration of soluble protein accumulation in terms of days after anthesis but not in terms of thermal time, whereas drought stress induced decreases in the duration both in terms of thermal time and days after anthesis. Heat or drought stress did not affect the rate of soluble and insoluble protein accumulation per degree-day, and the same equations can be used in a modeling approach. Studies have shown strong correlations between the leaf N content and grain protein content, particularly in wheat (Zhao et al., 2005), and suggested a technique to model grain protein on the basis of remotely sensing the leaf N content using vegetative index from the spectral reflectance data at the time of anthesis. Furthermore, they also showed that there was a strong negative relation between the reflectance data and leaf water content. This provides evidence that grain quality of the wheat can be estimated on the basis of the reflectance during anthesis stages; this might be particularly useful under conditions of drought, heat, or N stress.

Heat stress increased the percentage of shriveled seed and decreased seed size (Pan, 1996; Prasad et al., 2002, 2003). Seed composition and transcript abundance were also affected by heat stress (Thomas et al., 2003). Oil concentration increased with increasing temperature with an optimum at 25 to 28°C, above which the oil concentration declined (Dornbos and Mullen, 1992; Gibson and Mullen, 1996; Piper and Boote, 1999). Seed protein concentration of soybean was constant at temperatures between 16 and 25°C but increased at temperatures above 25°C (Wolf et al., 1982; Dornbos and Mullen, 1992; Gibson and Mullen, 1996; Piper and Boote, 1999). Oil and protein concentration were inversely related in response to heat stress during seed-fill (Piper and Boote, 1999). In contrast, quantifying the effects of temperature on oil and protein concentrations of soybean seed cultured *in vitro*, Pipolo et al. (2004) concluded that there was a similar quadratic response for oil and protein concentrations. Both protein and oil concentrations were a positively related and were a function of rate of dry matter accumulation of soybean seed. Therefore, temperature influence on seed size may result from changes in overall seed-growth rates, which in turn are likely to be dependent on carbon and nitrogen supply to the seeds (Pipolo et al., 2004).

Growth environment can also influence the nutritional quality such as accumulation of phytosterols and tocopherols (collectively called as tocols), which have health promoting effects (Britz et al., 2007; Wolf et al., 1982). Air tempera-

ture and soil moisture had obvious effects on absolute and relative amounts of the three major tocopherol species in soybean (Britz and Kremer, 2002). Slight increases in temperature combined with extreme drought caused a large increase in α -tocopherol that was almost precisely matched by decreases in δ -tocopherol and γ -tocopherol content (Britz and Kremer, 2002); thus, there was no effect on total tocopherol content. In contrast, drought caused small increases in tocopherol in one cultivar (cv. Williams), suggesting the responses were cultivar specific. Growth at elevated temperature significantly decreased isoflavins (Tsukamoto et al., 1995; Caldwell et al., 2005), while drought increased the isoflavon content (Caldwell et al., 2005).

In addition to decreasing seed size and seed composition, drought and/or heat stress can decrease the viability of the harvested seeds. Peanut seeds produced under drought stress had lower germination rate (Pallas et al., 1977). This was mainly attributed to insufficient calcium level that resulted from impaired calcium uptake under drought conditions (Cox et al., 1976). Similarly, soybean seeds obtained from plants grown at high day (35°C) and high night (30°C) temperatures had reduced subsequent seed germination and seedling vigor (Gibson and Mullen, 1996). The extent of reductions in seed germination and vigor by high temperature was influenced by duration of temperature and the phase of reproductive growth when the stress occurred. Greater reductions were observed with longer duration of exposure to high temperatures especially during seed fill and maturation. Studies on combined and interactive effects of drought and heat stress on seed quality of crops are limited and need further attention to better understand the impact of changing climates on a long-term basis.

Soil–Plant Water Relations

Drought causes changes in both soil and plant water potentials. Under drought conditions, soil water potential decreases; however, decreased soil water potential does not always lead to drought stress because the stress response is more dependent on the plant response. Therefore, measuring soil water potential may not be a good indicator of plant drought. High soil temperature generally causes increased evaporation and decreases soil water potential. Manifestation of drought in the plant often lags behind the soil water potential. Leaf water potential is often considered a reliable parameter for quantifying plant water stress. Leaf relative water content is a better indicator of drought stress than plant water potential. Plant water potential varies diurnally in response to transpiration; plant water potentials are greater during daytime than nighttime. There is a slight lag as water absorption responds slower than water loss from plant cells. When soil water potential is high, plant water potential approaches soil water

potential at night when stomata are closed. As soil dries under drought stress, hydraulic conductivity of soil decreases, and the rate of water movement toward root and absorption are slow to completely replace the water lost from the plant during the daytime because of transpiration. Thus, drought results in lower plant water potential. The effects of drought on leaf water potential are progressive rather than immediate. The changes in the plant water potential can be attributed to change in osmotic pressure or osmotic component of the water potential. When leaf water potential is low, it causes the stomata to close, which causes decreased transpiration which in turn leads to increased water potentials. However, if drought persists, the water potential will continue to decrease and reach a zero turgor (plant water potential = plant osmotic potential = soil water potential). This point is often referred to as permanent wilting point and is a function of osmotic potential of the plant. As mentioned above, the leaf water potential is influenced by transpiration and is also dependent on vapor pressure deficit (difference in vapor pressure from leaf and ambient air), which is affected by air and leaf temperatures.

Heat stress can also influence water relations of crops indirectly through faster depletion of soil water. Heat stress can deplete water faster from the soil through combination of increased evaporation by influencing soil temperatures and transpiration by increased vapor pressure deficit. There were no direct adverse effects of heat stress on osmotic adjustment; however, indirect effects of osmotic adjustment can occur through injury to photosynthesis, increased respiration, or decreased concentration of sugars in the cells. Machado and Paulsen (2001) found strong interactions between heat and drought stress on water relations. Water relations adjusted to heat stress when the soil was maintained at field capacity, whereas heat stress interacted strongly with drought and exacerbated its effects when water was withheld (Machado and Paulsen, 2001). This suggested that although drought is the only environmental stress that directly influences water status of the plant, the severity is highly dependent on temperature (Machado and Paulsen, 2001). The magnitudes of effects of heat stress on plant water relations were more severe under drought stress conditions. Crops respond differently to water relations under drought and heat stress. The interaction between heat and drought stress affected mostly relative water content and leaf water potential in sorghum, while in wheat these differences were smaller because of reduced plant growth under heat stress (Machado and Paulsen, 2001; Garrity et al., 1984). The reduced plant growth and smaller leaf area under drought stress decreases transpiration so that less water was removed from soil (Garrity et al., 1984). In sorghum, plant growth was increased under heat stress

(up to 35–30°C), leading to increased transpiration and decreased soil water content (Machado and Paulsen, 2001).

Nutrient Availability, Uptake, and Metabolism

At the molecular or cellular level, the photosynthetic capacity of plants is closely associated with leaf N. Both drought and/or heat stress can decrease N availability, plant N uptake, leaf N, and activities of N assimilatory enzymes. The two enzymes involved in assimilating intracellular ammonium into organic compounds are nitrate reductase (NR) and glutamine synthetase (GS). These changes in enzyme activities could be a result of changes in amino acid composition as altered by drought, heat, or combination of drought and heat (Rizhysky et al., 2004). Nitrate reductase activity, which plays an important role in regulating N metabolism, is decreased under heat stress (Al-Khatib and Paulsen, 1984; Singh and Sawhney, 1989). The decrease in extractable enzyme activity was slower than the decline in the soluble protein concentration in the leaves, indicating that nitrate reductase is less labile than most other protein to heat stress (Paulsen, 1994). Similarly, proteolytic enzyme activity which is commonly associated with senescence was increased under heat stress, particularly in mature leaves, which suggests a rapid mobilization of N compounds to grain (Al-Khatib and Paulsen, 1984). In plants, the carbon and nitrogen assimilation are coupled in plant metabolism, and the limitation of photosynthesis and growth by the interaction of stress factors, such as drought and heat, might be associated with an alteration of nitrogen levels and availability, aspects that have received little attention (Xu and Zhou, 2006). Temperature above optimum can impair nutrient uptake. The response of C_3 and C_4 plants can vary, and C_4 plants generally have greater efficiency for NO_3 uptake and assimilation than do C_3 plants because of highly organized cellular structure and spatial organization of N assimilatory enzymes (Oaks et al., 1990).

Drought stress due to decreased water availability and increased soil temperatures due to higher air temperature strongly influence nutrient absorption and uptake by plants. Although nutrient and water absorption processes are independent processes, the need for water for absorption and transport makes them highly dependent on each other. Most nutrients are absorbed by plant roots as ions and water is the medium of transport. Under fully irrigated conditions when soil water potential is high, the absorption and transport of water and nutrient are higher. Drought stress decreases nutrient transport by diffusion and mass flow to the root surfaces and nutrient absorption by roots, which is influenced by water potential. Under water stress, roots are unable to take up nutrients from the soil because of lack of activity of fine roots, water movement, and ionic diffusion of nutrients. Drought influences nutrient uptake not only

via effects of nutrient availability at the rhizoplane but also by altering nutrient capability of mycorrhizal or nonmycorrhizal roots (Rennenberg et al., 2006). Gessler et al. (2005) observed that in the long term, drought stress combined with increased soil temperature during growth season decreased maximum nitrate uptake capacity (V_{\max}) of mycorrhizal roots by a factor of 2 to 3, whereas ammonium uptake capacity was not affected. Nitrate uptake capacity was also reduced during severe short-term drought periods (Fotelli et al., 2002). Increased soil temperatures improve microbial mineralization of N and P, increasing its resupply to plants. Increased nutrient uptake capacities with increasing temperatures have been observed for NH_4^+ , NO_3^- , PO_4^- , and K^+ (Bassirirad et al., 1991; Bassirirad, 2000). Increased temperatures can cause increased nitrification and denitrification resulting in loss of N. In contrast, drought stress decreases microbial activity, which leads to lower nutrient availability. Since nutrient uptake by mycorrhizal or nonmycorrhizal plant roots is mainly an active transport process, it is likely that all energy-consuming enzymatic processes are highly temperature dependent. The amount of dissolved P and rate of dissolution are directly related to soil moisture content; thus, there is less P available under drought stress and increased soil temperature. Similarly, as indicated earlier, microbial activity which is responsible for release of N, P, S, and other micronutrient for root absorption are also highly dependent on water (Singh, 1998).

The direct effects of drought on nutrient transfer are limited and not clearly understood. Early studies have suggested that transport of ions from root to shoot is decreased under drought stress (Hsiao, 1973). However, as drought stress decreased the overall growth of the plants, it decreases the nutrient requirement. Nitrate and ammonium accumulation decreases under drought stress. The flow of nitrogen from roots to leaves slows down and higher concentrations of nitrate and ammonia build up in drought-stressed roots than in the roots of well-watered plants (Nilsen and Muller, 1981). The higher concentration of nitrogen ion in the roots of drought-stressed plants inhibits the accumulation of nitrogen from the soil (Nilsen and Orcutt, 1996). Therefore, the reduction in nitrogen accumulation is not due to specific effects of drought stress on transport proteins or accumulation mechanisms; rather, the changes in nitrogen use and flow results in conditions that inhibit nitrogen accumulation kinetics (Nilsen and Orcutt, 1996).

Generally, higher N levels in the leaves enhance photosynthesis and delay leaf senescence (Sinclair et al., 2000), and drought results in decrease in leaf N content (Sinclair et al., 2000). The absorption and assimilation of nutrients occur normally under optimum temperature conditions, and any changes below or above optimum can adversely affect these processes. Few studies have investigated the combined influence of drought and heat stress on nitrogen metabolism

(Xu and Zhou, 2006). These studies showed that drought decreased leaf N, heat stress did not influence leaf N, and, however, the total soluble protein content was decreased during drought, heat, and a combination of drought and heat. They concluded that heat stress induced suppression of photosynthesis by mainly decreasing the proportion of soluble protein to total leaf N, adversely affecting the Rubisco protein and activity. A combination of drought and heat stress can weaken the N pool because of a decline in free amino acids that contain many transfer substances involved in nitrogen metabolism (Lam et al., 1996) and other osmotic compounds (Morgan 1984). In addition, photosynthesis and thylakoid membrane damage as assessed by the efficiency of PSII photochemistry (Fv/Fm) are significantly correlated with leaf soluble protein, free amino acid, NR, and GS activity (Xu and Zhou, 2006).

The amount and type of nutrient availability to plants change with drought and temperature stress. Therefore, it is important to consider changes in fertilizer recommendations when the likelihood of plants experiencing heat or water stress increases. The interactions of climate variability, particularly those related to drought and heat stress with nutrient stresses or nutrient requirement have received far less attention and should be a focus of future research.

Sensitive Stages to Drought and Heat Stress

The impacts of drought or heat stress on crop growth and yield depend on the severity and duration of stress and the plant developmental stage at which the stress occurs. Drought and heat tolerance tends to be the greatest during early seedling stages and progressively decreases through later stages of development until the flowering and early seed-filling stages. The most sensitive stages of development to drought stress are generally during panicle development and during flowering in cereals and the period just before flowering and during flowering in legumes. However, most of the research on our basic understanding of stress tolerance and its application is focused on developmental stages other than stages just before flowering and at flowering (Valliyodan and Nguyen, 2006). In most cases, the reproductive parts of crop plants are the harvestable yields, and future success in producing drought and heat tolerant crop relies on intensive research to understand the mechanisms and processes influenced by stress and efforts to improve reproductive success (Valliyodan and Nguyen, 2006). Drought stress during flowering causes the largest decrease in yield when compared with that of other stages of crop development as shown for rice (Fig. 11–5; O'Toole, 1982), corn (Fig. 11–6a; Claassen and Shaw, 1970), and soybean (Fig. 11–6b). The sensitivity of crops to temperature stress is also somewhat similar to the sensitivity to drought

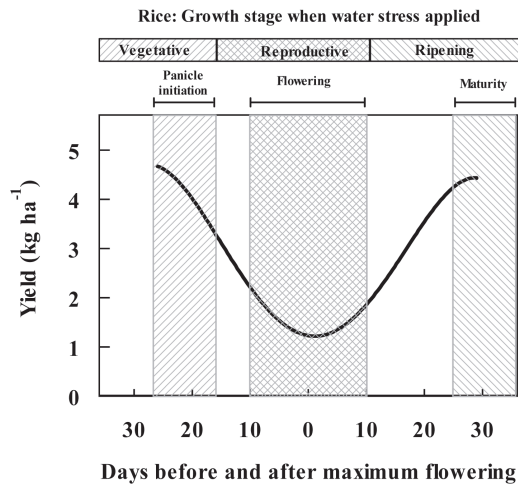


Fig. 11-5. Relative sensitivity of different growth stages of rice to water stress. Redrawn with permission from O'Toole (1982).

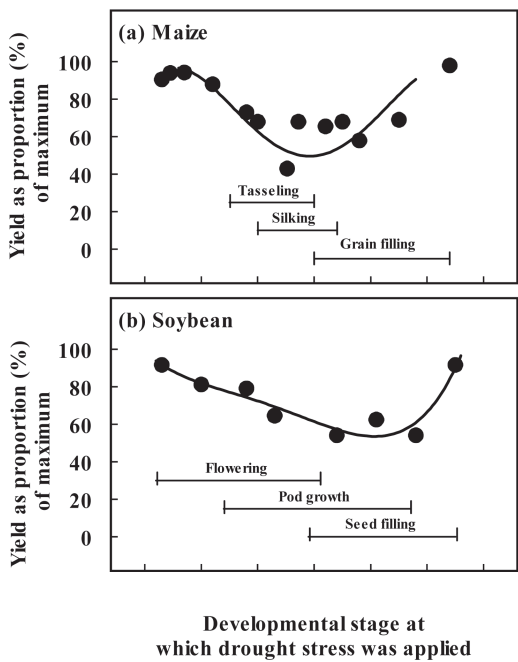


Fig. 11-6. Relative sensitivity of different growth stages of (a) maize and (b) soybean to water stress. Redrawn with permission from Claassen and Shaw (1970).

stress, in the sense that stages just before, during, and soon after flowering are more sensitive to high temperature stress than other stages, as indicated by an example seen in a legume (peanut; Fig. 11-7, Prasad et al., 1999a) and a cereal (sorghum, Fig. 11-8; Prasad et al., 2006a). The impacts of drought and heat stresses during these developmental stages were discussed in the earlier section. One of

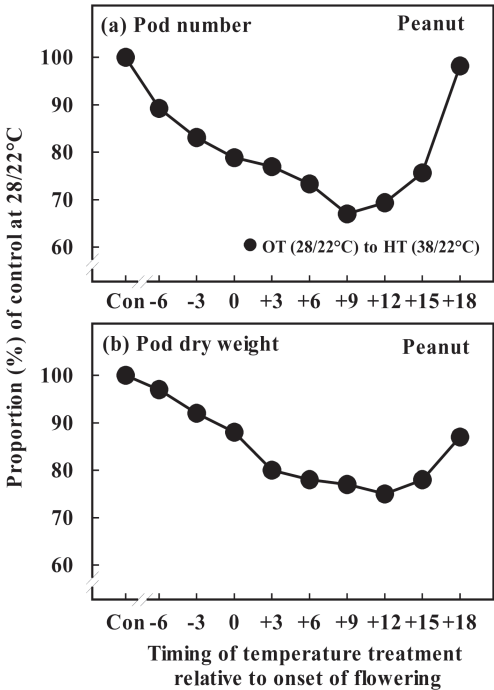


Fig. 11-7. Relative sensitivity of peanut in terms of (a) pod number and (b) pod dry weights in response to heat stress (38/28°C) during early and late flowering stages of peanut. Redrawn with permission from Prasad et al. (1999a).

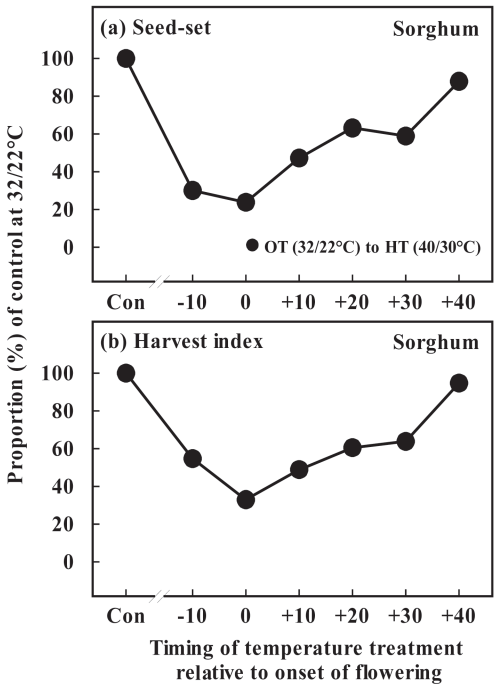


Fig. 11-8. Relative sensitivity of sorghum in terms of (a) seed-set and (b) harvest index weights in response to heat stress (40/30°C) during early and late flowering stages of sorghum. Redrawn with permission from Prasad et al. (2008).

the reasons for greater sensitivity of drought and heat stress during reproductive processes, relative to vegetative processes, is the fact that vegetative processes such as photosynthesis and development can acclimate to stress either by production of osmolytes and heat shock protein and by regulation of growth. However, the reproductive organs, particularly pollen and stigma, do not have the potential to acclimate because of their inability to produce heat shock proteins or other types of osmolytes that can either provide protection or increase acclimation potential of these organs.

Understanding the impacts of climate change and climate variability requires improved understanding of the impacts of increased mean temperatures as well as the impacts of short-term extreme temperatures (Wheeler et al., 2000). Long-term temperature increases over the season will change the duration and/or resource allocation (Roberts and Summerfield, 1987). The season-long impacts of temperatures on various crops have been documented for important legumes (e.g., dry bean, Prasad et al., 2002; peanut, Prasad et al., 2003; soybean, Baker et al., 1989) and cereals (rice, Baker et al., 1994; wheat, Wheeler et al., 1996; sorghum, Prasad et al., 2006a). The typical response of various crops to season-long growing temperatures under controlled environment conditions on seed size and harvest index are shown for rice and peanut (Fig. 11–9; Boote et al., 2005). In addition, the

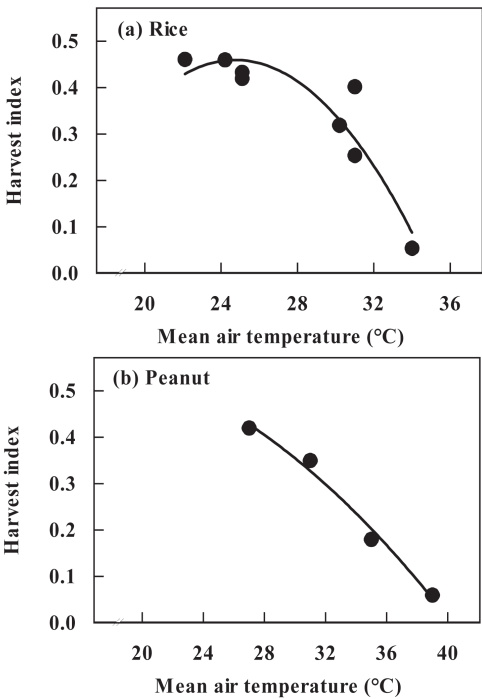


Fig. 11–9. Response of harvest index of (a) rice and (b) peanut in response to season long heat stress. Redrawn with permission from Boote et al. (2005) and Prasad et al. (2004).

impacts of short episodes of heat stress are more accurately quantified at sensitive stages for several legumes (for e.g., peanut, Prasad et al., 1999a, 2000b, 2001a; soybean, Ferris et al., 1999; cowpea, Ismail and Hall, 1999) and cereals (e.g., rice, Matsui et al., 2001; wheat, Ferris et al., 1998; sorghum, Prasad et al., 2006a). Similarly, the impact of continuous drought and short episodes of drought during sensitive stages are also understood (Saini, 1997). Maize is particularly sensitive to water stress at 7 d before and 15 d after flowering (Grant et al., 1989). The knowledge about the quantitative responses of drought and heat stress on reproductive processes and yield can now be incorporated into crop simulation models to improve their predictive capabilities. Such approaches are being recognized (Matthews et al., 1995; Semenov and Porter, 1995; Wheeler et al., 2000; Porter and Semenov, 2005; Challinor et al., 2005) and used in crop simulation models (Challinor et al., 2007) to improve their predictability in current and future climates.

Drought and Heat Compensating Traits and Tolerance Mechanisms

Plants show a wide range of compensating, escape, or tolerance mechanisms for drought and heat stress through various molecular, biochemical, physiological, or developmental or growth adaptations. The traits important for performance under drought and/or heat stress include enhanced root density and depth, transpiration efficiency, phenology and duration, rapid establishment, early vigor, lower stomatal conductance, slow wilting, leaf angle, leaf reflectance, delayed leaf senescence, accumulation and mobilization of carbohydrates and nitrogen from root to grain, osmotic adjustment, and heat shock proteins and dehydrins. Some of these mechanisms are described briefly in this section. We limited our discussion to whole-plant processes; however, we acknowledge that molecular and biochemical changes may be important or useful for stress tolerance. The examples and discussion is limited to those which can have an impact at whole-plant level rather than at cellular level. Although some of the survival traits are mentioned in the discussion (e.g., osmotic adjustment), generally survival traits do not improve potential yield under drought or heat stress conditions. Drought and/or heat tolerance is extremely complex and affects multigenic traits. Thus, oversimplification of the effects of drought and heat stress and aiming for one single trait may not be a viable solution.

Enhance Root Growth to Capture Soil Moisture

One of the important components of tolerance to drought is enhanced soil moisture capture, which is possible by increased exploration of soil by the roots. Deeper roots will enable water absorption from greater depth. This is particularly

true when the moisture is available at deeper depth. Typically soil dries from the top down; therefore, plants with deeper rooting systems will have longer periods of access to whatever water is available. Extensive root growth and distribution of roots will help explore larger soil volumes and thus may provide plants greater access to water and nutrients under drought conditions. Short periods of drought stress, particularly during the reproductive stages, can cause drastic reductions in grain yield. Cultivars with deeper root systems, when compared with shallow root systems, are generally more tolerant to drought stress during critical stages of crop development. Jordon and Miller (1980) suggest that sorghum cultivars with greater root length density at greater depths would increase water uptake and decrease water stress during grain-filling stages. Cultivars with larger root length densities and deeper rooting systems were found to be more tolerant to drought stress conditions in soybean (Hudak and Patterson, 1996; Sloane et al., 1990; Sponchiado et al., 1989) and wheat (Hurd, 1974). However, it is also important to consider that a plant with greater root length density may have greater access but use up the water rapidly, grow rapidly, and deplete the shallow water profile faster. Such cultivars may become severely stressed during later stages of reproductive development, which may result in lower yields. This is particularly important if the soil is shallow. Clearly, the selection trait is highly location specific and cannot be generalized for all locations and soils. Improved and better root growth may also be useful for heat stress conditions. Heat stress is often associated with high vapor pressure deficit, which increases the loss of water from the leaves. Plants will transpire more to keep the canopy cool; this cooling is only effective in the presence of water. Therefore, improved root systems will enable plants to transpire and keep the canopy cooler for longer periods of time. High soil temperatures can also directly decrease root growth (Prasad et al., 2000a) and nitrogen fixation (Prasad et al., 2001b), leading to lower yields.

Despite the importance of root growth and distribution on drought and/or heat tolerance, very little progress has been made in identifying cultivars with more efficient root systems or in breeding for improved root growth. This is because root growth is very difficult to measure and quantify, and quantification is labor intensive and destructive. In addition, destructive measures do not allow periodic samples over time; instead, it provides one time measurements, and taking multiple samples requires a large area and is labor intensive. There are some recently developed techniques such as root imaging through minirhizotron tubes that allow quantification of root growth over time. However, image quality and image analysis requires technical skills, extrapolation, and are expensive. There may be some other indirect traits which can be used as a surrogate measurement of root growth, such as lower canopy temperature or increased stomatal

conductance, which are indicative of increased water use under drought conditions. There are also some simple, inexpensive methods such as placement of herbicide deep in the soil between the rows of plants and monitoring the time taken for plants to respond to herbicide (Robertson et al., 1985). The plants with faster root development will reach the herbicide faster and show injury symptoms earlier than those with slower root development. This technique was used to identify genotypes with faster root system in cowpea (Hall and Patel, 1985) and peanut (Khalfaoui and Havard, 1993).

Transpiration Efficiency

Plant water-use efficiency (WUE) is a common trait associated with drought and is defined as the amount of biomass or yield accumulated per unit of water used. However, field determinations of water use frequently include evaporation, runoff, and drainage components of the soil water balance, which can confound evaluation of plant effects. Analyses focused on plants consider transpiration use efficiency, which is defined as the amount of biomass or yield accumulated per unit of water transpired. Tanner and Sinclair (1983) derived a formulation of transpiration efficiency from energy balance theory, introduced previously, and knowledge of plant biosynthesis. Assimilate requirements for biosynthesis of plant material depends on conversion of hexoses into plant constituents, e.g., the efficiency with which assimilates are converted into cellulose, proteins, fatty acids, and lignin. The derived relationship $Y/T = k/vpd$ holds that the ratio of assimilate (Y) to transpiration (T) is proportional to a conversion constant (k), adjusted for variation in vapor pressure deficit (vpd). The conversion constant differs for each crop type, depending on plant composition and associated conversion efficiency.

Intrinsic transpiration efficiency is the ratio of net photosynthesis to leaf conductance of water vapor. This ratio is proportional to the partial pressure of CO_2 in the substomatal cavity, a determinant of the ratio of CO_2 flux and H_2O efflux across stomata for a given set of environmental conditions. Transpiration efficiency is an important component of WUE. Increased transpiration efficiency can be obtained by either increasing biomass or photosynthesis or by decreasing transpiration or a combination of the traits. Often there are penalties associated with increasing or decreasing one trait. The challenge for physiologists and crop breeders is to increase photosynthesis and decrease transpiration.

Several studies have shown positive relations between WUE and yield [e.g., peanut (Wright et al., 1988; Wright, 1989) and cowpea (Craufurd et al., 1998)]. Genetic variation for WUE has been observed in several crops such as wheat (Farquhar and Richards, 1984; Merah et al., 2001), barley (Hubick and Farquhar, 1989), sorghum (Peng and Krieg, 1992), and peanut (Hubick et al., 1986). Improvement of

cultivars using this trait has not been very successful because of the complexity of the trait and also the difficulty in measuring WUE under field conditions (Ismail and Hall, 1992). With the advent of molecular breeding, identification of QTL and their use in the breeding programs may help develop new cultivars with drought tolerance. Recently, the ERECTA gene has been associated with transpiration efficiency (Masle et al., 2005). They showed that expression of ERECTA gene resulted in reduced stomatal frequency and conductance and greater photosynthetic rates, resulting in increased WUE under a wide range of water regimes.

Measurement of transpiration efficiency under field conditions is confounded by errors in the soil water balance; therefore, surrogate measures such as carbon isotope discrimination were developed. Carbon isotope discrimination provides information on the intrinsic transpiration efficiency on the basis of data from the time-integrated internal carbon dioxide concentration (Farquhar et al., 1982). Several studies have shown strong negative relations between carbon isotope discrimination and intrinsic transpiration efficiency (Morgan et al., 1993). There is a strong positive correlation between carbon isotope discrimination and grain yield (Fischer et al., 1998; Voltas et al., 1998), particularly under moderate post-anthesis drought or fully irrigated conditions (Monneveux et al., 2005). However, under severe drought stress, there are not even negative relationships (Ararús et al., 2003). Positive relationships and higher carbon isotope discrimination can be a result of greater access to water (root growth), increased water extraction capability (osmotic adjustment), higher remobilization of stem reserves, or early flowering, which allows the beginning of grain filling with more available water (Tambussi et al., 2007).

Shorter or Longer Growth Duration and Crop Phenology

Shorter life cycle and short growth duration can decrease the total water use by plants, compared with longer duration and larger leaves because of decreased transpiration. It is also important to consider that when leaf area decreases, there will be increased radiation reaching the soil surface, which enhances the evaporation from soil surface and increases the total water use (i.e., transpiration + evaporation). Several studies have shown that shorter-duration cultivars escape drought because they complete their lifecycle before the occurrence of drought, whereas long-duration cultivars have greater chances of being exposed to severe drought or heat stress, particularly, during the later stages of crop development. In contrast, cultivars with larger leaves and longer duration can decrease evaporation from the soil and increase water use through transpiration and can contribute to greater yields. Therefore, sufficient care should be taken while selecting the traits which will help ameliorate the drought conditions; this may be location

specific, depending on the rainfall distribution and solar radiation. In general for most crops, there is wide variability in phenology and thus duration of crops, and this trait is a single gene traits and its inheritance is relatively better known. This makes phenology an important breeding trait for use in commercial applications. It is important to consider that the occurrence of drought is very unpredictable under semiarid and dry regions; therefore, if drought occurs during the sensitive stages of these short life cycle cultivars, the impact can be more severe than the long-duration cultivars that might have accumulated greater dry matter and stored more carbohydrates for seed-fill, and the result may be higher yields.

With respect to the importance of phenology to heat stress, Tewolde et al. (2006) recently identified and quantified the characteristics of wheat cultivars adapted to production systems with risks of heat stress during the post-heading period. They conclude that early-heading cultivars outperformed later-heading cultivars because of two distinct advantages: the early-heading cultivars had a longer post-heading period and, therefore, a longer grain-filling period than the later-heading cultivars. In addition, early-heading cultivars would have completed a greater fraction of the grain-filling duration earlier in the season when air temperatures were lower and generally more favorable. The advantage of earlier-heading cultivar was also manifested in the amount of green leaves retained to anthesis. Earlier-heading cultivars produced fewer total leaves per tiller but retained more green leaves and lost fewer leaves to senescence at anthesis than later-heading cultivars. The results suggest that early heading is an important and effective single trait defining wheat cultivars adapted to production systems prone to high temperature stress during post-flowering period. However, this trait may not be beneficial if the region also suffers from drought stress during the grain-filling period. As discussed earlier, there is a strong correlation between the amount of dry matter produced before heading and drought tolerance of cultivar during postflowering stages. This is because most of the grain filling can occurs from stored carbohydrates. In addition, early heading may not be suitable to all locations, particularly in the regions where cool temperature or the occurrence of frost may limit the early-heading trait. Therefore, sufficient care should be taken while choosing or breeding stress tolerance cultivars for specific locations on the basis of the local environmental conditions.

Osmotic Adjustment

Maintenance of cell turgor by osmotic adjustment can decrease the impact of water stress. Lowering cell osmotic potential in response to drought is called osmotic adjustment or regulation. It is a physiological mechanism that can help maintain water absorption and cell turgor pressure, thus enabling plants to tolerate

drought stress. There is considerable evidence on the role of osmotic adjustment as a mechanism of drought tolerance in several crop species, e.g., wheat (Blum et al., 1999; Morgan, 2000) and sorghum (Santamaria et al., 1990; Tangpremsri et al., 1995). An increasing number of reports are providing evidence on the association between high rate of osmotic adjustment and sustained yield and biomass under water stress conditions (Blum, 2005). Osmotic adjustment helps maintain higher relative leaf water content at low leaf water potential, and it is evident that this helps sustain growth while the plant is meeting the transpiration demand by reducing its leaf water potential (Blum, 2005). Osmotic adjustment sustains turgor maintenance and hence the yield-forming processes during moderate to severe drought stress (Ali et al., 1999). However, its use as a valuable breeding and agronomic trait is questioned (Serraj and Sinclair, 2002). Although some studies have shown positive relations between the accumulated osmolytes and compatible solutes with yield and few physiological traits, the results are highly variable. The lack of consistent, positive relationships between those traits has limited their use in the breeding programs. Synthesis of osmolytes or compatible solutes is one mechanism of tolerance.

Serraj and Sinclair (2002) provided a comprehensive review of the practical application of osmotic adjustment for improving drought tolerance in crops and suggest that the osmotic adjustment occurs very late for the plant survival, and for agricultural conditions, crop survival is not an important issue because yields under such severe stress are so low that any putative benefits are not beneficial to the growers. They conclude that the advantage of osmotic adjustment is more in root tips. Osmolyte accumulation in roots can allow continued or even increased root development into deeper wet soil and can give plant access to an increased water reservoir on which the crop can be grown and/or survive (Serraj and Sinclair, 2002).

Delayed Senescence or Stay-Green

Leaves senesce early in response to drought and heat stress, particularly when these stresses occur during the postflowering stages of seed filling. Some genotypes tolerate drought during grain filling by keeping their leaves green; these cultivars are termed as stay-green types. Similarly, the stay-green character and chlorophyll retention in leaves under heat stress conditions was considered as expression of heat tolerance (Fokar et al., 1998). Stay-green genotypes retain chlorophyll in their leaves and maintain the ability to carry out photosynthesis longer than the senescent types, and are often shown to have a yield benefit (Borrell et al., 2001; Jordan et al., 2003). However, it has been suggested that stay-green trait is expressed under occurrence of drought stress. These stay-green genotypes are

different from some cultivars which have cosmetic stay-green, i.e., the cultivars which have green leaves but do not sustain photosynthesis for longer periods under drought conditions. It is also possible that stay-green genotypes can store large amounts of carbohydrates in stems, as these genotypes also often exhibit decreased lodging and have resistance to diseases such as charcoal rot [caused by *Macrophomina phaseolina* (Tassi) Goid]. The physiological basis of stay-green trait is not well understood and needs further investigation. Stay-green genotypes are known to have more sugars in stems (McBee and Miller, 1982) and contain higher cytokinin content (McBee, 1984). Borrell et al. (2001) showed that stay-green types assimilate more nitrogen and have greater specific leaf nitrogen content, suggesting the link between the stay-green and nitrogen. There is often no yield penalty associated with the stay-green trait (Borrell et al., 2001). However, it is unclear if the above mentioned traits are a consequence of stay-green or a secondary trait that is associated with general adoption of stay-green (Harris et al., 2007). The stay-green trait has been exploited in several crops. However, the progress of this trait in breeding is more obvious in corn and sorghum. In sorghum, several genotypes have been identified to possess stay-green trait (e.g., B-35). These genotypes have been used as a source of stay-green in several sorghum cultivars (Tuinstra et al., 1997, 1998), including in the development of several hybrids (Henzell et al., 2001). The genes responsible for stay-green have been identified in sorghum; the QTL are designated as Stg 1, Stg 2, Stg 3, and Stg 4 (Xu et al., 2000; Sanchez et al., 2002). Harris et al. (2007) recently have created near isogenic lines for Stg 1 through 4 to better understand physiological nature of stay-green trait. Both onset and rate of senescence were estimated for all the four Stg in near isogenic lines, and the slopes and intercept were compared under terminal drought conditions. These analyses showed that there are strong positive correlations between chlorophyll content (measured by a chlorophyll meter, SPAD) measured at 67 d after anthesis and SPAD predicted at 67 d after anthesis. They suggested three important components of tolerance were the SPAD reading at anthesis, the duration of senescence, and rate of senescence. They suggest that rate of senescence rather than onset of senescence is an important component of stay-green.

The stay-green trait and remobilization of stem carbohydrate reserves to grain have been explored under both heat (Fokar et al., 1998) and drought stress (Palta et al., 1994; Yang et al., 2000). However, few studies suggested that the high capacity to utilize stem reserves for grain filling might be linked with accelerated leaf senescence (Fokar et al., 1998; Yang et al., 2000). In addition, it is not clear whether accelerated leaf senescence and loss of chlorophyll from the leaves are also linked with the promotion of N remobilization from the stem. Tahir and Nakata (2005) studied the dynamics of stored total nonstructural carbohydrates

and N in leaves and stems under heat stress conditions. These results suggest that rate of chlorophyll loss from flag leaf is positively correlated with N and total nonstructural carbohydrates remobilization efficiencies under heat stress, suggesting a strong link between leaf senescence and remobilization efficiency. The duration of developing grain to receive carbohydrates may be limited by the life span of the phloem link. The phloem link to the grain may lose its function earlier than the chlorophyll disappearance in the leaves of stay-green genotypes. It is also possible that more rapid reallocation of stem carbohydrates is responsible for higher grain yield rather than stay-green characteristics (Dwyer et al., 1995). Stay-green (delayed senescence) is not necessarily associated with the full function of photosynthesis (Thomas and Smart, 1993). Therefore, in stay-green genotypes, in addition to being photosynthetically active, it is essential that the phloem is fully functional and translocates carbohydrates efficiently to the seeds. Although stay-green genotypes retain more photosynthates in leaves (Borrell and Hammer, 2000) and stems, rapid leaf senescence may be indicative of reserve mobilization to grain under stress conditions (Fokar et al., 1998; Yang et al., 2001). Therefore, there exists a delicate balance between stem reserve mobilization and stay-green, which involves carbohydrate and nitrogen metabolism; these phenomena are not clear (Blum, 2005) and need critical investigation.

Decreasing Loss of Water

One of the ways to improve drought and heat tolerance is to decrease loss of water. This could be achieved by decreasing leaf area, decreasing leaf temperatures, decreasing cuticular transpiration, decreasing nighttime transpiration, and decreasing water loss from soil by early vigor. Tambussi et al. (2007) provides a nice overview on these processes. Decreased leaf area and plant size is one of the mechanisms of moderating water loss from the canopy and reducing drought injury to the plant. However, drought moderation by reducing leaf area cannot sustain greater yields (Blum, 2005). The radiation energy falling on the canopy is dissipated by transpiration. A reduction in transpiration can be achieved by reducing net radiation by way of reflection or increasing crop albedo (Blum, 2005). Leaf temperature is an important component driving transpiration rate, and lower leaf temperature has an impact on WUE. Several morphological traits are linked to lower leaf temperature, such as epicuticular waxes, chlorophyll content, and leaf position (erect leaves). Plant surfaces such as epicuticular wax and hairs allow increased albedo and lower transpiration without decreasing stomatal conductance or photosynthesis. Low chlorophyll content to prevent photoinhibition has been associated with lower leaf temperature. The reduction in chlorophyll content did not cause any change in the photosynthetic capacity but is associated

with lower leaf temperatures particularly when stomata are closed. Furthermore, lower leaf temperatures under water stress could mitigate the heat stress associated with drought and reduce respiration as well as loss of water across the cuticle, thereby improving WUE (Tambussi et al., 2007). Similarly losses of water through cuticle are futile because it is not paired with carbon dioxide movement into leaves. Although these modifications often are beneficial under drought conditions to decrease water use, these traits are mostly associated with decreased photosynthesis and yield potential under normal growing conditions.

Cultivars Differences and Differential Mechanisms

Cultivars within crop species are known to differ in their responses to drought and heat stress. These responses can occur either during vegetative stages and/or during reproductive phases. Sometimes there may be a positive correlation between traits measured by means of vegetative tissue (e.g., membrane thermostability) and yield (e.g., in cowpea: Ismail and Hall, 1999; and wheat: Blum, 2005). Membrane thermostability during vegetative stages may not always lead to yield increases because tolerance based on vegetative tissue (cell membrane thermostability) is not generally associated with tolerance during reproductive stages—pollen viability or seed-set [e.g., peanut (Kakani et al., 2002); rice (Prasad et al., 2006b); or cotton (Kakani et al., 2005)].

Drought tolerance can often be associated with heat tolerance, since decreased transpirational cooling leads to increased tissue temperatures. Heat tolerance is a necessary auxiliary to drought tolerance under many conditions, since low-water potential causes stomatal closure that leads to decreased transpiration, which in turn increases tissue temperatures. Studying the performance of drought-tolerant cultivars under heat stress, Kakani et al. (2002) observed that peanut genotypes that were well established under tropics and semiarid tropics (e.g., 55–437 grown in sub-Saharan Africa) showed tolerance to drought stress. Furthermore, genotype Kadiri-3, a known drought tolerant cultivar, was highly susceptible to high temperature stress, whereas cultivar ICGV-86015, which is susceptible to drought, was tolerant to heat stress (Kakani et al., 2002). Similar results were also observed in wheat where a cultivar exhibiting greater performance under heat stress was highly susceptible to drought (Ristic, personnel communication). These studies indicate that even though drought and heat stress can occur together in most of the regions (particularly semiarid tropics), the possible physiological or biochemical mechanisms operating to induce escape or tolerance to each of these stresses may be different. Furthermore, the characteristics of traits associated with drought and heat stress could be different. Therefore, selection–production

of genotypes for tolerance to combined stresses of drought and heat must be performed under stress conditions that include both of these stresses.

Application of Existing and New Knowledge to Improve Drought and Heat Stress Responses

Most crop modeling efforts were initiated as a means of investigating the crop–environment interactions on plant growth and yield. To successfully simulate these complex plant–soil–environmental interactions, several key processes must be accurately simulated, and in particular, the effects of drought and temperature stress and their interactions. Accurate quantification and simulation of the various abiotic and biotic stresses and their interaction in the field conditions and plant responses to stress are some of the major challenges to crop modeling. At present, the majority of the existing crop models simulate plant growth on the basis of all or some of the physiological determinants of growth as outlined by Charles-Edwards (1982). This approach estimates daily above-ground dry matter production as a function of estimated light interception, light intensity, and a radiation-use efficiency coefficient. A majority of the plant simulation models estimate light interception as a function of leaf area and/or plant geometry. Since leaf dry weight, and subsequent leaf area, on a given day affects the amount of light intercepted that day, reductions in the production of new leaf area has a compounding effect on growth. Because of this, drought stress is often simulated by multiplying the potential new dry matter on a given simulated day by a stress multiplier. Water stress multipliers often range between 0 and 1, with 1 representing no stress and 0 representing extreme stress. The relationships used to quantify the stress vary but are typically a ratio of the amount of water demanded by the plant and the amount of water available in the soil for plant uptake.

Accurate estimations of soil water holding capacity and daily plant water use are necessary if simulated drought stress is to coincide with plant and soil metrics measured in the field. Plant water demands are traditionally simulated as a function of light interception and potential evapotranspiration (ET). It becomes quite obvious that errors in simulating leaf dry weight and leaf area accumulation will not only affect plant growth rates but also plant water use rates, resulting in errors in simulating drought stress timing and severity.

Daily reductions of accumulated dry matter through stress factors have a compounding affect by reducing the amount of dry matter partitioned to leaves, roots, and grain depending on estimated plant development stage. This method of simulating drought stress affects simulated plant growth in a manner similar to those discussed earlier in this chapter. It was state that drought reduces plant

leaf area and the mechanism for this reduction is either a reduction in leaf cell number or leaf cell expansion or both. Simulated drought stress has a similar effect; dry matter is reduced by a stress factor, which reduces new leaf area production, which reduces the amount of leaf area available to intercept light. As a result, simulated stress early in the growing season reduces leaf and root dry matter accumulation, but because these values are relatively small, short periods of drought have less impact on final grain yields.

Temperature stress multipliers are often more empirically based on observed plant responses to temperatures. Temperature stress multipliers often have a region where no stress is simulated (multiplier of 1) with temperature extremes that define this region being both species and growth stage specific. One area of simulating plant stress that may not mimic stress in actual plants is when both temperature and drought stress are simulated simultaneously. Simulations of interactions of temperature and drought stress in the crop models is a challenging task. Many crop models simulate these stresses separately and apply the minimum of the two to quantify the effects of growth and developmental processes. Simulating stress interactions with plant development stages is important in yield component models because yield component size (tiller no., seed head⁻¹ and seed size) is often estimated as a function of dry matter accumulation during specific periods. For example, in sorghum model (SORKAM, Rosenthal et al., 1989), productive tiller number is based on dry matter accumulation from emergence 8 d after emergence to 7 d after growing point differentiation. Seed number in each panicle is estimated as a function of dry matter production from 7 d after panicle initiation until 10 d after anthesis. This approach was developed so that stress during each of these periods would affect the size or number of the respective simulated yield component in much the same way that stress during these same time frames can affect the same yield components in reality.

The greatest challenge to crop modeling is accurately simulating the impacts of interactive effects of drought and heat stress on various plant processes, daily plant water use, soil dynamics, plant development, and sink strength. Some of the specific challenges and areas of research include.

1. Improve crop models to accurately simulate the impacts of both short-term and long-term drought and/or heat stress and interactions on growth and yield.
2. Incorporate and evaluate existing models for stage sensitivity to drought and/or heat stress on physiological, growth, and developmental processes and in determining components of yields.
3. Improve the ability of crop models to simulate the direct and interactive effects of drought and/or heat stress on phenology.

4. Improve our understanding of the physiological and/or biochemical mechanisms causing pollen and ovule sterility that lead to lower seed-set. Incorporate temperature functions to determine potential seed-set under stress conditions.
5. Improve our understanding of diurnal variation and seasonal changes in photosynthesis and respiration in response to short-term and long-term stress drought and heat stress.

Our review suggests a need to improve our understanding of the impacts, mechanisms of tolerance, and traits associated with multiple stresses. There is need to develop dedicated research programs aimed at enhancing the tolerance to combinations of different abiotic stresses and particularly those related to drought, high temperature, and global change (elevated carbon dioxide and ultra-violet-b radiation). Tolerance mechanisms for drought and heat may be different; therefore, an integrated approach should be taken for cultivar development. As we improve our knowledge and quantify the impacts of both short-term and season-long effects of drought and/or heat stress on various physiological, growth, development, yield, and quality of crops, the chances of incorporation of these effects into crop models will be improved and should be considered. Modeling growth, development, sink-source relation, grain yield, and grain quality of crops can assist in improving knowledge on the physiological and genetic nature of tolerance which can lead to improving grain yield and quality of crops. Improved models can enhance our understanding of performance of crop to future climates and also to identify traits that can potentially be improved to obtain higher and stable crop yields under stress environments.

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