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REVIEW

Plant adaptability to climate change and drought stress for crop growth and production

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Abstract

Abiotic factors pose a significant constraint for food security and agricultural production worldwide, and the issue has been exacerbated by extreme and rapid climate change. Heat and drought are the most important limiting factors that have a significant influence on crop growth and production. For better management, it is critical to understand the biochemical, ecological and physiological responses to these stresses. Plant responses to these challenges may be divided into three categories: phonological, physiological and biochemical. This review gives a thorough description of plant adaptations towards drought and heat stress, with a particular emphasis on identifying similarities and variations. As a result of physical damage, biological disruption and biochemical abnormalities, suboptimal water supplies and unusual temperatures negatively impact crop development and yields. However, both of these stressors have a wide range of impacts and are thus complex to explain in terms of mechanics. More profound knowledge of how plants respond to various challenges can lead to more practical solutions and management. A distinctive aspect of the phenomenon is comparing fundamental behaviour with abiotic stresses.

Keywords: heat, drought, climate change

Introduction

Climate changing is adversely affecting agricultural crop productivity, which is a significant constraint on world food security on one side and acceleration of human population on other side (Raza *et al.*, 2019). Furthermore, according to an FAO global assessment conducted in connection with population growth, an additional 70% food will be required by 2050 (Food and Agricultural Organization (FAO), 2009). It is highly challenging for agriculturists to overcome future food uncertainty in this most populous world. Global warming and potential climatic irregularities mean crops often have an increasing number of biogenic and abiogenic stresses that significantly influence crop productivity. Heat and drought are the most severe climate change-related impacts for agriculture output and food security.

All plants have specific range of optimum temperature to grow. Temperature above this range have negative impacts on growth stages and development. The gradual rise in mean annual temperature or heat is one of the most threatening abiotic stresses. Elevated temperatures may alter the developmental and biological plant processes, which affect yield and quality of produce (Calleja-Cabrera *et al.*, 2020). Although higher temperature is beneficial for some crops of cooler regions, overall, elevated temperature has negative impact on crop production throughout the world and causes yield decline to a large extent.

Extended intervals without rain that are linked to rising temperatures are projected to cause more frequent drought. Drought is increasing worldwide, due to lower precipitation and changing rainfall pattern. At reproductive or growth phases, drought stress has the most destructive influence on crop output. Droughts impair plant growth, reproduction and physiology, which significantly impact agricultural outputs (Fahad *et al.*, 2017). They produce embolism at the xylem, which hinders water movement from the ground to the leaves, and can potentially lead to plant mortality via hydraulic collapse if uncontrolled (Sevanto, 2014). According to a study that examined data from research published between 1980 and 2015, drought has reduced wheat and maize yields by up to 40% over the world (Daryanto *et al.*, 2016). Lobell *et al.* (2011) report that the production of wheat dropped by 5.5% and the output of maize decreased by 3.8% globally between 1980 and 2011. In addition, between 1880

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and 2012, the average combined ocean and terrestrial temperature rose by 0.85°C (Pachauri *et al*., 2014). Every decade is expected from now on an average increase of 0.2°C. Increased meditation of greenhouse gases (CO_2, CH_4, etc.) is the major contributor to global climate change. A 30–150% increase in CO_2 and methane concentrations has been seen over the last 250 years (Prentice *et al*., 2001). More than any other environmental factor, these stresses limit plant development and output. For instance, it was projected that every 1°C rise in temperature would result in a 6% loss in global wheat yield. Different models predict a yield loss of 6–10% for every 1°C increase in the average temperature of the growing season, because of these two and other stressors (Guarino and Lobell, 2011). Even though rising temperatures are favourable for crop productivity in certain colder parts globally, generally, effects on world nutrition safety remain unfavourable. Furthermore, climate change poses a major effect on the stability of agricultural production. The top ten global crops, which include sugarcane, palm, soybean, wheat, maize and rice, have seen a significant impact on yields in many places throughout the world (Ray *et al*., 2019).

Drought vs. climatic stress

Drought, excessive salinity and cold may all cause a cellular dehydration that manifests as symptoms of physiological dehydration. Drought stress occurs when soil and atmospheric humidity are low and the ambient air temperature is above normal. In this situation, the evapotranspiration flux is out of balance with the soil's absorption of water (Suzuki *et al*., 2016). When the temperature of the soil and air rises over a certain threshold level for a certain period of time, it is referred to as heat stress. Temperature affects yields in a comprehensive multi-location research. Plant growth and agricultural yield of important crops are being adversely affected by these unfavourable circumstances, which cause the development of drought-prone regions (Suzuki *et al*., 2016; Ray *et al*., 2019). Both drought and heat must be evaluated together since their combined impact is greater than that of each of them alone. Numerous genes influence the body's response to abiotic stress, such as heat or drought, whereas the underlying processes are more complicated than those for biotic stress, which tend to be characterized by monogenic resistance. Heat and drought responses may be complicated further by various environmental factors, both biotic and abiotic, which make research more difficult. Due to oxidative, osmotic and thermal stressors caused by water scarcity and soil salinity, these issues are indisputably important obstacles to production in agriculture (Barnabás *et al*., 2008). It has also been noted that the lower stomatal conductance and transpiration under these circumstances may cause heat stress when leaf temperatures increase. Growth and performance of plants deteriorate significantly in tropical and subtropical areas when there is a lack of water and high temperatures (Suzuki *et al*., 2016).

Direct and indirect impacts of heat and drought on plant parts

Droughts affect plants when root water supplies are insufficient or water loss is excessive due to transpiration. Drought damage is frequently unanticipated due to a number of factors such as evapotranspiration losses rainfall patterns and water storage capacity. Drought alters the connections between nutrients, growth and water, assimilates partitioning and photosynthesis, and considerably reduces crop yield. According to Demirevska *et al*. (2009), reaction of plants to water scarcity differs across plant species, depending on the plant's stage of growth and development and other environmental variables. Furthermore, it also disrupts the hormonal balance of the plants. Excessive reactive oxygen production, which result in oxidative stress, is one of the primary consequences of heat stress (Hasanuzzaman *et al*., 2012). The primary variables that diminish plant yield are a decrease in the soil humidity level and reduction in PAR absorption, lower efficiency of radiation and a low harvest index (Earl and Davis, 2003). To deal with the severe consequences of drought stress, plants show adaptation in their physiological processes and growth (Wang *et al*., 2020). Climate change and drought alter plant function in number of ways as shown in Fig. 1.

The biochemical, hormonal, physiological and morphological changes caused by heat stress significantly affect plant growth and production. Increases in atmospheric temperature, referred to as heat shocks, have become the most significant limiting factors in agricultural output on a global scale. The changing seasons and distribution of crops may be affected by increased temperature (Porter, 2005). Proteins may be severely damaged, their synthesis disrupted, necessary enzymes inactivated and membranes damaged due to heat stress. Heat stress may affect cell division considerably as well (Smertenko *et al*., 1997). All of these variables may impair plant growth and possibly contribute to oxidative damage. Additionally, short-term heat exposure during seed filling may result in rapid seed filling, resulting in low quality and decreased yield. We looked at the primary responses of crop plants to drought and climate change or heat stress. Aquaporins, which are integral membrane proteins that serve as channels for the transport of specific tiny solutes and water, regulate all of these parameters. Furthermore, heat and drought reduced the internal CO_2 contents of the plants, vegetative growth, and early maturity and inhibits the enzyme activities including Rubisco involved in ATP synthesis. Severe heat and drought stop the movement of water resulting less nutrients uptake and almost all the plan parts damaged (Orians *et al*., 2019). Indirect effects included weeds that are already responsible for 34% of crop losses, with insects accounting for 18% and disease for 16%. Weeds, insects and disease already have a huge detrimental influence on our agricultural production system because of climate change (Skendžić *et al*., 2021). Insect pests thrive in warmer climates because they may complete their life cycles faster, reducing the amount of time they spend in susceptible phases (Ding *et al*., 2011). Insect, weed and disease populations are expanding northward as a result of the warming climate. Crops are more susceptible to disease because of the increasing climate effects on temperature and moisture stress. Figure 2 represents the indirect heat and drought effects on plants and soil system.

Direct and indirect impacts of heat and drought on soil

A healthy soil ecosystem is critical to a farm or ranch's natural productivity. Extremes of temperature and precipitation may harm soils as a result of changing climatic conditions. Temperature rises may disrupt ecosystem services supplied by soil, such as water holding capacity, carbon sequestration and nutrient uptake by plants and animals. The frequency and severity of severe precipitation events has already increased and is likely to continue to rise, which will lead to increased soil erosion if conservation strategies are not implemented (Kiem *et al*., 2016). At times when rainfall exceeds the soils capacity to infiltrate, erosion occurs. Topsoil is carried away by water that cannot penetrate the soil; thus, it flows off the land as a result. Crops can no longer rely on the water and soil that discharge after high rainstorm storms. Climate change-induced shifts in rainfall patterns are expected to lead to more frequent and powerful rainstorms. In Iowa, for example, even though the state's yearly precipitation has remained flat, the number of days with significant rainfall has grown dramatically (Gelybó *et al*., 2018). Sediment contamination is further exacerbated by severe precipitation events, which causes soil erosion. Soil erosion may be reduced by using agricultural leftovers, mulch, or cover crops to keep soil covered. A rise in the frequency and severity of intense precipitation will need better soil management strategies.

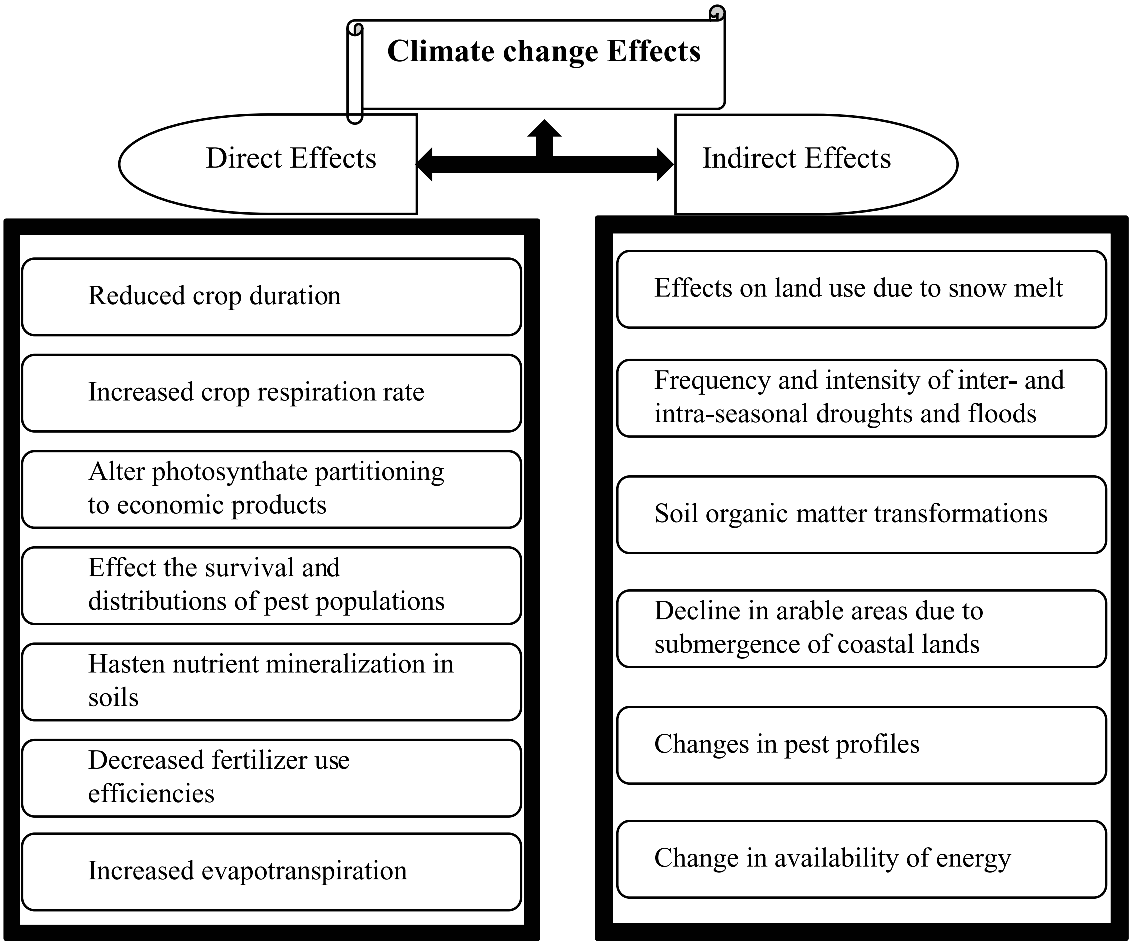

Figure 1. Effects of climate change on plant parts or processes.

Phonological adaptation of plants towards abiotic stresses

EFFECTS OF DROUGHT ON CROP GROWTH

Drought causes poor germination and seedling establishment, which are the primary causes of less seedling development from increased area. Several studies have indicated that drought stress negatively impacts planting germination and growth (Jaleel *et al*., 2009). Drought stress has been linked to a reduced seed germination potential, hypocotyl length, early seedling, dry mass of the root, and vegetative development in various main field crops such as rice, lucerne and pea. Cell division, expansion and differentiation are the primary mechanisms by which plants grow. Drought inhibits cell elongation and mitosis, resulting in slowed growth (Hussain *et al*., 2008). Depletion slows cell growth, owing to the reduction in turgor. Aridity inhibits cell elongation because of the restricted water transport from the xylem to neighbouring cells. Drought conditions can reduce the size and quantity of individual leaves. The amount of assimilates available and the turgor pressure determines how much the leaf expands. Water deficit inhibits leaf expansion due to a poor rate of photosynthesis and reduced turgor pressure. Fresh and dry biomasses are also severely decreased during periods of water scarcity. The height, stem, leaf size and breadth of maize plants were significantly reduced under water-stressed circumstances (Kamara *et al*., 2003). Kamara *et al*. (2003) observed in a further investigation that the accumulation of maize biomass was significantly decreased during moisture deficient circumstances applied at numerous phases of growth.

EFFECTS OF TEMPERATURE ON CROP GROWTH

The additional chief restrictive factor for plant growth and improvement in hot climates is excessive radiation and high temperatures. High temperatures can cause growth inhibition, twigs and leaves to scorch, leaf senescence, and decoloration of leaves and fruits, as well as sunburn-like symptoms. High temperatures can decrease the germination potential of seeds, leading to poor germination and standing. The time, duration and degree of thermal stress affect cereal crops more strongly. Under comparable conditions, high-temperature stress lowered the spikes number and florets in rice per plant, and the seed in sorghum under the same environmental circumstances was also considerably affected. Anthers and pollens in interior florets were more vulnerable to high temperatures than ovules. The sterility of the floret has been associated with inadequate pollen shedding, poor germination of pollen grains, dehiscence, reduced elongation of the pollen tube and decline in *in vivo* pollen germination at high temperatures (>30°C). In maize and sugarcane under high-temperature stress, a significant decrease was noted in growth and net assimilation rate. The deposit of biomass, internodal length and early sugarcane leaf senescence were reported to decrease significantly because of high temperatures (Ebrahim *et al*., 1998). Sunburn of leaves, leaf abscission and senescence, scorching, fruit damage and discoloration, twigs, root, stem and shoot growth inhibition are the most common phonological indications of extreme heat stress (Rodríguez *et al*., 2005). Abnormal plants, plant emergence, lower germination rates, poor showing strength and decreased radicles are the main effects of heat stress in numerous plant species that are grown (Kumar *et al*., 2011). The

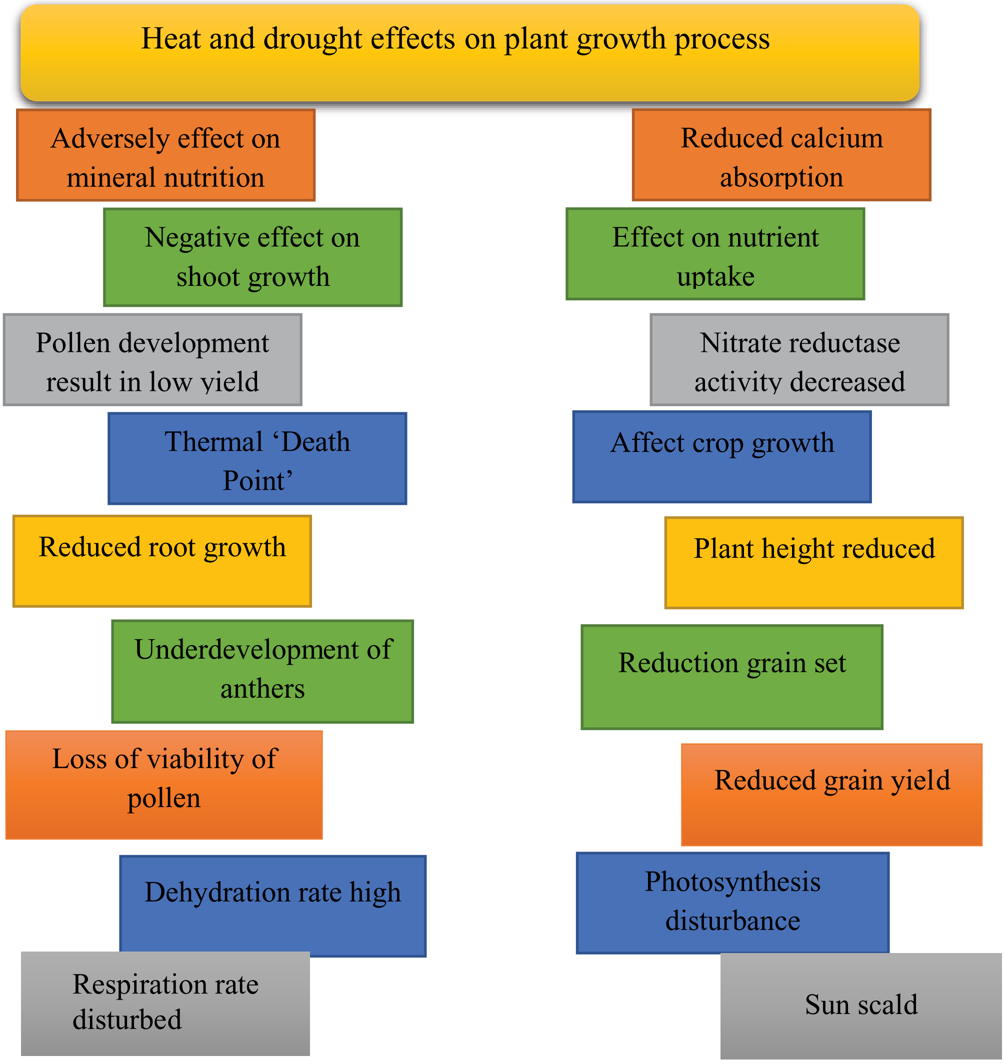

Figure 2. Effects of drought and heat on plants parts and soil processes.

germination rate of wheat was explicitly prohibited at extremely high temperatures (45°C) and caused cell death, where the seedling rate was lowered (Cheng *et al*., 2009). The number of tillers, plant height and biomass of rice crop reduced significantly due to heat stress (Mitra and Bhatia, 2008). Other issues include reducing the net assimilation rate that has been established in sugarcane and millet, as the major cause of the poor growth rate (Srivastava *et al*., 2012).

EFFECTS OF DROUGHT ON CROP PRODUCTION

Yield is the result of a combination of various physiological and phonological processes. Drought stress has a deleterious impact commonly on these processes. Drought stress resulted in significant output losses in major field crops. Pre-anthesis drought lowers anthesis time, but after anthesis, drought lessened the grain filling period for cereals. Taiz and Zeiger (2006) described four major enzymes that control the grain filling process in cereals, namely adenosine diphosphate, sucrose synthase, starch synthase, starch branching enzyme and glucose pyrophosphorylase, Drought effects have been observed to reduce the activity of these enzymes, which has a negative influence on primary cereal crop yield (Ahmadi and Baker, 2001). Drought stress during flowering can cause total sterility in pearl millet caused by a disruption in assimilating transport for the developing ear (Yadav *et al*., 2004). A drought-related decline in yields may be due to various factors, including disturbed assimilation, reduced photosynthesis and poor flag leaf formation. Drought circumstances during the tasseling stage of maize resulted in significant yield losses (Anjum *et al*., 2011). Drought stress in cotton caused an impressive decrease in bollard production and abortion of produced bollards, affecting the steak yield (Pettigrew, 2004). Drought conditions resulted in a significant reduction in barley grain yield, owing to a lower number of viable tillers and grains and a lower 1000-grain weight. Drought stress during the flowering stage of the pigeon pea resulted in a 50% drop in seed output (Nam *et al*., 2001).

EFFECTS OF TEMPERATURE ON CROP PRODUCTION

Almost all plant tissues are vulnerable to high heat throughout all developmental and growth phases; the multiplicative tissues are particularly sensitive, and unusual temperature fluctuations during the reproductive phase can result in the loss of the entire grain production cycle (Lobell *et al*., 2011). Higher temperature shock waves during the propagative stage of major cereals can cause significant yield reductions in temperate sites. Heat stress has a detrimental impact on the value of the end product in oilseed and cereal crops because it reduces the oil, protein contents and starch significantly. Ferris *et al*. (1998) found that under high-temperature conditions, the grain weight (1000-grain weight) and total grains number of wheat crop decreased significantly. Heat stress affected the performance of several rice growth and yield aspects, resulting in lower rice output.

Heat stress for very short periods, during the reproductive phase, may lead to significant reduction in flowers and floral buds: however, a great disparity in sensitivity among and within plant varieties and species exists (Sato *et al*., 2006). Lower production of flowers or flower production without seed or fruit may result from a short spell of heat during propagative stage (Maheswari *et al*., 2012). Fahad *et al*. (2017) described that the rice tillering phase was highly responsive to higher night temperatures. Heat induction caused ample yield losses in groundnut and common beans. Heat stress has a remarkable impact on fertilization, growth of fertilized embryos and meiosis in tomato crop, resulting in significant yield losses. Heat, drought and stress reduce the growth and output of various major crops; however, the damage varies depending on the intensity of the stress and the crop's growth phase. Unfertilized embryo and pro-embryo, anomaly in style and stigmatic positions, compromised meiosis in female and male tissues, impaired pollen tube and pollen germination growth, distressed fertilization procedures, unfertilized embryo, reduced ovule viability, hindrance in growth of endosperm and condensed pollen grains engaged by the stigma are all the problems of abiotic stresses including excessive heat (Cao *et al*., 2008). Generally, the propagative stage is more susceptible to this stress, resulting in a significant loss in yield. The rise in the seasonal average temperature at 1°C has shown a drop in grain yields of cereals of 4.1–10.0% (Wang *et al*., 2012). In relation to tolerant varieties, sensitive crop variants are more seriously damaged by heat stress. Heat stress changes the early dough, and maturity affects the kernel drying process and causes the loss of wheat grain yield (Saitoh, 2008). Heat also decreases the weight of the single kernel and contributes mostly to the loss in return (Kutcher *et al*., 2010).

Physiological responses

EFFECT OF DROUGHT ON NUTRIENT AND WATER RELATIONS

The leaf water potential, leaf stomatal conductance, transpiration rate, substomatal conductance and canopy temperature influence water relations. Drought stress affects all of these parameters in plants, although stomatal and substomatal conductance is the most valuable in this regard (Farooq *et al*., 2009). Under drought conditions, there was a considerable decrease in transpiration rate and water potential, increased canopy and leaf temperature. The water-efficiency ratio of dry matter generated by water consumed is also a critical component in plant physiological control. This increase in water efficiency is primarily due to the accretion of dry matter by overwhelming minimum water through the closure of stomata and a reduced evaporation rate. Potato showed lower water use efficiency when faced with a water shortage early in the season, resulting in poor biomass development and yield. Drought stress has a substantial influence on the interaction between plant nutrients. Plant roots absorb several vital minerals, such as calcium, silicon, magnesium and nitrogen along with water; however, dry circumstances block the transfer of these elements by diffusion and mass flow, limiting the plant development (Barber, 1995).

Plants increase the surface area and length of their roots and change their architecture to catch less transportable nutrients. A shortage in moisture level might hamper the root development and reduce the consumption of more minor moving minerals such as phosphorous. In a plant's nutritional linkages, root-microbe interactions are equally crucial. Reduced oxygen and carbon flow to nodules, as well as nitrogen build-up owing to drought stress, decreased the capacity of some legumes to fix nitrogen. A shortage of water in the soil affects the structure and activity of soil microbial colonies, disrupting plant feeding interactions. The responses of different crop species to nutrient uptake under water stress differ. Under drought conditions, N uptake rises, P uptake decreases and potassium uptake stays unaffected. However, nutritional connections are more complex as several nutrients interactively affect one another and overall plant physiology. This element requires a thorough molecular investigation.

HEAT STRESS

The status of water in plants is of significant relevance under changing climatic circumstances. Usually, when adequate water is available, plants tend to balance their tissue water content independently of temperature fluctuations, but the increase in temperature becomes disastrous with less water. Unfortunately, heat stress is often connected with water shortages on the soil, especially in tropical and subtropical regions. Although there was adequate amount of water in the soil, sugarcane demonstrated a dramatic loss of water content in leaf tissue when exposed to hot temperatures. It recommends that heat stress might have a detrimental impact on root conductivity. Tomato showed a comparable decrease in root conductivity and water content during heat stress. When plants are exposed to heat, water loss is often higher throughout the day owing to a higher rate of transpiration, which eventually impairs various critical plant physiological systems. Heat stress affects the bulk, volume and growth of roots, restricting nutrients and water for above-ground plant components (Huang *et al*., 2012). There is less evidence on the direct impact of heat stress on crop nutrients.

The activity of essential food metabolic enzymes, such as nitrate reductase, can be drastically decreased under high-temperature stress. Because of several factors, including a nutrient intake per unit surface of the root, decreased root mass and nutrition intake may decrease under thermal stress (Basirirad, 2000). Overall, heat and drought stress harm the plant nutritional cycle, availability and absorption by interacting with various physiological processes. Photosynthesis in plants affected by drought and excessive heat is one of the principal physiological processes (Farooq *et al*., 2009). Defective photosynthetic machinery functioning, reduction in leaf expansion and leaf ageing are the primary variables affecting it (Wahid *et al*., 2007). Under drought conditions, stomatal closure limits the availability of CO_2, making plants more vulnerable to photodamage. The reduction of humidity causes unfavourable changes in photosynthetic machinery, impacts photosynthetic pigments negatively and impairs significant enzyme functions, leading to large losses in yield and growth (Zandalinas *et al*., 2016). Heat stress would also affect photosynthetic processes by disrupting pigment photosynthesis, reducing photosystem II activity and decreasing the ability of RuBP for regeneration (Sharkey, 2005). Some of the significant impacts on photosynthesis are described below of drought and heat stress.

EFFECT OF DROUGHT ON PHOTOSYNTHETIC PIGMENTS

Drought has various impacts on thylakoid membranes and photosynthetic pigments (Kumar *et al*., 2011). Drought conditions have also been linked to decreased chlorophyll concentration. Several researchers have found that when cereals are subjected to moisture stress, their chlorophyll content decreases. It differs with cultivar and crops, e.g. during water stress, chlorophyll concentrations in specific cultivars of black gram raised while they dropped in other crops. The difference in behaviour was related to changes in enzymatic activities involved in chlorophyll synthesis. The quantity of chlorophyll in the dry plant was shown to be higher than the concentration of chlorophyll b. Chlorophyll a concentration under drought-stressed plants was greater than that of chlorophyll b. The chlorophyll a/b ratio in *Brassica* species was revealed to be lower under drought conditions.

EFFECT OF TEMPERATURE ON PHOTOSYNTHETIC PIGMENTS

High-temperature revelation generally results in a decrease in chlorophyll production. Lower chlorophyll accumulation in plants may be caused by the increased breakdown and reduced chlorophyll production or a combination of both during extreme heat stress (Allakhverdiev *et al*., 2008). Inhibition in chlorophyll synthesis under extreme heat is strictly linked to the inactivation of several enzymes. In wheat, enzymatic activities, i.e. 5-aminolevulinate dehydratase needed for pyrrol production, reduced dramatically and the chlorophyll contents in cucumber was decreased 60% at temperature 42°C due to the inhibition of 5-aminolevulinate synthesis (Ashraf and Karim, 1991). Under higher temperatures, the output of the protochlorophyllide was reduced by 70%. Heat stress enhanced the breakdown of chlorophyll a, as well as b in mature leaves (Maroco *et al*., 1997). These effects on chlorophyll pigments and other photosynthetic machinery are thought to be related to oxidative damage. In heat-tolerant tomato and sugarcane varieties, the chlorophyll a/b ratio increased, but the chlorophyll to carotenoid ratio decreased significantly. This demonstrates that the alteration in the balance of the photosynthetic pigment also has a function in heat shock tolerance.

EFFECT OF DROUGHT ON THE PHOTOSYNTHETIC PROCESS

To minimize water loss through transpiration, practically all the plants' first and predominant response to water stress is stomatal closure. Stomatal closure may occur in response to a drop in leaf water potential or a decline in atmospheric moisture level (Fiscus *et al*., 2005). The stomatal closure reduces CO_2 uptake, resulting in no assimilation due to oxidative stress, and also improves heat dissipation in leaves (Vu *et al*., 1999). Interestingly, soil moisture status has a more significant impact on stomatal control than leaf water content, which might explain why stomata respond to ABA generated by roots under dry circumstances. However, under drought conditions, stomatal responses vary greatly among plant species. Reduced stomatal conductance limits photosynthesis in light drought, but reduced Rubisco activity becomes the most important factor affecting photosynthesis (Porter, 2005; Jaleh, 2017). Water scarcity induces cell shrinkage, resulting in reduced cell volume; thus, the cellular substance becomes extra sticky, leading to protein denaturation.

Higher solute concentration in the cytoplasm may also lead to ionic toxicity, which negatively influences enzymatic functions that can take part in various plant functions, including photosynthesis. The rate at which the Rubisco enzyme is created and eliminated determines its absorption in leaves. Because it has a half-life of many days, it is very stable even in times of severe water scarcity. Rubisco's diminished synthesis, on the other hand, causes severe damage due to a reduction in its small subunits (Parry *et al*., 2003). Under drought stress, the binding of inhibitors such as 2-carboxyaribinitol 1-phosphate to the catalytic site of Rubisco is also prevalent, affecting enzyme activity (Lawlor and Cornic, 2002).

Similarly, drought and heat stress harm other essential photosynthetic enzymes. Under mild drought, reduced phosphorylation and inadequate ATP generation have been identified as the fundamental causes limiting photosynthesis (Marchand *et al*., 2005). Under drought circumstances, the lower generation of nicotinamide adenine dinucleotide phosphate decreases ATP synthesis due to depressed regulation of the non-cyclic electron transport chain.

EFFECT OF TEMPERATURE ON THE PHOTOSYNTHETIC PROCESS

Higher temperature affects the light-dependent chemical processes in the carbon metabolism and thylakoid in the stroma, which are significant sources of damage (Haag, 2019). The membrane of the thylakoid is extremely vulnerable to heat stress and in chloroplasts, major changes occur, such as changes in thylakoids' structural organization, loss of granum stacking and swelling of grana (Rivas and Barber, 1997). The PSII's thermo-tolerance adjustment is controlled by enhanced photon flux density and leaf temperature. The PSII is very sensitive to temperature, and its activity is considerably involved even in partially heat stress. Under higher temperatures, the oxygen-evolving complex is also severely damaged, leading to an uneven distribution of electrons to the PSII acceptor site. Denaturation of the D_1 and D_2 proteins occurs at higher temperatures (Toth *et al*., 2005). Heat stress caused damage to several PSII components in barley and wheat (Yang *et al*., 2006). Cotton's photosynthetic activity was further hampered by a halt in RuBP regeneration and a reduction in the electron transport chain. The PSII stromal enzymes and chloroplast are mostly stable at high temperatures, and the PSII electron transmission system is functioning. In recent research, Fahad *et al*. (Ray *et al*., 2019) have discovered that the photosynthetic activity of two rice cultivars has declined dramatically at high day and night temperatures. High temperature has more impact on the photosynthetic efficiency of C_3 plants than that of C_4 plants (Rogiers *et al*., 2012).

Photosynthesis was reduced due to chlorophyll pigment degradation, a blockage of the PSII reaction center, a drop in quantum efficiency, a drop in leaf nitrogen contents, electron transport and down-regulation of PSII photochemistry. High-temperature stress has a significant impact on starch and sucrose synthesis because key enzymes such as sucrose phosphate adenosine, diphosphate-glucose pyrophosphorylase, invertase and synthase have lower activity. Due to reducing the active state of the CO_2 binder enzyme Rubisco, net photosynthesis is hampered for some plant species. At the same time, the catalytic activity of Rubisco increases with temperature, and its weak affinity to CO_2 and its ability to bind to O_2 limit the increase in its net photosynthetic rate. Despite all of the harmful consequences of higher temperatures on photosynthesis, the ideal temperature needs for photosynthesis are anticipated to rise as CO_2 levels increase in the atmosphere. Rogiers *et al*. (2012) noticed a decline of 60% with an increase from 25 to 45-degree temperature in average rates of photosynthesis of *Vitis vinifera* leaves. This photosynthetic decrease has been related to stomach closure of 15–30%.

EFFECT OF DROUGHT ON ASSIMILATE PARTITIONING

Drought disturbs the balance of assimilated products, as most are moved into the roots to improve water consumption. The rate of photosynthesis and the concentration of sucrose in the leaves are used to transport assimilates from the source to the sink. Dryness impacts photosynthesis and reduces the sugar content, reducing the export rate between sources. Drought also reduces the sink's ability to digest incoming agents appropriately. The invertase acid activity that impacts phloem loading and unloading is also decreased. As a result, moisture stress affects dry matter partitioning (Dinar and Rudich, 1985).

EFFECT OF TEMPERATURE ON ASSIMILATE PARTITIONING

The heat stress reduces the sources and sinks, which have substantial impacts on growth and, in the end, economic production. In assimilating heat stress partitioning, however, considerable variation in distinct genotypes of wheat was reported. In two heat-sensitive tomato cultivars, Dinar and Rudich (1985) found carbon transportation to the apex was drastically reduced.

Wardlaw (1974) examined the reactions of the source of wheat, the sink and the transportation track to high-temperature stress and found the photosynthetic rate to be ideal between 20 and 30°C, but a rapid drop over 30°C was observed. The flags were loaded according to the same manner (Tietjen *et al*., 2017). The motion inside the trunk, however, showed that the temperature was 1 to 50°C independent. It was discovered that, in addition to a lower photosynthetic rate, the impact of temperature stress on the wheat division was associated with the questionable source and sink activity. From these results, it may be concluded that improving the mobility efficiency of leaf and other plant components of assimilates might constitute an essential strategy to enhance grain filling in cereals.

Oxidative damage: A communal response

Most abiotic stresses in plants are usually in a sequential stage of oxidative damage. Drying stress causes oxidative damage to the plants by allowing reactive oxygen species (ROS) to grow. ROS represents a significant danger that proteins and lipids will be destroyed for cell functioning. According to Moran *et al*. (1994), during drought conditions, the pea plant's protein and lipid peroxidation increased fourfold compared to normal conditions. The ROS is primarily produced in chloroplasts; however, oxygen interactions with electron transport chain (ETC) elements in mitochondria also produce ROS. ROS-generating processes can be either non-enzymatic or enzymatic. Under high-temperature stress, ROS generation has also been documented. Plants often rely on antioxidant defence, which can be non-enzymatic or enzymatic, to deal with oxidative stress. Enzymatic protection is often regarded as the most effective. The POD, GR, CAT and SOD are the major enzymes involved in this system. Aside from these enzymes, non-enzymatic components such as glutathione and carotenoid can also contribute to the antioxidant system. Enzymes such as SOD, CAT and POD either directly scavenge ROS or indirectly protect plants by controlling non-enzymatic defence (Pettigrew, 2004). An increased level of malondialdehyde has been seen in response to ROS, which is a strong indicator of drought-induced oxidative damage. As a result, maintaining more significant levels of antioxidants can be a practical approach for plants to combat the detrimental effects of ROS. Plants use phytohormones, which are natural defensive compounds that help them sustain more significant amounts of antioxidants under stress conditions. They aid plant adaptation towards the varying environment by modulating growth, source or sink transitions, nutrient allocation and development (Fahad *et al*., 2017).

Conclusion

Abiotic stresses are reducing crop yield all across the world. Drought and heat stress cause plants to respond in a variety of ways, the most notable of which is by altering their development and morphology. Despite the fact that drought and heat stress may have a negative impact on the plant's growth and development, reproductive growth is the most affected. Anthesis or grain filling stress may have a major impact on crop production if it is mild. Damage to the photosynthetic machinery, oxidative stress and membrane instability are also caused by these forces. The capacity of plants to withstand these pressures differs significantly across species. Recent advances have been achieved in limiting the adverse consequences of these abiotic stressors, either through the use of genetic methods or by the induction of stress tolerance.

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CONFLICT OF INTEREST

None.

References

Ahmadi, A. and Baker, D.A. (2001) The effect of water stress on the activities of key regulatory enzymes of the sucrose to starch pathway in wheat. *Plant Growth Regulation* 35, 81–91.

Allakhverdiev, S.I., Kreslavski, V.D., Klimov, V.V., Los, D.A., Carpentier, R. *et al*. (2008) Heat stress: An overview of molecular responses in photosynthesis. *Photosynthesis Research* 98, 541–550.

Anjum, S.A., Xie, X.Y., Wang, L.C., Saleem, M.F., Man, C. *et al*. (2011) Morphological, physiological and biochemical responses of plants to drought stress. *African Journal of Agricultural Research* 6(9), 2026–2032.

Ashraf, M. and Karim, F. (1991) Screening of some cultivars/lines of black gram (Vigna mungo L. Hepper) for resistance to water stress. *Tropical Agriculture* 68, 57–62.

Barber, S.A. (1995) *Soil Nutrient Bioavailability: A Mechanistic Approach*, 2nd edn. Wiley, New York, NY.

Barnabás, B., Jäger, K. and Fehér, A. (2008) The effect of drought and heat stress on reproductive processes in cereals. *Plant, Cell & Environment* 31(1), 11–38.

Basirirad, H. (2000) Kinetics of nutrient uptake by roots: Responses to global change. *New Phytologist* 147, 155–169. DOI: 10.1046/j.1469-

Calleja-Cabrera, J., Boter, M., Oñate-Sánchez, L. and Pernas, M. (2020) Root growth adaptation to climate change in crops. *Frontiers in Plant Science* 11, 544.

Cao, Y.Y., Duan, H., Yang L.N., Wang, Z.Q., Zhou, S.C. *et al*. (2008) Effect of heat stress during meiosis on grain yield of rice cultivars differing in heat tolerance and its physiological mechanism. *Acta Agronomica Sinica* 34, 2134–2142.

Cheng, L., Zou, Y., Ding, S., Zhang, J., Yu, X. *et al*. (2009) Polyamine accumulation in transgenic tomato enhances the tolerance to high temperature stress. *Journal of Integrative Plant Biology* 51(5), 489–499.

Daryanto, S., Wang, L. and Jacinthe, P.A. (2016) Global synthesis of drought effects on maize and wheat production. *PLoS One* 11(5), e0156362.

Demirevska, K., Zasheva, D., Dimitrov, R., Simova-Stoilova, L., Stamenova, M. *et al*. (2009) Drought stress effects on Rubisco in wheat: Changes in the Rubisco large subunit. *Acta Physiologiae Plantarum* 31(6), 1129.

Dinar, M. and Rudich, J. (1985) Effect of heat stress on assimilate partitioning in tomato. *Annals of Botany* 56, 239–248.

Ding, Y., Hayes, M.J. and Widhalm, M. (2011) Measuring economic impacts of drought: a review and discussion. *Disaster Prevention and Management: An International Journal* 20(4), 434–446.

Earl, H.J. and Davis, R.F. (2003) Effect of drought stress on leaf and whole canopy radiation use efficiency and yield of maize. *Agronomy Journal* 95(3), 688–696.

Ebrahim, M.K., Zingsheim, O., El-Shourbagy, M.N., Moore, P.H. and Komor, E. (1998) Growth and sugar storage in sugarcane grown at temperature below and above optimum. *Journal of Plant Physiology* 153, 593–602.

Fahad, S., Bajwa, A.A., Nazir, U., Anjum, S.A., Farooq, A. *et al*. (2017) Crop production under drought and heat stress: plant responses and management options. *Frontiers in Plant Science* 8, 1147.

Farooq, M., Wahid, A., Kobayashi, N., Fujita, D. and Basra, S. (2009) Plant drought stress: Effects, mechanisms and management. *Sustainable Agriculture* 29(1), 153–188.

Ferris, R., Ellis, R.H., Wheeler, T.R. and Hadley, P. (1998) Effect of high temperature stress at anthesis on grain yield and biomass of field grown crops of wheat. *Annals of Botany* 82,631–639.

Fiscus, E.L., Booker, F.L. and Burkey, K.O. (2005) Crop responses to ozone: Uptake, modes of action, carbon assimilation and partitioning. *Plant, Cell & Environment* 28, 997–1011.

Food and Agricultural Organization (FAO) (2009) http://www.fao.org/news/archive/news-by-date/2009.

Gelybó, G., Tóth, E., Farkas, C., Horel, Á., Kása, I. *et al*. (2018) Potential impacts of climate change on soil properties. *Agrokémia és Talajtan* 67(1), 121–141.

Guarino, L. and Lobell, D.B. (2011) A walk on the wild side. *Nature Climate Change* 1, 374–375. DOI: 10.1038/nclimate1272

Haag, J. (2019) Molecular and biochemical enhancement of chlorophyll in sports turf. Lulu.com.

Hasanuzzaman, M., Hossain, M.A., da Silva, J.A.T., Fujita, M. (2012) Plant responses and tolerance to abiotic oxidative stress: antioxidant defenses is a key factor. In: Bandi, V., Shanker, A.K., Shanker, C. and Mandapaka, M. (eds) *Crop Stress and Its Management: Perspectives and Strategies*. Springer, Berlin, Germany, pp. 261–316.

Huang, B., Rachmilevitch, S. and Xu, J. (2012) Root carbon and protein metabolism associated with heat tolerance. *Journal of Experimental Botany* 63, 3455–3465.

Hussain, M., Malik, M.A., Farooq, M., Ashraf, M.Y. and Cheema, M.A. (2008) Improving drought tolerance by exogenous application of glycinebetaine and salicylic acid in sunflower. *Journal of Agronomy and Crop Science* 194(3), 193–199.

Jaleel, C.A., Manivannan, P.A., Wahid, A., Farooq, M., Al-Juburi, H.J. *et al*. (2009) Drought stress in plants: A review on morphological characteristics and pigments composition. *International Journal of Agriculture and Biology* 11, 100–105.

Jaleh, D. (2017) Metabolic adjustments, assimilate partitioning, and alterations in source-sink relations in drought-stressed plants. Photoassimilate Distribution in Plants And Crops. Routledge, pp. 407–420.

Kamara, A.Y., Menkir, A., Badu-Apraku, B. and Ibikunle, O. (2003) The influence of drought stress on growth, yield and yield components of selected maize genotypes. *The Journal of Agricultural Science* 141, 43–50.

Kiem, A.S., Johnson, F., Westra, S., van Dijk, A., Evans, J.P. *et al*. (2016) Natural hazards in Australia: droughts. *Climatic Change* 139(1), 37–54.

Kumar, S., Kaur, R., Kaur, N., Bhandhari, K., Kaushal, N. *et al*. (2011) Heat-stress induced inhibition in growth and chlorosis in mungbean (*Phaseolus aureus* Roxb.) is partly mitigated by ascorbic acid application and is related to reduction in oxidative stress. *Acta Physiologiae Plantarum* 33, 2091–2101.

Kutcher, H.R., Warland, J.S. and Brandt S.A. (2010) Temperature and precipitation effects on canola yields in Saskatchewan, Canada. *Agricultural and Forest Meteorology* 150, 161–165.

Lawlor, D.W. and Cornic, G. (2002) Photosynthetic carbon assimilation and associated metabolism in relation to water deficits in higher plants. *Plant Cell Environment* 25, 275–294.

Lobell, D.B., Schlenker, W. and Costa-Roberts, J. (2011) Climate trends and global crop production since 1980. *Science* 333(6042), 616–620

Maheswari, M., Yadav, S.K., Shanker, A.K., Kumar M.A. and Venkateswarlu, B. (2012) Overview of plant stresses: Mechanisms, adaptations and research pursuit. *Crop Stress and Its Management: Perspectives and Strategies*. Dordrecht, The Netherlands, Springer, pp. 1–18.

Marchand, F.L., Mertens, S., Kockelbergh, F., Beyens, L. and Nijs, I. (2005) Performance of high arctic tundra plants improved during but deteriorated after exposure to a simulated extreme temperature event. *Global Change Biology* 11, 2078–2089.

Maroco, J.P., Pereira, J.S. and Chaves, M.M. (1997) Stomatal responses to leaf-to-air vapour pressure deficit in Sahelian species. *Australian Journal of Plant Physiology* 24, 381–387.

Mitra, R. and Bhatia, C.R. (2008) Bioenergetic cost of heat tolerance in wheat crop. *Current Science* 94, 1049–1053.

Moran, J.F., Becana, M., Iturbe-Ormaetxe, I., Frechilla, S., Klucas, R.V. *et al*. (1994) Drought induces oxidative stress in pea plants. *Planta* 194, 346–352.

Nam, N.H., Chauhan, Y.S. and Johansen, C. (2001) Effect of timing of drought stress on growth and grain yield of extra-short-duration pigeonpea lines. *The Journal of Agricultural Science* 136, 179–189.

Orians, C.M., Schweiger, R., Dukes, J.S., Scott, E.R. and Müller, C. (2019) Combined impacts of prolonged drought and warming on plant size and foliar chemistry. *Annals of Botany* 124(1), 41–52.

Pachauri, R.K., Allen, M.R., Barros, V.R., Broome, J., Cramer, W. *et al*. (2014) Climate change 2014: Synthesis report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. IPCC, p. 151.

Parry, M., Andralojc, P., Mitchell, R.A., Madgwick, P. and Keys, A. (2003) Manipulation of rubisco: The amount, activity, function and regulation. *Journal of Experimental Botany* 54, 1321–1333.

Pettigrew, W.T. (2004) Physiological consequences of moisture deficit stress in cotton. *Crop Science* 44, 1265–1272. DOI: 10.2135/cropsci2004.1265

Porter, J.R. (2005) Rising temperatures are likely to reduce crop yields. *Nature* 436(7048), 174–174.

Prentice, I.C., Farquhar, G.D., Fasham, M.J.R., Goulden, M.L., Heimann, M. *et al*. (2001) The Science of Climate Change. Contributions of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, pp. 183–237. https://www.ipcc.ch/site/assets/uploads/2018/03/WGI_TAR

Ray, D.K., West, P.C., Clark, M., Gerber, J.S., Prishchepov, A.V. *et al*. (2019) Climate change has likely already affected global food production. PLoS ONE 14(5), e0217148.

Raza, A., Razzaq, A., Mehmood, S.S., Zou, X., Zhang, X. *et al*. (2019) Impact of climate change on crops adaptation and strategies to tackle its outcome: A review. *Plants* 8 (2), 34.

Rivas, J.D.L. and Barber, J. (1997) Structure and thermal stability of photosystem II reaction centers studied by infrared spectroscopy. *Biochemistry* 36, 8897–8903.

Rodríguez, M., Canales, E. and Borrás-Hidalgo, O. (2005) Molecular aspects of abiotic stress in plants. *Biotecnología Aplicada* 22, 1–10.

Rogiers, S.Y., Greer, D.H., Hatfield, J.M., Hutton, R.J., Clarke, S.J. *et al*. (2012) Stomatal response of an anisohydric grapevine cultivar to evaporative demand, available soil moisture and abscisic acid. *Tree Physiology* 32, 249–261.

Saitoh, H. (2008) Ecological and Physiology of Vegetable. Nousangyoson Bunka Kyoukai, Tokyo, Japan.

Sato, S., Kamiyama, M., Iwata, T., Makita, N., Furukawa, H. *et al*. (2006) Moderate increase of mean daily temperature adversely affects fruit set of *Lycopersicon esculentum* by disrupting specific physiological processes in male reproductive development. *Annals of Botany* 97, 731–738.

Sevanto, S. (2014) Phloem transport and drought. *Journal of Experimental Botany* 65(7), 1751–1759.

Sharkey, T.D. (2005) Effects of moderate heat stress on photosynthesis: Importance of thylakoid reactions, rubisco deactivation, reactive oxygen species, and thermotolerance provided by isoprene. *Plant, Cell & Environment* 28, 269–277.

Skendžić, S., Zovko, M., Živković, I.P., Lešić, V. and Lemić, D. (2021) The impact of climate change on agricultural insect pests. *Insects* 12(5), 440.

Smertenko, A., Dráber, P., Viklický, V. and Opatrný, Z. (1997) Heat stress affects the organization of microtubules and cell division in *Nicotiana tabacum* cells. *Plant, Cell & Environment* 20(12), 1534–1542.

Srivastava, S., Pathak, A.D., Gupta, P.S., Shrivastava, A.K. and Srivastava, A.K. (2012) Hydrogen peroxide-scavenging enzymes impart tolerance to high temperature induced oxidative stress in sugarcane. *Journal of Environmental Biology* 33, 657–661.

Suzuki, N., Bassil, E., Hamilton, J.S., Inupakutika, M.A., Zandalinas, S.I. *et al*. (2016) ABA is required for plant acclimation to a combination of salt and heat stress. *PLoS One* 11(1), e0147625.

Taiz, L. and Zeiger, E. (2006) Plant Physiology, 4th edn. Sinauer Associates Inc Publishers, Sunderland, MA.

Tietjen, B., Schlaepfer, D.R., Bradford, J.B., Lauenroth, W.K., Hall, S.A. *et al*. (2017) Climate change-induced vegetation shifts lead to more ecological droughts despite projected rainfall increases in many global temperate drylands. *Global Change Biology* 23(7), 2743–2754.

Toth, S.Z., Schansker, G., Kissimon, J., Kovacs, L., Garab, G. *et al*. (2005) Biophysical studies of photosystem II-related recovery processes after a heat pulse in barley seedlings (*Hordeum vulgare* L.). *Journal of Plant Physiology* 162, 181–194.

Vu, J.C.V., Gesch, R.W., Allen, L.H., Boote, K.J. and Bowes, G. (1999) CO_2 enrichment delays a rapid, drought-induced decrease in Rubisco small subunit transcript abundance. *Journal of Plant Physiology* 155, 139–142.

Wahid, A., Gelani, S., Ashraf, M. and Foolad, M.R. (2007) Heat tolerance in plants: An overview. *Environmental and Experimental Botany* 61, 199–223.

Wang, J.Z., Cui, L.J., Wang, Y. and Li, J.L. (2012) Growth, lipid peroxidation and photosynthesis in two tall fescue cultivars differing in heat tolerance. *Biologia Plantarum* 53, 247–242.

Wang, Y., Duan, L., Liu, T., Li, J. and Feng, P. (2020) A Non-stationary standardized streamflow index for hydrological drought using climate and human-induced indices as covariates. *Science of the Total Environment* 699, 134278.

Wardlaw, I.F. (1974) Temperature control of translocation. In Bielske, R.L., Ferguson, A.R. and Cresswell, M.M. (eds) *Mechanism of Regulation of Plant Growth.* Bull Royal Society, Wellington, pp. 533–538.

Yadav, R.S., Hash, C.T., Bidinger, F.R., Devos, K.M. and Howarth, C.J. (2004) Genomic regions associated with grain yield and aspects of post flowering drought tolerance in pearl millet across environments and tester background. *Euphytica* 136, 265–277.

Yang, X., Chen, X., Ge, Q., Li, B., Tong, Y. *et al.* (2006) Tolerance of photosynthesis to photoinhibition, high temperature and drought stress in flag leaves of wheat: A comparison between a hybridization line and its parents grown under field conditions. *Plant Science* 171, 389–397.

Zandalinas, S.I., Rivero, R.M., Martínez, V., Gómez-Cadenas, A. and Arbona, V. (2016) Tolerance of citrus plants to the combination of high temperatures and drought is associated to the increase in transpiration modulated by a reduction in abscisic acid levels. *BMC Plant Biology* 16, 1–16.