REVIEW

Crop responses and management strategies under shade and drought stress


College of Agronomy, Sichuan Agricultural University, 211-Huimin Road, Wenjiang District, 611130 Chengdu, China*
Sichuan Engineering Research Centre for Crop Strip Intercropping System, Key Laboratory of Crop Ecophysiology and Farming System in Southwest China (Ministry of Agriculture), Sichuan Agricultural University, Chengdu, China**
Rice Research Institute and Key Laboratory for Major Crop Diseases, Sichuan Agricultural University at Wenjiang, Chengdu, China***
CAS Key Laboratory of Mountain Ecological Restoration and Bioresource Utilization, Ecological Restoration Biodiversity Conservation Key Laboratory of Sichuan Province, Chengdu Institute of Biology, Chinese Academy of Sciences, P.O. Box 416, 610041 Chengdu, China#
Agricultural Institute, ELKH Centre for Agricultural Research, 2462 Martonvásár, Brunszvik u. 2, Hungary##
Department of Agronomy, Pir Mehr Ali Shah Arid Agriculture University, Rawalpindi, Punjab, Pakistan###

Abstract

The occurrence of shade and drought stress either individually or simultaneously causes altered morphophysiological and molecular responses in crops. Nevertheless, responses of crop plants to combined shade and drought stress are unique as compared to those of individually occurring stress which urges need to study and identify distinctions, commonalities, and the interaction between responses of plants to these concurrent stress factors. In the present review, we outlined currently available knowledge on responses of plants to shade and drought stress on a shared as well as the unique basis and tried to find a common thread potentially underlying these responses. Then, we briefly described some plausible mitigation strategies to cope with these stresses along with future perspectives. A deeper insight into plant responses to co-occurring shade and drought stress will help us to generate crops with broad-spectrum stress tolerance and increased resilience to such stresses in high planting densities or intercropping systems, thus, ensuring food security.

Keywords: cooccurring stress; crop; individual stress; morphophysiological and molecular responses; stress management.

Highlights

- Crop responses to co-occurring and individual shade and drought stress
- Mitigation strategies to cope with stresses along with future perspectives
- Deeper knowledge of plant responses to co-occurring stresses is indispensable

Abbreviations: DEG – differentially expressed genes; LEA – late embryogenesis abundant proteins; PHY – phytochrome; PIFs – phytochrome-interacting factors; Pn – net photosynthetic rate; QTL – quantitative trait locus; R:FR – red:far-red; ROS – reactive oxygen species; RWC – relative water content; SARs – shade avoidance responses; WUE – water-use efficiency; ψw – plant leaf water potential.

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*Corresponding author
e-mail: f.yang@sicau.edu.cn

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Introduction

In the present era of global warming and climate change, plants on Earth are continuously being challenged by their surrounding environment, forcing them to acclimate for the sustenance of their survival. In addition, the continuous deterioration of limited available arable land area by humans is further threatening global food security. As there is a rapid increase in the world population, the demand for food is also increasing likewise, which necessitates the need to grow more resilient plants to feed the increasing population. Under such critical circumstances, one alternative is to grow crop plants at higher densities or in intercropping systems, while keeping intact the individual plant productivity (Courbier and Pierik 2019). However, this option is not as straightforward as it seems to be, as various challenges come with this option, the most important being the shade stress characterized by low red:far-red (R:FR) ratio and low light intensity, as a result of which plants compete with each other for light (Hussain et al. 2019a).

R and FR light are perceived by plants via a family of photoreceptors (PHY) photoreceptors that exist in two interconvertible forms; Pfr – which is active FR light-absorbing form and Pr – which is inactive R light-absorbing form. Five different phytochromes (PHYA–E) have been characterized so far in Arabidopsis thaliana. PHY B is considered as the main modulator of low R:FR-mediated shade avoidance responses (SARs) along with PHY D and E. FR light inactivates phytochromes, reduces phytochrome-mediated degradation of phytochrome interacting factors, leads to rapid induction of gene expression, and triggers biosynthesis and signal transduction of numerous plant hormones, such as auxin, gibberellin, brassinosteroid, and ethylene ultimately promoting elongation growth which is a characteristic of SARs (Keuskamp et al. 2010). SARs involve regulation of metabolic and transcriptional networks which facilitates elongated growth but at the cost of enhanced apical dominance and that of leaf development, thus enabling young growing tissues to get away from shade (Franklin 2008). In general, shade inhibits leaf growth as the proportion of biomass distributed to leaves in comparison to stem decreases under shade stress (Wu et al. 2017). Reduced stomatal conductivity and density are also typical of shade conditions that lead to poor transport of CO₂ (Tan et al. 2021). Furthermore, the movement of electrons from PSII to PSI is blocked and the number and activity of enzymes participating in Calvin cycle changes (Shafiq et al. 2021), i.e., decreased level of reduced thioredoxins in chloroplast stroma is associated with an increased level of oxidized CP12 (chloroplast peptide: a small nuclear-encoded chloroplast protein), which forms PRK/DAPH/CP12 complex leading to reduced activity of glyceraldehyde-3-phosphate dehydrogenase and phosphoribulokinase, thereby affecting carbon fixation rate in Calvin–Benson cycle under shade conditions (López-Calcaño et al. 2014).

With higher planting densities or cultivation of crops in intercropping systems, the challenge of water deficit stress or drought comes, which severely restricts crop growth (Iqbal et al. 2019). Drought stress is usually represented by the reduction of plant leaf water potential (ψw), closure of stomata, reduced cell growth and enlargement, reduced turgor pressure, and reduced relative water content (RWC) (Soltys-Kalina et al. 2016). It is well documented that drought alters numerous physiological and biochemical processes, i.e., photosynthesis, chlorophyll biosynthesis, metabolism of various nutrients, uptake of ions and translocation of elements, respiration, and carbohydrates metabolism (Ashraf and Harris 2013). Additionally, it results in the production of reactive oxygen species (ROS), further damaging the normal functioning of the photosynthetic machinery, leading to serious yield reductions (Green-Tracewicz et al. 2011). At a molecular level, it modulates the production of various genes, transcription factors, heat-shock proteins, aquaporins, late embryogenesis abundant (LEA) proteins, dehydrins, etc. (Kaur and Asthir 2017).

When shade and drought stress co-occur simultaneously, physiological, structural, and biochemical changes occur in plants at the leaf as well as the whole plant level (Holmgren 2000). Such stresses might result in different plant responses, i.e., additive, synergistic or antagonistic (Zhang et al. 2011), that may or may not hamper plant growth and vary from species to species. Research work on shade (Chen et al. 2019, 2020; Ferroni et al. 2021) and drought (Lawlor and Tezara 2009, Zivcak et al. 2014a, Anjum et al. 2017), occurring as individual stress factors in several crops, is well cited in the literature. However, not much attention has been given to their combined effects and whether the crop responses to both of these stresses are shared or unique also remains ambiguous (Shafiq et al. 2020). An understanding of the responses of plants to cooccurring stress factors is necessary to enhance plants' adaptation under field conditions. The present review is an effort to comprehend the current understanding of the effect of shade and drought stress, individually on crop plants. Furthermore, it sheds light on the shared and unique responses of crop plants to shade and drought stress and discusses some feasible alleviation strategies to survive these stresses and to minimize the harm caused by these stresses to the crop plants.

Plant responses to shade stress

The incidence of shade stress at any stage of plant growth negatively affects the growth and development of the plant. The intensity of injury owing to the stress, however, depends on the magnitude of the stress and its duration as well as the plant growth stage. The consequences of shade stress on plant's morphophysiological, biochemical, as well as molecular processes are elicited below.

Plant phenotypes

Shade negatively affects various morphological and growth parameters in crops, such as winter wheat (Triticum aestivum; Li et al. 2010), rice (Oryza sativa; Liu et al. 2014), soybean (Hussain et al. 2019a), and maize (Gao et al.
dissolution and transport of CO₂ (2008), leading to a structure that is not conducive to the dissolution and transport of CO₂ (Terashima et al. 2001).

Smaller and thinner leaves in response to shade stress is a common characteristic observed in many plant species, such as soybean (Wu et al. 2017), sunflower (Helianthus annus; Granier and Tardieu 1999), Chenopodium album (Yano and Terashima 2004), rice (Murchie et al. 2005), Arabidopsis (Kozuka et al. 2005), Eurya japonica (Mishio and Kawakubo 2015), Juglans regia (Atanasova et al. 2003), Carya illinoensis (Lombardini et al. 2009), and tomato (Solanum lycopersicum; Fan et al. 2013). Such leaf structure results in lower harvesting of light (Yang et al. 2014, Wu et al. 2017). The low R:FR ratio under shade also affects leaf angle as shade on the adaxial side promotes the elongation of the cells on that side through adjustment of Pfr content, thus changing the leaf angle to increase the light interception in leaf (Fujita et al. 2008).

Leaf cuticle and epidermal appendages like trichomes play an important protecting role against light interception (Karabourniotis et al. 2021). In comparison to sun leaves, shade leaves have a thinner cuticle membrane (Wu et al. 2020). Non-glandular trichomes form dense layers on plant organ surfaces and have distinct optical characteristics (Werker 2000). Liakoura et al. (1997) found that trichome density and its UV-B protective potential are affected by shading. Under low irradiance or low angles of incidence, trichome layers may limit light harvesting for photosynthesis. Trichomes may thus influence light propagation into the mesophyll, thereby influencing the characteristic of the internal light microenvironment and the extent of light-saturated photosynthesis in the internal cell layers (Gorton and Vogelmann 1996).

Low R:FR ratio causes stem elongation as it enhances the expression of flavin monooxygenase which increases the content of auxin that is then transported from leaves to stem, thus leading to extension of internodes as well as an increase in plant height (Liu et al. 2019). Furthermore, a low R:FR ratio also increases gibberellin content which accelerates the cell division and cell elongation of the stem, thus leading to increased plant height (Kamiya and Garcia-Martinez 1999). It decreases the diameter of the stem since more carbon is allocated to the stem and petiole elongation thus impairing the development of roots and leaves (Gommers et al. 2013). Shade also decreases stem strength by reducing the biosynthesis of lignin which is a major component of the cell walls, resulting in weak and elongated stems having poor mechanical strength and susceptibility to lodging leading to loss of yield (Hussain et al. 2020a).

Shade also affects the root morphology; it reduces the root length, surface area, and volume (Hussain et al. 2019b). Generally, under shade conditions, the growth of roots is reduced more than the growth of the aerial parts as the photosynthates are distributed preferentially to shoots during leaf extension to increase the interception of light (Hébert et al. 2001, Gommers et al. 2013, Gundel et al. 2014). This ultimately leads to a decrease in the root/shoot ratio (Zhou et al. 2020). Light not only influences root morphology by regulating the synthesis and partitioning of photosynthates but also acts as a signal to directly regulate root growth (van Gelderen et al. 2018a). For example, far-red light detection in the shoot of Arabidopsis regulates lateral root growth via the HY5 transcription factor (van Gelderen et al. 2018b).

Shade reduces the growth of plants along with its metabolic activities which influence the agronomic and yield parameters of the plants. During the rice filling stage, it causes a decrease in yield and degrades the grain quality (Chen et al. 2019). In another study, shade increased the chalkiness by delaying the development of caryopsis and disturbing the characteristics of starch in rice grains thus reducing the market price and quality of rice grain (Deng et al. 2018). In winter wheat, a shade between jointing and maturity stage caused yield reduction (Li et al. 2010). Similarly, in cotton (Gossypium hirsutum), shade stress between flowering and boll-opening stage resulted in the decrease of cotton boll's number and mass, strength of the fiber, and the micronaire that led to poor yield and quality of cotton (Chen et al. 2017). However, the effect of shade on yield parameters of crops may differ based on the shade's duration and magnitude, crop growth stage, and local ecological environment.

**Photosynthetic performance**

Shade is well reported to influence the performance of plant photosynthesis and other leaf gas-exchange parameters. Under shade stress, light-intercepting and utilization ratio as well as the activity of PSII increases, but the photosynthetic capacity is inhibited as transport of energy from PSII to PSI is hindered (Zivcak et al. 2014b) (Fig. 1). Shade stress in soybean, during the vegetative growth phase, disrupted the normal photosynthetic rate due to decreased energetic pressure generation at PSII, thus minimizing electron transport rate, reducing the amount of ATP produced as well as the Rubisco activity. It affected the photochemical activity, assimilation of CO₂ and decreased the quantum efficiency of PSII and quantum yield (Hussain et al. 2019b). Poor photosynthetic rates in crop plants grown under shade are also attributed to (1) poor mesophyll and stomatal conductance of CO₂, (2) impaired chloroplast development, and (3) hindered photosynthesis due to inhibited leaf growth caused by controlled cell multiplication (Wu et al. 2017).

Shade results in lower leaf and canopy temperature together with decreased transpiration rate and stomatal conductance. It might also reduce stomatal opening (Knapp and Smith 1990) as in guard cells the content of abscisic acid increases and binds to soluble receptors triggering the closing of stomata (McCourt and Creelman 2008). Activation of abscisic acid receptor enhances the activity of respiratory burst oxidases due to increased phosphorylation (Mustilli et al. 2002) which leads to a brief outbreak of ROS in the stomatal guard cells (Pei et al. 2000) that open calcium ion influx channels (Mittler 2002).
and Blumwald 2015), thus activating cell membrane's ion efflux channels. Such alterations in the concentration of ions cause water efflux, increasing the flaccidity of guard cells which causes stomata to close (Chen et al. 2010). Shade also affects the Chl antenna size. Under low light conditions, when Chl a/b ratio decreases and the light-harvesting center to PS-core ratio increases, the Chl antenna size increases, and this serves as a dynamic compensation response to shade conditions (Leong and Anderson 1984, Melis 1991).

Reactive oxygen species and antioxidant activity

When plants experience shade, they undergo oxidative stress and enhanced ROS production. The stress leads to increased levels of photorespiration and enhances the activity of the mitochondrial electron transport chain (mETC) (Blokhina et al. 2003, Lawlor and Tezara 2009). Earlier research reports the enhanced ROS production in plants under shade stress (Apel and Hirt 2004, Volkov et al. 2006, Zhu et al. 2017). Shade results in increased auxin contents and auxin-regulated ROS production has also been reported; it plays a role in root gravitropism (Joo et al. 2001). To mitigate the oxidative damage and maintain cellular homeostasis, plants produce an elaborate arsenal of enzymatic (superoxide dismutase, ascorbate peroxidase, peroxidase, catalase, glutathione reductase, glutathione S-transferase, guaiacol peroxidase, etc.) and nonenzymatic (reduced and oxidized glutathione, ascorbic acid, α-tocopherol, and carotenoids) antioxidants under unfavourable conditions such as shade and drought stress (Shafiq et al. 2021). These antioxidants not only interrupt the cascades of uncontrolled oxidation by ROS but also help in the maintenance of an appropriate balance between their production and removal that allows an optimum functioning of photosynthesis (Foyer 2018). Various enzymatic and nonenzymatic antioxidants have been known for inducing shade tolerance as reported in pine needles (Anderson et al. 1992), spruce (Polle and Rennenberg 1992, Doulos et al. 1993), olive (Mohammad et al. 2019), Taxus × media cv. Tauntonii (Verhoeven et al. 2005), etc. The high contents of antioxidants in response to stresses show that they contribute towards stress tolerance in plants.

Plant-related gene and protein expression

Shade modulates plant responses at the molecular level as well. Under shade stress, phytochromes perceive altered R:FR light while cryptochromes sense changes in light to control the adaptive developmental approaches (Casal 2012). This is followed by signal transduction which is then cascaded through phytochrome interacting factors (PIFs), circadian clock protein TOC1, circadian clock basic helix-loop-helix protein PIL1, and various transcription factors belonging to DELLA families to activate the alterations of gene expression (light signal genes, hormone-related genes, and stress-induced genes), and prompt series of shade-avoidance syndrome responses (Salter et al. 2003, Wang et al. 2011, Gendron et al. 2012, Gallemí et al. 2016). The end-of-day far-red treatment induces many auxin or brassinosteroid responsive genes and both auxin [big and
shade avoidance 3 (sav3)/tryptophan aminotransferase of Arabidopsis 1 (taa1)) and brassinosteroid [rotundifolia3 (rot3)] mutant showed decreased shade-induced expression of genes as well as the petiole elongation (Kozuka et al. 2010). Li et al. (2017) reported that shaded conditions downregulated the expression of gibberellin biosynthesis genes in a shade-tolerant mutant of perennial ryegrass compared to wild type which demonstrated the function of gibberellin in dwarfism and tolerance to shade. The microarray analysis disclosed that shade regulated the expression of genes that were involved in cell wall carbohydrate metabolism, responses of auxin, and the flavonoids in the stem of tomato (Cagnola et al. 2012). Similarly, RNA-Seq based transcriptome analysis of the conifers grown under shade stress showed gene regulations on the signalling of hormones and biosynthesis of pigments (Ranade et al. 2019). Shade stress in peanut (Arachis hypogaea) downregulated the expression of various genes for photosynthesis pathways, and the key genes in the metabolism of sucrose and starch, and the hormonal signal pathways (Chen et al. 2020). Heavy shade in soybean lead to expression downregulation of key genes participating in the lignin biosynthesis which reduced the lodging resistance (Wen et al. 2020). To conclude, shade profoundly alters a plant’s genetic expression.

Plant responses to drought stress

Similar to shade stress, the incidence of drought stress at any stage of plant growth also negatively affects the growth and development of plants. The consequences of drought stress on morphophysiological, biochemical, as well as molecular processes in plants are elicited below.

Morphological parameters

The key crop phenotypic indicators of drought stress include plant height and leaf area. Drought results in shorter plants and restricted leaf growth (Paredes et al. 2014). It hampers the flow of water from the xylem to other elongating cells as well as causes reduced turgor pressure that results in a reduction of cell division, cell elongation, and cell expansion leading to a smaller leaf area in crop plants (Pereyra-Irujo et al. 2008, Skirycz et al. 2010). Reduced leaf expansion is helpful for plants under such stress, as it reduces the area of leaf exposed, which results in reduced rates of transpiration, thus preventing water loss. Drought increases the endogenous abscisic acid content which accelerates the leaf senescence process as observed in rice (Ray et al. 1983). Similarly, increased concentrations of ethylene under water stress were correlated with increased senescence and abscission of leaves in Vicia faba (El-Beltagy and Hall 1974). This mechanism of accelerated senescence and abscission in old leaves of mature plants under water deficit stress is called leaf area adjustment (Mahajan and Tuteja 2005).

Water deficit stress also alters root morphology and architecture and causes a reduction in root to shoot ratio (Shi et al. 2015, Anjum et al. 2016a). It has multiple effects on root growth, for example, Catharanthus roseus and sunflower enhanced their root length when exposed to water deficit stress (Tahir et al. 2002, Jaleel et al. 2008) while no effect was observed in maize and wheat. The increase in root length under water deficit might be attributed to increased root abscisic acid content (Manivannan et al. 2007). However, drought effects on root architecture vary between drought-tolerant and sensitive plants (Manschadi et al. 2006). In general, extensive and prolific root system enhances the ability of plant in sustaining growth and yield in a drought environment (Chandra Babu et al. 2001). Nevertheless, at regular but lower amounts of precipitation, the moisture is not sufficient enough to make deeper fractions of soil wet, hence a subsurface root architecture is more desirable under such conditions.

Drought in legumes limits flower and pod production, enhances flower and pod abortion rate, reduces seed size, thus, causing a dramatic loss of seed yield (Fang et al. 2010). Water deficit in soybean greatly reduces branch number and the total yield of seed (Frederick et al. 2001). A 33% drought-induced reduction in global chickpea (Cicer arrietum) production is expected (Kashiwagi et al. 2015). In comparison to legume or root crops (such as Dioscorea alata, Beta vulgaris, etc.), cereals had lower drought-induced yield reduction (Daryanto et al. 2017). Drought caused a yield reduction in other crops, such as cotton, peanut, sunflower, wheat, and maize (Tahir et al. 2002, Kamara et al. 2003, Pettigrew 2004, Vasantha et al. 2005, Barnabás et al. 2008, Furlan et al. 2012).

C3 and C4 plant photosynthesis

Lack of water availability affects various metabolic processes including photosynthesis. It causes a significant reduction in C3 and C4 photosynthesis (Fig. 2). The core processes of C3 and C4 photosynthesis are the same, including light-harvesting complexes, electron transport components, and the C3 cycle. As a result, C3 and C4 plants are expected to respond similarly to drought stress; nevertheless, the two photosynthetic types are significantly different, which may result in differing responses. C4 plant leaves have a CO2-concentrating mechanism that provides them with greater water-use efficiency (WUE) contrary to C3 plants. However, it is still debatable if C4 plants having higher WUE can withstand more drought stress in comparison to C3 plants. Similarly, though the CO2-concentrating mechanism provides better-buffering capacity to C4 photosynthesis against CO2 shortages due to limited closing of stomata during drought, yet C4 photosynthesis biochemistry is considered to be at least as sensitive or even more sensitive as compared to C3 photosynthesis (Ghamnoum 2009). Generally, drought reduces the leaf area and causes the closing of stomata that lowers the leaf intercellular CO2 concentration, thus imposing limitations on CO2 assimilation. Drought stress also lowers mesophyll conductance (Genty et al. 1989, Flexas et al. 2004). The mesophyll conductance refers to the flow of CO2 from the intercellular air spaces to the carboxylation site in the chloroplasts of mesophyll cells, and it takes into account the intricate routes of the cell wall, plasma membrane, chloroplast envelope, and stromal
thylakoids (Ethier et al. 2006). Recent research suggests that mesophyll conductance plays an important function in photosynthetic regulation (Fleck et al. 2010, Ferroni et al. 2021). Reduced mesophyll conductance values during water stress may lead to a delayed restoration of net photosynthetic rate, making it a critical limiting factor in net photosynthetic rate recovery (Olsovska et al. 2016). It is assumed that mesophyll conductance accounts for up to 40% of the CO$_2$ diffusional constraints on entire photosynthesis (Warren 2008). Stomatal closure in response to drought stress results in a disproportion of photochemical activity at PSII and electron requirement for the process of photosynthesis (Runion et al. 1997, Zivcak et al. 2014a), hence increasing the vulnerability to photodamage (He et al. 1995, Guo et al. 2018). It damages and reduces the synthesis of photosynthetic pigments (Oneto et al. 2016) and declines the Rubisco activity (Lawlor and Tezara 2009), thus, limiting the plant photosynthesis. Another reason for the reduced net photosynthetic rate in response to water deficit is the generation of ROS. Water deficit limits intercellular CO$_2$ concentration. This accumulates the components of reduced photosynthetic electron transport which can potentially reduce the molecular oxygen. This generates ROS which damage the photosynthetic apparatus (Hussain et al. 2019c). To conclude, drought has detrimental effects on the light-harvesting mechanism and photosynthetic apparatus in plants.

**Plant water and nutrient relations**

Water deficit significantly lowers the RWC, turgor pressure, $y_s$, and $E$ which is well documented in various crop species (Siddique et al. 2000, Liu et al. 2004, Reddy et al. 2004, Nayyar and Gupta 2006, Yang and Miao 2010, de Campos et al. 2011). It also hinders mineral nutrient uptake and translocation from roots to shoots (Suriyagoda et al. 2014). It reduces the growth of root per unit of root length and root biomass, as well as the rate of inflow of the nutrients (Kuchenbuch et al. 1986). Water scarcity affects the cation active transport and membrane permeability which reduces the cation absorption through roots (Hu and Schmidhalter 2005). Drought also affects the metabolism of the nutrients, for instance, it hinders the functioning of enzymes that take part in the assimilation of nutrients (Ashraf and Iram 2005). It might also cause micronutrient deficiency for manganese, iron, and molybdenum (Hu and Schmidhalter 2005), however, as soon as the soil is well watered, these micronutrients are converted into more soluble and reduced forms to be used by plants (Havlík et al. 2016). In conclusion, the occurrence of drought stress in plants decreases nutrient availability, uptake, translocation, and their metabolism.

**Reactive oxygen species, antioxidants, organic solutes, and phytohormones**

Drought results in excessive ROS generation which serves as an adaptive mechanism in stressed plants (Hossain et al. 2021). Excessive ROS generation causes oxidative injury in plant cells (Sgherri et al. 1993, Boo and Jung 1999). It enhances the ROS generation through various ways, e.g., limited CO$_2$ fixation reduces the NADP$^+$ production via the Calvin cycle which lessens the photosynthetic electron transport chain (Cruz de Carvalho 2008). It enhances the photorespiratory pathway, particularly when RuBP oxygenation is at maximum because of the restrictions on CO$_2$ fixation. Furthermore, under conditions of water deficit, photorespiration contributes to more than 70% of total H$_2$O$_2$ production (Noctor et al. 2002). Various
enzymatic and nonenzymatic antioxidants have been known for inducing drought tolerance as reported in rice (Sharma and Dubey 2005), transgenic rice, and tobacco (Nicotiana tabacum) (Badawi et al. 2004, Prashanth et al. 2008), in wheat (Keleş and Öncel 2002), transgenic wheat, soybean, and petunia (Petunia hybrida; Yamada et al. 2005, Simon-Sarkadi et al. 2006, Vendruscolo et al. 2007), transgenic tobacco (Yan et al. 2003), cotton (Ratnayaka et al. 2003), beans (Türkan et al. 2005), etc. Plants also produce enzymatic and nonenzymatic antioxidants to inhibit ROS accumulation. Drought-tolerant wheat genotypes can reduce O₂ oxidative damage by maintaining higher contents of carotenoids during drought stress, according to a previous study by Balouchi (2011). Under drought stress, Ma et al. (2014) found that the amount of flavonoids in wheat leaves is increased due to the higher expression of flavonoid biosynthesis genes. Apart from ROS and antioxidants, plants produce a variety of compatible organic solutes in response to drought stress (Boscaiu and Fita 2020). Plant cells use osmotic adjustment to preserve water status in their tissues during drought stress. The biosynthesis of osmotically dynamic substances, such as proline (Faraooq et al. 2017), glycine betaine (Gupta et al. 2014), sugar alcohols, soluble sugars, organic acids (Farshadfar et al. 2008), chloride ions, calcium, and potassium, is involved in osmotic adjustment (Farshadfar et al. 2008). Moreover, plants produce phytohormones such as abscisic acid to control stomatal opening under guard cells and protect plants from excessive water loss thus facilitating plant acclimatization to drought stress (Schachtman and Goodeger 2008).

Responses at the molecular level

Molecular alterations in response to environmental stresses negatively affect the growth and development of crops. Several genes are upregulated or downregulated by water deficit conditions. Water deficit alters the level of expression of LEA (dehydrin-type genes) as Sivamani et al. (2000) found; tolerance to drought was enhanced in rice roots and wheat leaves by overexpression of barley group 3 LEA gene HVA1. Furthermore, synthesis of the molecular chaperone (Close 1997, Bhargava and Sawant 2013), dehydration-responsive-element (having A/GCCGAC as a core sequence) (Seki et al. 2001), homeodomain leucine zipper protein's expression (that interacts with CaCBF1B) (Mahajan and Tuteja 2005), and expression of H1-S (histone H1variant which is known to function in regulating stress modulated genes and aid closing stomata) (Scioppa et al. 2004, Bhargava and Sawant 2013) are all reported to be regulated under drought conditions. Abscisic acid production in roots is also regulated under drought stress. It is transported to shoots which causes the closure of stomata, thus restricting the growth of plants (Mittler and Blumwald 2015). Likewise, water scarcity and abscisic acid have been shown to rapidly elevate calcium levels in plant cells, activating a signalling pathway that activates a number of genes that help maintain cellular homeostasis (Sanders et al. 1999, 2002). Enhanced tolerance to drought stress was observed in rice by upregulation of Oryza sativa WRKY11 under control of the heat-shock protein 101 (HSP101) promoter (Wu et al. 2009). Drought stress upregulated miR398, whereas it reduced the level of expression of Cu/Zn SOD isoforms in peanut (Park and Grabau 2017). Similarly, drought stress regulated the gene expression of transcription factors associated to bZIP, MYB, bHLH, NF-Y, EAR, NAC, and ZPT2, AP2/ERF, HD-ZIP families (Yang et al. 2010).

Plant responses to co-occurring shade and drought stress

The morphological and physiological responses to shade and drought, including structural and biochemical variation, have been well documented at the single-leaf and whole-plant levels but what impact does the co-occurring shade and drought stress have on the plant growth, it still remains unclear. To date, there has been no consistent conclusion on this issue, but several contrasting hypotheses have been proposed. First, the trade-off hypothesis, which predicts that shade increases the effect of drought on plants. This is so as plants allocate more resources to leaves and shoots in comparison to roots under shade stress which eventually increases the light-capture capacity but reduces water absorption in plants (Smith and Huston 1999). Additional mechanisms for a trade-off have also been indicated in specific cases (Marshall 1986, Vance and Zaerr 1991, Kusibake et al. 1996). By contrast, the influential facilitation hypothesis predicts that shade might reduce air and leaf temperature, leaf vapor-pressure deficit, and oxidative stress. Thus, shading can help to alleviate the negative effects of drought on plants (Holmgren 2000) but the degree to which deep shade can be facilitative is unclear. The third hypothesis is the interplay hypothesis which suggests that drought has a relatively stronger impact under high irradiance and deep shade, with moderate shade alleviating the negative effects of drought (because of facilitation) (Holmgren et al. 1997). Finally, an independent-effects model predicts that the effects of shade and drought are independent, i.e., orthogonal, as drought reduces relative growth rate (RGR) by a given proportion at any irradiance (Sack and Grubb 2002, Sack 2004). Some limited literature available (mostly on woody seedlings) regarding the effect of co-occurring shade and drought stress on plant growth is elicited below.

How plant morphophysiology responds to co-occurring shade and drought stress

Carneiro et al. (2015) found that when shade (70%) grown Jatropha curcas plants were subjected to long-term water deficit conditions (irrigation withheld until signs of stress, i.e., leaf tipping and wilting became evident), the biomass allocated to roots was lowered by > 40% though the root length did not change. However, the leaf size of plants grown in co-occurring shade and drought stress was considerably greater than those grown under full sun and drought environment. The reduction in biomass allocation to roots showed that exposure of Jatropha plants to co-occurring shade and drought stress could
hamper plant development whereas larger leaf area under shade was probably due to reduced demand of evaporation in the shaded environment that led to the maintenance of leaf size in drought conditions. Ammissah et al. (2015) reported that seedlings of ten different Ghanaian trees species under drought stress (withholding water for nine weeks), survived better in shade (20% irradiance) than those in full light as better microclimatic conditions in the shaded environment under drought conditions (i.e., shade lowered the temperature of air and leaves, thus hampering overheating, and reduced the transpirational demands of plants; also shaded plants exposed to drought have higher relative water content in comparison to those plants grown under full light) enhanced the plant performance under drought conditions thus supporting facilitation hypothesis. The facilitation hypothesis was also supported by examples of red oak and yellow poplar seedlings grown in a combination of shade and drought stress (Kolb et al. 1990). When discussing the yield components, shade and drought stress occurring individually generally have negative effects on plant yield, however, when both the stresses occur simultaneously, the effect on yield is often not the same. Shade stress, in some cases, may serve useful to alleviate negative consequences of water deficit stress on the yield of crops as reported earlier in soybean (Zhang et al. 2011, Shafiq et al. 2020).

Plant photosynthetic response to co-occurring stresses might also vary in comparison to individual stress. Transpiration rate ($E$), stomatal conductance ($g_s$), and net photosynthetic rate ($P_n$) in plants did not decrease when exposed to drought stress (55 ± 2% field capacity) and low irradiance (PPFD = 500–600 μmol m$^{-2}$ s$^{-1}$ at noon) whereas a decrease was observed in plants that were kept in medium or high irradiance which depicts a positive role of shade under drought conditions (Shafiq et al. 2020) and supports the facilitation hypothesis (Holmgren 2000). The results of this research propose that the degree of influence of drought stress on a plant’s photosynthetic capacity depends on the irradiance in the environment. In the co-occurrence of shade and drought stress, the production of reductants, such as glutathione reductase, thioredoxin reductase as well as ascorbate, decreased due to shade. This decreased reduction capacity is associated with increased ROS-driven oxidative damages induced by drought (Ali et al. 2005, Baier et al. 2005, Ahmed et al. 2009). The damages caused by ROS lead to numerous physiological and biochemical dysfunction in plants. Contrastingly, Asghar et al. (2020) reported lesser ROS production (under drought stress) in soybean plants exposed to shade in comparison to those grown under normal light; the possible explanation could be that shade pretreatment enhanced the exogenous auxin that played role in ROS detoxification. Furthermore, they reported that drought stress in soybean seedlings leads to increased proline content, soluble and reducing sugars, however, the increase was greater in plants under a pre-shade treatment in comparison to plants grown under normal light. This increase in osmoprotectant accumulation in shaded plants occurred due to the increment in abscisic acid contents and the enhancement of auxin contents which helped the plants in better survival under drought conditions (Pardos and Calama 2018).

Which genes and proteins respond to co-occurring shade and drought stress

In conditions of co-occurring drought and shade stress, the molecular changes that occur may or may not be the same as those which occur in response to individual stresses. For instance, in drought conditions, DELLAs proteins enhance abscisic acid sensitivity in stomatal guard cells due to the inhibition of gibberellic acid biosynthesis which interferes with abscisic acid receptors, thus leading to an earlier closure of stomata in tomato plants (Nir et al. 2017). However, a beneficial function of phytochrome B and DELLAs in the plant’s drought tolerance may reverse under shade stress where low R:FR ratio of light causes phytochrome B inactivation and upregulation of gibberellic acid signalling (resulting in increased bioactive gibberellic acid) that eventually causes degradation of DELLAs (Djakovic-Petrovic et al. 2007). Hence, drought stress may lessen or diminish the advantages of shade avoidance in a field environment (Huber et al. 2004). Contrastingly, (Asghar et al. 2020) reported shade-induced expressional upregulation of AAO3 and NCED3 (abscisic acid biosynthesis genes) and ABI4 and ABI5 (abscisic acid signalling genes), which helped to overcome the far-reaching implications of water deficit in soybean. The increased synthesis of abscisic acid could be due to high sugar contents which ultimately lead to the signalling of abscisic acid. ABI4 transcription factor performs an essential function in abscisic acid–sugar connection and its expression is upregulated by the availability of higher sugar content (Arenas-Huerto et al. 2000). Nevertheless, this predicted association between abscisic acid and sugar content together with the role of the studied genes needs to be examined further under varying environmental conditions. Most of the research available has been conducted on plant morphophysiological and molecular responses to individual stress, however, as it is obvious from the above-cited literature, further studies on the range of species (specifically field crops) are required for a profound understanding of the changes in plant responses under co-occurrence of simultaneous shade and drought stress.

Management strategies for drought and shade

Drought and shade stress adversely affect plant growth and productivity. Such effects can be managed and minimalized by various efforts.

Selection and breeding strategies

A combination of traditional, molecular, and omics-based techniques could be used to generate shade and drought-tolerant genotypes (Maqbool et al. 2017). The use of molecular and biotechnological means for selecting preferred materials (such as in conventional breeding),
along with the production of genetically engineered crops, helps assemble material for shade and water-deficit tolerance (Fig. 3). Liu et al. (2017) used metabolomic analysis of isoflavones based on the OPLS-DA (orthogonal partial-leastsquares discriminant analysis) model for predicting shade tolerance of soybean seedlings of various germplasm without actually conducting tedious field experiments. This provided an easier alternative for evaluating and screening shade-tolerant soybean germplasms. Yuan et al. (2012) found two important QTLs (quantitative trait loci) for plant height and ear height; qPH4 and qEH4a simultaneously at two different locations under shade and full-light treatments in maize. These QTLs were found to be insensitive to shade stress in maize cultivars, hence, it was suggested that these QTLs could be used for selecting shade-tolerant and/or high planting density-tolerant maize hybrids in maize breeding programs. Li et al. (2017) used transcriptome analysis to identify differentially expressed genes (DEGs) of a shade-tolerant mutant of perennial ryegrass (Lolium perenne) called ‘shadow-1’ under shade stress. They found 329 DEGs that were unique to shadow-1 plants grown in a shaded environment and also the gibberellin-biosynthesis genes were downregulated compared to wild type. The data provided could be used by breeders to develop shade-tolerant dwarf ryegrass cultivars. Other physiological and morphological characteristics used for screening shade-tolerant crops include reduced elongation responses, the longevity of leaf, specific leaf area, root/shoot ratio, rate of dark respiration, and relative growth rate (Gommers et al. 2013).

In the case of drought stress conditions, the ‘final grain yield’ is the most commonly used parameter for screening drought-tolerant crops in the conventional breeding approach (Verulkar et al. 2010). Since yield (a quantitative trait) has low heritability, this approach remains ineffective (Ouk et al. 2006). However, a profound understanding of physiological and molecular basis might aid in targeting the key traits restricting the crop yield. QTL analysis and segregation mapping provide us with the molecular basis of tolerance to water deficit stress (Lanceras et al. 2004). Identifying QTLs involved in drought tolerance aid in MAS (marker-assisted selection) of crops with preferred characters (Rahman et al. 2011, Varshney et al. 2012). Though, a considerable number of QTLs for numerous drought-tolerant traits have already been reported, yet the discovery of epistatic QTLs and epiQTLs in the future could be potentially used for molecular breeding (Gupta et al. 2017). Apart from conventional breeding, the classical breeding approach is also in practice (Chandra Babu et al. 2003). Selecting putative drought-adaptive secondary traits in classical breeding is reported to be useful for developing drought-tolerant cultivars. Earlier, much research regarding the genetic analysis of secondary traits (i.e., root system architecture, wnw, panicle water potential, osmotic adjustment, and RWC) has been conducted, however, such traits have low heritability just like yield under drought stress (Ludlow and Muchow 1990, Atlin and Lafitte 2002, Jongdee et al. 2002).

**Biological engineering technology**

At present, plants are commonly bioengineered for drought tolerance using various transgenic approaches (Bahieldin et al. 2005, Nakashima et al. 2014). The expression of involvement of DREB2A and DREB2B (drought-induced transcription factors) were found to be involved in the expression of numerous genes involved in tolerance against drought stress in crops (Cui et al. 2011, Ali et al. 2017). Responses of abscisic acid-responsive elements-binding proteins (AREB) to water deficit at transcriptional and post-transcriptional levels were found to be also the determinants of plants’ abilities to tolerate drought (Kaur and Asthir 2017). Overexpression of AtWRKY57 induced tolerance against drought stress in Arabidopsis (Li et al. 2013). Expression of AtWRKY63 and BdWRKY36 imparted tolerance against drought stress through the abscisic acid-signalling pathway in transgenic tobacco
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(Sun et al. 2015). Drought tolerance was enhanced in rice by overexpression of OsLEA-3-1 and OsLEA-3-2 genes (Xiao et al. 2007, Duan and Cai 2012). The LEA group protein gene HVA1 which (during the maturation stage of seed) accumulates in the aleurone layers and embryos of barley, increased the transgenic rice plants' tolerance against water deficit stress (Xu et al. 1996). Aquaporins assist in the regulation of the plant–water relations, hence can be used to develop drought-resistant plant genotypes (Alzal et al. 2016). Considerable literature is available and shows that the transgenic expression of specific stress regulatory genes resulted in enhanced crop tolerance to drought, but the enhanced expression of these genes is also often related to growth retardation which limits its practical applications. Therefore, developing water deficit-resistant crops will necessitate a profound apprehension of the genetic basis of drought tolerance along with the recognition of transcriptions factors linked to resistance to drought stress (Xiong et al. 2006).

Though much research has been conducted to identify genes responsive to individual stress, further efforts are required to identify genes expressed by both shade and drought stress concurrently. The combination of traditional breeding with modern-day techniques, i.e., genetic engineering, marker-assisted selection, and molecular breeding, will assist in developing and improving crop resistance against individual and concurrent environmental stress factors (Fleury et al. 2010).

Induction of shade and drought resistance

Resistance to shade and water deficit could be imparted in plants by taking several agronomic and physiological measures. Of these, adjustment of row configuration in the intercropping system and planting densities in the monocropping system, exogenously applied various plant growth regulators, osmoprotectants, mineral nutrients, seed priming, etc., have proven to be beneficial in mitigation of the negative implications of shade and drought stress. An account of these measures is given below.

Optimum planting pattern

Shade is not just an issue for the growth of plants growing in forest understories but also for the short-statured crops growing in intercropping systems or the crops growing at higher densities in the sole cropping system. In high planting densities, erect leaves serve as a vital adaption to obtain a higher leaf area index, enhancing photosynthetic rate (Sinclair and Sheehy 1999). In the case of intercropping systems, adjustment of row configuration and use of appropriate planting patterns should be taken into consideration to avoid shade stress (Maitra et al. 2021). Maize–soybean relay-intercropping has been preferred over strip intercropping which helps the short-statured soybean crop avoid shade for most of its growth period and prevent lodging and thus yield loss (Yang et al. 2017, Fan et al. 2018). Feng et al. (2019) suggested that selecting an optimum planting pattern could help increase the interception of light and affect the distribution of light between maize and soybean rows in relay-intercropping thereby reducing the shade avoidance response in short-statured soybean and leading to a significant improvement in productivity of the intercrops. Likewise, Raza et al. (2019a,b) also documented such results. Adjustment of planting geometry in the intercropping system helped in enhancing the water-use efficiency of the intercrops (Rahman et al. 2017a,b). In the case of monocropping, adjustment of planting densities should be taken into account to prevent the shade from neighbouring plants (Roig-Villanova and Martinez-Garcia 2016, Fiorucci and Fankhauser 2017). Under drought stress, adjusting planting densities can help in lowering the competition of water and nutrients among plants. Higher planting densities under drought conditions increase competition for water among seedlings that can cause their death. It is preferable to use lower planting density under such conditions that increase distance among plant roots and ensure adequate water availability for each plant (Cordero et al. 2021). Selecting an optimum row to row and plant to plant distance can also help in reducing competition for water and other resources. Reduced row to row distance results in lower canopy temperature and controlled transpiration via leaf cooling pathways (Crawford et al. 2012). It will also lower ROS production and photodamage caused by high light and temperature that are usually accompanied by drought stress (Cordero et al. 2021).

Application of plant growth regulators

Various natural or synthetic plant growth regulators have been proven to have potential effects in increasing the ability of plants to acclimatize against various abiotic stresses. Pons et al. (2001) reported that shade caused a decline in leaf expansion, but cytokinin application to shaded leaves restored the leaf expansion. Tegg and Lane (2001) showed that ‘Primo’ (trinexapac-ethyl), a plant growth regulator, significantly improved the shade adaptation of several turfgrass species commonly used in high-quality turf surfaces. Similarly, paclobutrazol, a growth regulator and an inhibitor of gibberellin biosynthesis, has been studied in many crops to reduce stem elongation in a shaded environment. Its application in tomato plants decreased the seedling height (Seleguini et al. 2013) whereas, in Schizolobium amazonicum, it provided compact seedlings with larger dry root phytomass (Binotti et al. 2019). While the exogenous application of plant growth regulators has not been much explored in shade environments, considerable literature is available regarding their role in the amelioration of drought stress conditions. For example, treating seeds with gibberellic acid improved yield parameters in drought-stressed rapeseed (Brassica napus) (Khan et al. 2020). Exogenously applied gibberellic acid led to improved tolerance in cotton against water deficit stress (Kumar et al. 2001) and Sitka spruce (Picea sitchensis; Philipson 1992). Foliar application of various types of jasmonates enhanced drought tolerance as reported by other reports (Alam et al. 2014, Anjum et al. 2016b, Zheljazkov et al. 2013). Benzyl adenine, an active cytokinin, is documented to potentially enhance the
drought resistance of different crops (Prerostova et al. 2018). Similarly, exogenous application of 1-aminocyclopropane-1-carboxylic acid improved the tolerance against drought stress by hampering the process of ageing (Young et al. 2004), while salicylic acid imparted drought tolerance in wheat by increasing its catalase activity (Hováth et al. 2007). Under co-occurring drought and shade stress, the use of plant growth regulators needs to be explored yet. The possible use of gibberellins and auxin under co-occurring shade and drought stress could be explored as earlier research suggested that application of gibberellins and auxin regulates soybean hypocotyl elongation under co-occurring shade and high-temperature stress (which is usually accompanied by drought stress in most cases) (Bawa et al. 2020).

Application of osmoprotectants

Asghar et al. (2020) found that a pre-shaded environment enhanced the accumulation of osmoprotectants, such as proline, soluble sugars, and reducing sugars, in soybean seedlings which later enhanced the drought tolerance of the seedlings when exposed to drought stress. This increase is likely because of an increase in abscisic acid contents or an increase in auxin contents in pre-shaded treatment. Similarly, numerous literature has documented an increase in proline (Sperdouli and Moustakas 2012, Cvikrová et al. 2013, Filippou et al. 2014), soluble sugars (Pinheiro and Chaves 2011, Anjum et al. 2017, Du et al. 2020), and glycine betaine (Quan et al. 2004, Zhang et al. 2012) following water deficit stress. Ali et al. (2013) reported that proline applied exogenously under water stress conditions lead to improved composition, oil quality, and oil antioxidant activity of maize seeds. Sakamoto and Murata (2002) reported improved plant growth in drought stress due to foliar-applied glycine betaine as it maintained the leaf water status by improving osmoregulation, gs, and Rubisco activity, which resulted in better photosynthesis. To conclude, it is evident from the above-mentioned literature that osmoprotectants can help impart resistance in plants against shade and drought stress.

Application of mineral nutrients

The role of mineral nutrients in relieving crops has been widely documented. Wu et al. (2018) found that phosphorous and nitrogen application mitigated negative effects of drought stress on Moso bamboo (Phyllostachys edulis) through enhancing its membrane integrity, water-use efficiency, and rate of photosynthesis. Phosphorous application in Phoebe zhennan facilitated and improved drought tolerance through physiobiochemical adjustments (Tariq et al. 2017). Zährer et al. (2017) found that the potassium nutrient management strategy could diminish the effects of drought stress in cotton as its application regulated the translocation process and associated enzyme activities together with the photoassimilation in cotton. The foliar application of Ca²⁺ was found to be a promising fertilization strategy for the improvement of sugar metabolism, redox state, and the efficiency of mineral nutrients, thereby, enhancing tolerance to water deficit in sugar beet (Beta vulgaris; Hosseini et al. 2019). Sulfate application in form of K₂SO₄ mediated drought tolerance in water-stressed maize plants by positively influencing their leaf gas-exchange parameters, leaf water status, and antioxidant mechanism (Usmani et al. 2020). Selenium, though not considered essential for plant growth, improved tolerance to drought in wheat seedlings (Yao et al. 2009) and corn plants (Bocchini et al. 2018). Similarly, silicon, which is the second most abundantly present element in the soil, has not been yet considered an essential plant nutrient mainly due to its poorly understood function in plant biology (Epstein 1994). However, recently, the improvement of crop resistance against water scarcity due to the added silicon in the growth medium has been studied extensively (Hattori et al. 2005, Zhu and Gong 2014, Coskun et al. 2016, Helaly et al. 2017, Thorne et al. 2020). The role of silicon in increasing lodging resistance in shade-grown soybean has also been studied recently. Silicon was found to affect the structural composition of the various components of plant cell walls primarily by changing linkages of noncellulosic polymers and lignin, thus, enhancing lodging resistance and preventing yield losses (Hussain et al. 2020b). Similar to silicon, researchers have looked into the vitality and function that titanium plays in improving crop performance over the last century, but it has not yet been recognized as an essential phytounitnutrient. Hussain et al. (2019b) reported that a moderate foliar application of ionic titanium enhanced the Chl pigments, biomass production, electron transport rate, and photochemical efficiency of PSII in shade-grown soybean. They suggested that titanium use could help alleviate shade stress, especially in intercropping systems. In conclusion, the above-mentioned data suggest the use of plant mineral nutrients to be a potential source for the achievement of better crop growth and productivity as well as for alleviation of the deleterious impacts of shade and water deficit stress.

Seed priming

Seed priming is considered one of the most pragmatic approaches to improve the abiotic stress tolerance, especially drought stress, in a range of plant species (Chen and Arora 2013). It involves hydration of the seed to activate the pregerminative metabolic and biochemical activities without radical protrusion during phase two of seed germination (Paparella et al. 2015). This technique can particularly, be very useful for the improvement of rice to be grown in water scant areas, as in the newly introduced aerobic rice culture, the frequency and intensity of drought may increase manifold. Sufficient literature has documented the use of seed-priming treatments for drought resistance in various plant species (Du and Tuong 2002, Harris et al. 2002, Kaur et al. 2005, Kaya et al. 2006, Farooq et al. 2009, Hasanuzzaman and Fujita 2011, Goswami et al. 2013, Samota et al. 2017). However, the effectiveness of priming varies widely depending on the crop species being treated as well as the selected priming technique. Under
low light conditions, Jiang et al. (2020) found that shade-induced hypocotyl elongation in soybean is modulated by gibberellins, which are produced in response to the mutual promotion of auxin and brassinosteroids. The use of such plant growth regulators under shade stress can be explored as the above-mentioned evidence suggests a promising role of this technique in conferring drought stress tolerance.

Future perspectives and conclusion

Shade is a common abiotic stress in crop production and has a serious negative impact on the quality and yield of the crops produced. Unfortunately, although the shade is lethal for crop growth and crops often experience it during their life span (specifically in intercropping systems and high-density monocropping systems), little attention has been paid to this stress. Plants respond to shade through various complex biochemical, physiological, and molecular mechanisms, together with posttranscriptional regulation via miRNA. Recently, a range of biotechnological tools have been used to better understand the mechanisms by which plants respond to shade stress, nevertheless, these approaches need to be explored further. Modern computational and systems biology tools can be used for recognition of the vital genes, proteins, and metabolites, etc., which could be then utilized for engineering plants that are tolerant to shade. Furthermore, the identification of miRNAs as important regulators of the gene expression under shade stress underscores that miRNA-based biotechnology has great potential for the development of plants that can tolerate shade. Similar to shade, drought stress also has deleterious effects on crop growth. Though, the physiological mechanisms of plants' tolerance against drought have been comparatively described in great detail in the literature, yet we require comprehensive research regarding the responses of roots (involving the root–shoot signalling) under conditions of water scarcity. Moreover, the use of modern era genomic, proteomic, and transcriptomic approaches for a thorough insight of drought stress is also imperative. Fundamental knowledge of molecular responses and tolerance mechanisms will help to engineer crops that can withstand drought stress and produce adequate economic yield under such conditions.

Under field conditions, plants encounter multiple stresses simultaneously. Consequently, the occurrence of shade and drought stress simultaneously rather than the occurrence of individual stress, is a major challenge for crop production. Both these stresses alter the growth and development at various growth stages of a plant throughout its life span. The above-reviewed literature provides evidence that plant responses to the co-occurrence of shade and drought stresses may be unique or shared. For example, being unique, shade stress results in stem elongation whereas drought stress results in shorter plant height. In contrast, the consequences of both the stresses include a decrease in flower and pod yield, an increase in flower and pod abortion rate, and a decrease in seed size, all of which leads to a dramatic reduction in seed yield. Although, plant responses to drought and shade stress at morphological and physiological levels, including the structural and biochemical changes, have been well documented at individual leaf and whole-plant levels but what impact does shade has on plant growth under drought conditions, remains unclear. So far, there are no consistent conclusions to date as to whether the interaction of shade and drought stress is antagonistic, synergistic, or additive, as it varies from species to species, the growth period of the plant, and the stress intensity factor. The interactive effect of shade and drought stress is considerably well documented in woody plants and forest species in comparison to the field crops. Therefore, much research is needed on field crop responses to the co-occurrence of shade and drought stress. Proper field experiments should be designed under field conditions to clearly understand the responses. Furthermore, modern-day novel molecular and biotechnological approaches should be used for the development of genetically engineered plants that can respond specifically to shade and drought stress. The use of bioinformatics and genomic sequencing, transcriptomics, and proteomics analysis could further assist in determining shared and unique genes that are regulated under abiotic stress conditions thereby helping improve plants’ resistance against individual and concurrent shade and drought stress.

References


Cykrova M., Gemperlová L., Martincová O., Vatková R.: Effect of drought and combined drought and heat stress on polyamine metabolism in proline-over-producing tobacco

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RESPONSES OF CROP PLANTS TO COMBINED SHADE AND DROUGHT STRESS

Daryanto S., Wanga L., Jacinthe P.-A.: Global synthesis of drought
de Campos M.K.F., de Carvalho K., de Souza F.S. et al.: Drought
tolerance and antioxidant enzymatic activity in transgenic
calkiness by postponing caryopsis development and
Djakovic-Petrovic T., de Witt M., Voorhees L.A.C.J. et al.: DELLA protein function in growth responses to
Doulis A., Hausladen A., Mondy B. et al.: Antioxidant response
Du L.V., Tuong T.P.: Enhancing the performance of dry-seeded
rice: effects of seed priming, seedling rate, and time of
seeding. – In: Pandey S., Mortimer M., Wade L. (ed.): Direct
International Research Institute, Manila 2002.
Du Y., Zhao Q., Chen L. et al.: Effect of drought stress on sugar
metabolism in leaves and roots of soybean seedlings. – Plant
Duan J., Cai W.: OsLEA3-2, an abiotic stress induced gene of
Durlis A., Hausladen A., Mony B. et al.: Antioxidant response
as determinants of the photosynthetic decline of ageing
Ferroni L., Brestit M., Živčák M. et al.: Increased photosynthesis
from a deep-shade to high-light regime occurs by enhanced
CO2 diffusion into the leaf of Selaginella martensii. – Plant
Fleck I., Peña-Rojas K., Aranda X.: Mesophyll conductance to
CO2 and leaf morphological characteristics under drought
Fleur D., Jefferies S., Kuchel H., Langridge P.: Genetic and
Flexas J., Bota J., Cifre J. et al.: Understanding down-regulation
of photosynthesis under water stress: future prospects and
searching for physiological tools for irrigation management. –
Foyer C.H.: Reactive oxygen species, oxidative signaling and the
2008.
Frederick J.R., Camp C.R., Bauer P.J.: Drought-stress effects
on branch and mainstem seed yield and yield components of
Fujita K., Takagi S., Terashima I.: Leaf angle in Chenopodium
album is determined by two processes: induction and
Furlan A., Llanes A., Luna V. et al.: Physiological and biochemical
responses to drought stress and subsequent rehydration in the
symbiotic association peanut-Bradyrhizobium sp. – ISRN
Gallelli M., Galstyan A., Paulišić S. et al.: DRACULA2 is a
dynamic nucleoporin with a role in regulating the shade
avoidance syndrome in Arabidopsis. – Development 143:
1623-1631, 2016.
Gao J., Shi J., Dong S. et al.: Grain yield and root characteristics
of summer maize (Zea mays L.) under shade stress condi-
circadian clock protein, TOC1, is a DNA-binding transcription
quantum yield of photosynthetic electron transport and
quenching of chlorophyll fluorescence. – BBA-Gen. Subjects
Ghasemzadeh A., Jaafar H.Z.E., Rahmat A. et al.: Effect of
different light intensities on total phenolics and flavonoids
synthesis and anti-oxidant activities in young ginger varieties
(Zingiber officinale Roscoe). – Int. J. Mol. Sci. 11: 3885-
3897, 2010.
Gommer C.M.M., Visser E.J.W., St Onge K.R. et al.: Shade
tolerance: when growing tall is not an option. – Trends Plant
Gorton H.L., Vogelmann T.C.: Effects of epidermal cell shape
and pigmentation on optical properties of Antirrhinum petals
at visible and ultraviolet wavelengths. – Plant Physiol. 112:
879-886, 1996.
Goswami A., Banerjee R., Raha S.: Drought resistance in rice
seedlings conferred by seed priming: Role of the anti-oxidant

677
Granier C., Tardieu F.: Leaf expansion and cell division are affected by reducing absorbed light before but not after the decline in cell division rate in the sunflower leaf. – Plant Cell Environ. 22: 1365-1376, 1999.


Gupta N., Thind S.K., Bains N.S.: Glycine betaine application modifies biochemical attributes of osmotic adjustment in drought stressed wheat. – Plant Growth Regul. 72: 221-228, 2014.


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Nakashima K., Yamaguchi-Shinozaki K., Shinozaki K.: The


Schachtman D.P., Goodegr.J.Q.: Chemical root to shoot signaling
Seki M., Narusaka M., Abe H.
Scippa G.S., Di Michele M., Onelli E.
Simon-Sarkadi L., Kocsy G., Várhegyi Á.


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