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Review article

# Turfgrass response to environmental stress: I. Cool-season turfgrasses

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## Abstract

Cool-season turfgrasses are widely utilized in transitional urban green spaces and sports landscapes, where they often face a variety of abiotic stresses, including drought, salinity, heat, cold, and shade. Over the last thirty years, numerous studies have explored the morpho-physiological and biochemical responses of various turfgrass species to these environmental challenges, aiming to identify stress-specific resilient cultivars and enhance grass management practices. Cool-season turfgrasses exhibit a range of responses at cellular and whole-organism levels under stress conditions. This article reviews the existing mechanisms of abiotic stress tolerance in these turfgrasses, focusing on the integration of findings from diverse studies to offer a comprehensive overview of turfgrass adaptation strategies. Key stress indicators such as proline accumulation, antioxidant enzyme activity, chlorophyll content, and water-use efficiency are discussed concerning specific stress types. Furthermore, emerging evidence suggests that combined stress conditions can occasionally yield unexpected synergistic or antagonistic effects, affecting plant responses differently than single stress exposures. Understanding these intricate responses is crucial for breeding climate-resilient cultivars, especially given the anatomical limitations of turfgrass species and the necessity for genetic compatibility in gene transfer. This review emphasizes the significance of species-specific knowledge in turfgrass science and lays the groundwork for future research aimed at sustainable grass management under climate change pressures.

**Keywords**: Drought, Heat, Low temperature, Salinity, Shade, Turf quality.

## Abbreviations

ABA, Abscisic acid; APX, ascorbate peroxidase; CAT, catalase; CK, cytokinin; d, day; DHAR, dehydroascorbate reductase; EL, electrolyte leakage; ET, evapotranspiration; GA, gibberellic acid; GABA, gamma aminobutyric acid; GADPH, glyceraldehyde phosphate dehydrogenase; GB, glycine betaine; h, hour; IBPs, ice-binding proteins; IDH, isocitrate dehydrogenase; $P_{n,}$ net photosynthetic rate; $g_s$, gaseous exchange; MDH, malate dehydrogenase, MDA, Membrane lipid peroxidation; MHAR, monodehydroascorbate; reductase; PN, potassium nitrite; PBZ, Paclobutrazol; POD, Peroxidase; PA, phosphatidic acid; ROSs, reactive oxygen species; RWC, relative water content; SDH, succinate dehydrogenase; SDL, short day length; SNP, sodium nitroprusside; SOD, superoxide dismutase; SRL, specific root length; TNC, total nonstructural carbohydrates, TQ, turf quality; tricarboxylic acid, TCA, WSCs, water-soluble carbohydrates; WUE, water-use efficiency.

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## Introduction

Turfgrass represents one of the predominant plant species used to cover open land in urban and suburban environments, with significant contributions to environmental enhancement and protection. One of the sustainable methods of overcoming the diverse environmental conditions is the use and selection of turfgrass-tolerant varieties (Huang *et al*., 2014). Cool-season grasses exhibit optimal growth under low-temperature conditions and tend to remain productive over a longer portion of the year compared to warm-season grasses. Cool-season turfgrasses are primarily distributed in regions north of 30◦N latitude that experience cool climates, including humid, semi-humid, semi-arid, and transitional zones (referring to a geographic belt marked by overlapping climatic extremes—hot, humid summers and cold winters—where neither cool-season nor warm-season turfgrasses perform optimally year-round, posing unique management challenges) (Fry & Huang, 2004). Cool-season turfgrasses are also characterized by their $C_3$ carbon fixation pathway in photosynthesis, dark green foliage, and strong tolerance to cold stress while sensitive to temperatures above 30 ˚C (Salehi & Khosh-Khui, 2004). The optimum growth for cool-season turfgrasses occurs at temperatures of 18 and 24 ◦C for shoot growth and 10 and 18 ◦C for root growth (Fry & Huang, 2004). Frequently chosen $C_3$ turfgrass species encompass tall fescue (*Festuca arundinacea* Schreb.), Kentucky bluegrass (*Poa pratensis* L.), perennial ryegrass (*Lolium perenne* L.), fine fescues (*Festuca rubra* var. *commutata*, *Festuca ovina* var. *duriuscula*), and creeping bentgrass (*Agrostis stolonifera* L.). Less common cool-season turfgrass species include annual ryegrass (*Lolium multiflorum* Lam.), rough bluegrass (*Poa trivialis* L.), and supine bluegrass (*Poa supina* Schrad.).

One of the greatest challenges in cool-season turfgrass growth and production is to maintain turf quality (TQ) under extreme heat climatic conditions with minimal inputs and environmental impacts (Sun *et al*., 2024). This challenge could be addressed through management techniques, including selecting suitable species and overseeding to create a balanced year-round turf (Akbari *et al*., 2011). Global warming increasingly puts cool-season grasses in the transition zone under heat stress and osmotic stress, potentially resulting in their replacement by more stress-tolerant species. Moreover, turfgrass species with low-input adaptability while maintaining acceptable quality are gaining attention among lawn managers, as they help reduce maintenance costs, particularly those associated with mowing and environmental impact (Mirzaei & Esmaeili, 2025).

Although there is a handful amount of information regarding turfgrass tolerance to abiotic stresses, efforts that could enhance our understanding of the physiological effects of environmental stress can provide guidelines for practical management strategies that promote the maintenance of high-quality turfgrasses under adverse environmental conditions. In this paper, we mostly tried to gather recent information on the morpho-physiological, anatomical, and biochemical responses of both commercial and native cool-season turfgrasses after being exposed to adverse environmental conditions. Additionally, this review highlights a critical knowledge gap in our understanding of turfgrass responses to combined abiotic stresses, a complexity frequently neglected in single-stress studies, and underscores the necessity of integrated, multidisciplinary approaches to enhance stress resilience in turfgrass breeding programs. More than 35 research studies evaluating the response of common cool-season turfgrasses were covered in this review, trying to provide an overview of cool-season turfgrass adaptation strategies to various abiotic stresses, relying on the available data.

## Drought stress

### Morpho-physiological and biochemical responses to drought stress

Drought is progressively developing, not only in arid or semi-arid areas but also in transitional areas, mainly due to irregular distribution of precipitation and climate change (Huang *et al*., 2014). Turfgrass landscapes offer various environmental and health advantages, including a

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positive impact on human well-being, improved surface water quality, and reduced nutrient runoff. However, despite these benefits, irrigated turfgrass areas often face criticism and scrutiny from water resource managers and environmental advocates (Fry & Huang, 2004). Also, non-irrigated areas experience unprecedented dry periods, showing the necessity of characterizing turfgrass varieties that can maintain acceptable performance in dry conditions.

Many studies have investigated the varying drought tolerance of cool-season turfgrasses (Alizadeh *et al.*, 2009; Salehi & Salehi, 2012; Bizhani & Salehi, 2014; Boogar *et al.*, 2014; Salehi *et al.*, 2014; Sarmast *et al.*, 2015; Mahdavi *et al.*, 2018; Esmailpourmoghadam & Salehi, 2021; Esmaeili *et al.*, 2025). Those turfgrasses that can maintain green color, uniformity of growth, and functionality under stress conditions are considered the most drought tolerant (Esmailpourmoghadam & Salehi, 2021; Esmaeili *et al.*, 2025). Drought tolerance in turfgrasses is closely associated with their morphological and physiological aspects (Sarmast *et al.*, 2015; Esmaeili *et al.*, 2025).

## Morphological responses

Understanding morphological, anatomical, and physiological adaptations of roots when exposed to drought stress may provide substantial privilege to find improved selection traits for breeding programs, leading to the introduction of cultivars with root-based drought tolerance strategies.

Root architecture traits serve as valuable indicators for proxies that can enhance crop productivity, emphasizing the critical role of root systems in optimizing resource uptake. These traits also play a significant role in improving drought tolerance under water-limited conditions (Rahnama *et al.*, 2024a). Water deficit can develop specific anatomical, morphological, and physiological characteristics in the roots of turfgrasses to enhance drought resistance. These different drought-induced characteristics of roots contribute to the variability in the shoot, similar to results in other studies (Rahnama *et al.*, 2024a).

Viability of roots with proper growth and maintenance of roots, turgid pressure under drought stress conditions, are important factors influencing turfgrass drought resistance. Pirnajmedin *et al.* (2017) stated that the continual access to water by tall fescue's deep and expansive root system contributes to its higher performance during drought stress. Severe drought stress reduces total root length and mass and increases root mortality. Root distribution throughout the soil profile may be altered as water deficit develops. Roots of drought-tolerant genotypes can extract more water from the soil, enabling the maintenance of higher stomatal conductance during water stress compared to other genotypes (Rahnama *et al.*, 2024a). Reduction in moisture content near the soil surface reduces root growth near the soil surface, but in return empowers the root growth in the lower surface, where water is adequate. This phenomenon has been observed in several turfgrass species, including perennial ryegrass, tall fescue, and Kentucky bluegrass (Yang *et al.*, 2013; Martin, 2021) (Table 1).

## Physiological responses

### Photosynthesis, chlorophyll, and water relations

Photosynthesis is a key metabolic process, regulating plant response to drought stress and plant regrowth upon re-watering (Chaves *et al.*, 2009). Photosynthesis is controlled by photochemical reactions, facilitating energy production, gas exchange for $CO_2$ absorption, as well as carbon fixation and assimilation. Inhibitory effects of drought on photosynthesis are generally associated with low $CO_2$ availability caused by diffusion limitations through stomata and mesophyll tissues (Zhong *et al.*, 2019). Stomatal conductance, a key determinant of photosynthetic efficiency, serves as an indicator of osmotic stress tolerance and overall plant water status (Rahnama *et al.*, 2010). Although stomatal closure protects plants from excessive water loss, it simultaneously limits $CO_2$ diffusion into photosynthetic tissues. Under prolonged

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or intense drought, a significant decrease in the activities of key enzymes like Rubisco and Rubisco activase contributes to reduced photosynthetic capacity (Hu *et al.*, 2010). The activity levels of these enzymes differ across plant species and cultivars, with drought-tolerant plants often maintaining higher enzymatic activity (Carmo-Silva *et al.*, 2012). For instance, Xu *et al.* (2013) found that the drought-tolerant Kentucky bluegrass cultivar 'Midnight' showed significantly higher net photosynthetic rate (Pn), greater glyceraldehyde phosphate dehydrogenase (GAPDH) activity, and increased Rubisco transcript levels during short-term drought. Upon rewatering, this cultivar also exhibited a faster activation of Rubisco, enabling quicker recovery of photosynthetic function. Mahdavi *et al.* (2020) also found that chlorophyll content, RWC, and phosphorus content of two tall fescue cultivars ('J-r' and 'H-d') exposed to 21d of drought stress declined. In a comparative study involving IPT-transgenic lines and natural accessions of perennial ryegrass, plants that demonstrated superior drought tolerance consistently maintained higher RWC, TChl concentrations, and photochemical efficiency. These physiological attributes contributed to enhanced drought resilience. Notably, the Fv/Fm ratio—an indicator of photosystem II efficiency—proved to be a reliable marker for identifying drought-tolerant genotypes across both transgenic and non-transgenic lines (Esmaeili *et al.*, 2025). Furthermore, correlation analysis revealed strong positive associations ($r > 0.8$) between Fv/Fm, RWC, TChl, and VQ, underscoring the potential of these traits as effective indicators of turf performance under drought stress in perennial ryegrass (Esmaeili *et al.*, 2025).

**Table 1. Overview of adaptation strategies and beneficial traits of cool-season turfgrasses under various abiotic stresses.**

| Salinity stress | Drought stress | Low Temperature stress | Shade stress | Heat stress |
|---|---|---|---|---|
| Osmolyte accumulation | Osmolyte accumulation | Osmolyte accumulation | Proline accumulation | Antioxidant enzyme activity |
| Antioxidant enzyme activity | Antioxidant enzyme activity | Antioxidant enzyme activity | Antioxidant enzyme activity | Water-use efficiency |
| Chlorophyll content | Chlorophyll content | Chlorophyll content | Chlorophyll content | ↑ Stomatal conductance (Short-term heat) |
| Water-use efficiency | Water-use efficiency | Water-use efficiency | Wide and thin leaves | ↓ Stomatal conductance (Prolong heat) |
| Stomatal conductance | Stomatal conductance | Altering membrane lipid composition | Dwarfism | Extensive rooting |
| Thick cuticle | Thick cuticle<br>Deep root development<br>Root/tiller ratio | Carbon and nitrogen reserves | Photosynthesis-respiration balance (Pn:Rd) | RuBP content<br>$P_n$<br>Chlorophyll content |
| Early leaf aging | Maintain $P_n$<br>PSII protection | Total and individual amino acid accumulation | Shallow rooting | TNCs availability<br>HSP accumulation |
| Salt accumulation | Moderate ROS | Phytohormone regulations | Phytochorome response | CK response regulation |
| Salt extrusion | Improvement through PGPR | Dehydrins accumulation | Prolong vegetative growth | Dark leaves |

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### Stability of the cell membrane

Cellular membrane stability serves a critical role during plant dehydration (Xu *et al.*, 2011). Electrolyte leakage (EL) is a common parameter usually used to estimate cellular membrane integrity, especially under water stress conditions (Rachmilevitch *et al.*, 2006). The results obtained by Xu *et al.* (2013) indicated that ‘Midnight’ Kentucky bluegrass maintained greater membrane stability with less physical damage compared to ‘Brilliant’ Kentucky bluegrass at the same level of drought stress (10d). EL declined rapidly for ‘Midnight’ Kentucky bluegrass cultivar upon re-watering, suggesting rapid membrane repair and recuperative ability, whereas EL ability of ‘Brilliant’ Kentucky bluegrass did not recover and instead continued to increase to 87%. These results support the idea that ‘Brilliant’ Kentucky bluegrass experienced permanent membrane damage when leaf RWC dropped to 22% during drought stress.

Hatamzadeh *et al.* (2015) explored the role of nitric oxide (NO), applied as sodium nitroprusside, in alleviating drought stress in two turfgrass species: creeping bentgrass and tall fescue. Under 40 d of drought, NO treatment helped maintain higher RWC, reduced ion leakage, and preserved chlorophyll and proline levels compared to untreated controls. Drought stress decreased the activity of antioxidant enzymes like SOD and APX, but NO application counteracted this decline by boosting their activity. During the recovery phase, NO-treated plants showed better RWC and chlorophyll levels, while APX activity remained higher than in controls (Hatamzadeh *et al.*, 2015).

Esmaeili et al. (2025) found a strong negative correlation ($r > 0.7$) between the levels of antioxidant enzymes—SOD and CAT—as well as isopentenyl adenine, with EL and MDA content in both IPT-transgenic and local accessions of perennial ryegrass following 10 d of drought stress. This suggests that enhanced antioxidant activity and cytokinin levels are closely associated with reduced cellular damage under drought conditions. Additionally, their recovery-phase analysis revealed that CAT and SOD activities in most plants did not return to baseline levels even after 14 d of rewatering, whereas POD activity declined significantly during the same period. These findings suggest that CAT and SOD play a more prominent and sustained role than POD in mediating drought adaptation and post-stress recovery in perennial ryegrass.

### Biochemical responses

### Antioxidant enzyme activity

Plants have developed a wide range of defense systems to survive whenever faced with drought stress (Shao *et al.*, 2005). One of the earliest responses of plants to stresses such as water-deficiency is the accumulation of reactive oxygen species (ROSs) such as superoxide, hydroxyl radicals, hydrogen peroxide, and singlet oxygen that can damage the plant cells (Salvi *et al.*, 2021). ROSs are generated during standard aerobic metabolic processes when electrons from the electron transport chains within mitochondria and chloroplasts are released and interact with molecular oxygen in the absence of alternative electron acceptors (Podlešáková *et al.*, 2019).

In the Chang *et al.* (2016) study, ROSs activity was quite stable in the well-watered creeping bentgrass plants but significantly increased during the water stress condition, as such $H_2O_2$ and $O_2^-$ contents experienced a 3 and 2-fold increase, respectively, in the last day of the stress period. However, plants generally can eliminate superoxide with the help of superoxide dismutase (SOD), which catalyzes the dismutation of superoxide into hydrogen peroxide and oxygen, and is important in preventing the reduction of metal ions and hence the synthesis of hydroxyl radicals. Catalases (CAT) catalyze the decomposition of hydrogen peroxide into water and oxygen, primarily found within peroxisomes (Mhamdi *et al.*, 2010). The activity and content of antioxidant enzymes, including SOD, CAT, and peroxidase (POX), as well as proline,

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exhibit an increase in plant cells in response to drought stress, serving a crucial function in the defense against oxidative stress.

The practice of withholding irrigation for a duration of up to 8 d in certain tall fescue cultivars demonstrated that a significant portion of the superoxide generated due to drought stress was transformed into $H_2O_2$ by SOD, which was subsequently detoxified by ascorbate peroxidase (APX) into water (Sarmast *et al.*, 2015). Peroxidases are responsible for the detoxification of $H_2O_2$ within vacuoles, the cell wall, and the cytosol, although they do not function within organelles. In contrast, APX, glutathione reductase (GR), monodehydroascorbate reductase (MHAR), and dehydroascorbate reductase (DHAR) participate in the ascorbate-glutathione cycle (AsA-GSH cycle), where they convert $H_2O_2$ to $H_2O$ through reduction processes that involve ascorbate and glutathione (Sun *et al.*, 2024). An augmented level of ROSs during drought stress adversely affected growth and development. ROSs highly deactivate cellular metabolism by oxidative damage to membranes, proteins, and nucleic acids; they also cause lipid peroxidation, protein denaturation, and DNA mutation.

DaCosta & Huang (2007) reported that SOD and CAT activities have decreased in leaves of three bentgrass (*Agrostis* spp.) species, which were subjected to severe drought stress. Higher capacity of the antioxidant enzymes SOD and CAT was linked to decreased lipid peroxidation of leaves, higher TQ, leaf RWC, and photosynthesis efficiency for a longer duration of drought stress. In another study that was conducted by Xu *et al*. (2011), APX, MHAR, and DHAR increased in the leaves, and CAT, GR, and MHAR in roots, but a reduction was observed in the activities of SOD and DHAR in the roots of drought-stressed Kentucky bluegrass. Positive correlation of antioxidant activity and drought tolerance has been reported in different turfgrass species, although the specific enzymes imparting drought tolerance may differ between species or cultivars (Huang *et al.*, 2014). Xu *et al.* (2011) reported that APX and CAT enzyme activities in leaves were associated with drought tolerance in Kentucky bluegrass exposed to drought stress. In addition, GR, MHAR, and DHAR were found to be associated with superior drought tolerance of Kentucky bluegrass, while CAT, POD, and APX also contributed to post-drought recovery upon re-watering (DaCosta & Huang, 2007).

GABA application had no significant effect on the activity of superoxide dismutase and catalase in perennial ryegrass under well-watered and drought conditions. Further study is needed to determine the role of GABA in antioxidant response regulation and reactive oxygen scavenging under abiotic stress conditions (Krishnan *et al.*, 2013).

Plant growth-promoting rhizobacteria (PGPR), as bio-fertilizers, are also important in terms of decreasing and improving the harmful effects of abiotic stress, especially drought stress in plants. These bio-fertilizers improved the drought tolerance of tall fescue ‘J-r’ and ‘H-d’ cultivars through antioxidant enzyme activities such as SOD and POX (Mahdavi *et al.,* 2018) (Table 1).

## Amino Acid and Amid

Osmolytes are important in cell osmotic adjustment in many plant species throughout their life cycle. They predominantly include non-protein amino acids (e.g., proline), ammonium compounds (glycine betaine), sugars (fructans, sucrose), polyols (mannitol), organic acids (malate), inorganic ions (potassium, calcium), and hydrophilic proteins (late embryogenesis abundant) (Chaves *et al.*, 2009).

Accumulation of proline compounds in leaf tissue in response to drought stress is well established and correlates with drought resistance in many cool-season turfgrass species, including *Lolium* spp. and *Festuca* spp. grasses (Esmaeili *et al.*, 2025; Salehi *et al.,* 2014; Sarmast *et al.*, 2015; Mahdavi *et al.*, 2018, 2020). Proline is an important compatible osmolyte that serves as a protectant for enzymes and cellular structures of tall fescue cultivars under severe drought stress (Sarmast *et al.*, 2015; Mahdavi *et al.*, 2018, 2020). The accumulation of

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proline has been demonstrated to effectively enhance drought tolerance in various cool-season turfgrass species (Sarmast *et al.*, 2015; Mahdavi *et al.*, 2020; Esmailpourmoghadam & Salehi, 2021). Mahdavi *et al.* (2020) evaluated the impacts of *Pseudomonas fluorescens* inoculation and water deficit conditions on the performance of two tall fescue cultivars named 'H-d' and 'J-r', and the findings indicated that 'J-r' accumulated a higher amount of proline and glycine betaine than 'H-d' in 21d drought stress. Moreover, *Pseudomonas fluorescens* treatment increased proline and glycine betaine amounts in 'J-r' tall fescue under severe drought stress (21d). A several-fold increase in proline content of some *F. arundinacea* cultivars subjected to short water scarcity was also observed by Sarmast *et al.* (2015). In another study, Chapman *et al*. (2022) demonstrated that foliar application of GABA, proline, or their combination enhanced the dark green color index and stolon elongation in creeping bentgrass under drought stress. Notably, proline treatment alone led to a greater increase in RWC, suggesting that both GABA and proline contribute to drought tolerance, with proline having a more pronounced effect on maintaining plant water status.

## Carbon metabolism

In $C_3$ grass species, starch represents the predominant form of non-structural polysaccharides. It serves as a crucial energy reserve, particularly under drought stress conditions when the production of water-soluble carbohydrates (WSCs), such as fructose, glucose, and sucrose, is limited due to reduced photosynthetic activity (Fry & Huang, 2004). Carbohydrates fulfill diverse physiological roles in plants. Soluble sugars such as sucrose, fructose, and glucose contribute to maintaining cellular turgor and may help protect proteins and membranes from stress-induced damage. Contrarily, storage carbohydrates like starch and fructans primarily function as energy reserves (Yang *et al.*, 2013). Drought stress has been shown to alter the accumulation patterns of both water-soluble carbohydrates (WSCs) and storage compounds, including fructans and starch (Kaur *et al.*, 2007).

The plant response to drought stress is influenced by multiple factors, including species-specific traits, the nature of carbohydrate compounds involved, and the duration or severity of the stress conditions (Da Silva & Arrabaca, 2004). According to Ma *et al.* (2020), WSCs are crucial for tall fescue plant growth when drought stress is present. Total nonstructural carbohydrates (TNCs) buildup in perennial grasses subjected to extended drought spells aided in the recovery of plants upon rewatering. According to the literature review, drought stress raised the concentration of TNCs in several $C_3$ turfgrass species (Chakrabarti *et al.*, 2022; Chandregowda *et al.*, 2022). By comparing how different types of carbohydrates responded to drought stress and rewatering in two cultivars of Kentucky bluegrass, Yang *et al.* (2013) discovered that two cultivars responded differently to drought stress and rewatering in terms of the amount of storage carbohydrates (fructans and starch) and water-soluble sugars (glucose, fructose, and sucrose). 'Midnight' maintained a higher fructan content after three days of rewatering and a higher sucrose content after ten days of drought stress. The increased sucrose accumulation in phosphate synthase and sucrose synthase was unrelated to the activity of the enzyme acid invertase, which breaks down sucrose. Based on their findings, they concluded that while higher fructan accumulation may help Kentucky bluegrass recover quickly after a drought, higher sucrose accumulation brought on by the maintenance of active sucrose synthesis may be linked to better turf performance during drought stress.

Another study investigated the effect of the endophytic fungus *Epichloë occultans* on the drought response of the annual reygrass. Under well-watered conditions, endophyte-free plants produced more biomass, but their growth was significantly reduced under drought, resulting in similar biomass between both groups under water-deficient conditions. Isotope data revealed that intrinsic water use efficiency increased only in endophyte-infected plants during drought, indicating better maintenance of photosynthesis. Moreover, endophyte presence reduced root

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length but enhanced root hydraulic conductivity (Manzur *et al.*, 2022). Overall, the endophyte improved drought tolerance by modulating shoot and root architecture and physiology, hence helping maintain photosynthetic performance and water use efficiency under stress.

## Abscisic acid (ABA), Cytokinin (CK), and other hormones

Drought stress triggers various cellular responses in plants, notably altering phytohormone levels. ABA, a key stress hormone, accumulates in response to drought through regulating gene expression and adaptive processes, such as stomatal closure to reduce water loss. In contrast, CK often decreases during drought, and the opposing roles of ABA and CK contribute to managing water balance under stress (Davies, 2010). The foliar application of exogenous ABA in tall fescue and Kentucky bluegrass resulted in improved drought resistance through the induction of stomatal closure and the enhancement of osmotic adjustment (Wang *et al.*, 2003). While ABA's role in stress tolerance is well-studied in many species, its connection to drought resistance in turfgrasses remains unclear. In monocots, drought often leads to reduced leaf function and early senescence of mature leaves. The application of a synthetic CK, 6-Benzylaminopurine (6-BA) at a concentration of 25 μM resulted in an increase in stomatal aperture and conductance following the re-watering of Kentucky bluegrass leaves that had experienced complete stomatal closure due to drought stress (Hu *et al.*, 2012). In a recent study on tall fescue, Rasaei *et al.* (2025) demonstrated that under severe drought conditions, foliar application of 6-BA resulted in a more pronounced reduction in sugar content in leaves compared to roots. Moreover, total starch concentrations in both roots and leaves were consistently higher in 6-BA-treated plants than in untreated controls, particularly under 50% and 25% water-holding capacity under 14 d of stress exposure. These findings suggest that in the absence of 6-BA treatment, drought-stressed plants mobilized starch reserves more extensively, with WSCs likely being channeled toward osmotic regulation and ATP synthesis to support survival under water-deficit conditions.

Gamma-aminobutyric acid (GABA) is a four-carbon non-protein amino acid that is conserved across both prokaryotic and eukaryotic organisms (Shelp *et al.*, 2012). The role of GABA in plant species remains inadequately understood, especially concerning its function during abiotic stresses in grasses. Several studies have revealed that GABA frequently and swiftly accumulates in plants when subjected to various abiotic and biotic stresses, such as drought, salinity, mechanical injury, hypoxia, thermal shock, and pathogen invasion (Fait *et al.*, 2005; Podlešáková *et al.*, 2019; Tang *et al.*, 2020; Cheng *et al.*, 2024). However, it is not yet fully known whether this accumulation serves as a mechanism for stress protection or is a consequence of cellular damage. Krishnan *et al.* (2013) studied the effects of foliar spray of GABA at concentrations of 50 or 70 mM on perennial ryegrass ‘CSI’ under conditions of adequate watering and drought stress within a controlled environment growth chamber. Perennial ryegrass subjected to GABA treatment and subsequently exposed to drought stress exhibited elevated RWC, TQ, and peroxidase activity, alongside reduced wilt rating, canopy temperature depression, EL, and lipid peroxidation in comparison with the untreated specimens. GABA is produced from glutamate via the action of glutamate decarboxylase, subsequently undergoing conversion to succinic semialdehyde and succinate before it enters the tricarboxylic acid cycle (Shelp *et al.*, 2012). Under conditions of drought stress, various metabolites, including GABA, sugars, sugar alcohols, amino acids, and amines, have been observed to accumulate in multiple plant species (Seki *et al.*, 2007; Cheng *et al.*, 2024).

## Salinity stress

### Morpho-physiological and biochemical responses to salinity stress

Salinity is a major challenge in agriculture, negatively impacting both crops and turfgrass (Pessarakli & Kopec, 2009). Globally, around 833 million hectares of land are salt-affected,

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including 8.7% of the Earth's surface (Chen *et al.*, 2025). Salinity disrupts osmotic balance, causing cell dehydration and death (Tada *et al.*, 2014). Its harmful effects, especially in arid and semi-arid regions, stem from low soil osmotic potential, nutrient imbalances, and ion toxicity (Bizhani & Salehi, 2014; Yang *et al.*, 2022). Depending on severity and duration, salinity stress leads to ion imbalance, physiological drought, and cellular damage (Amombo *et al.*, 2018; Esmailpourmoghadam *et al.*, 2023). Under salinity stress, osmotic stress occurs rapidly due to high external salt concentrations that lower soil water potential and limit water uptake, while ionic stress develops more gradually as toxic ions such as $Na^+$ and $Cl^-$ accumulate in plant tissues, impairing enzymatic functions and disrupting cellular homeostasis (Munns & Tester, 2008; Acosta-Motos *et al.*, 2017). Salinity negatively impacts plant growth both physiologically and biochemically (Bizhani & Salehi, 2014). In the short term, osmotic stress limits cell expansion, while long-term salt accumulation leads to ionic stress and early leaf aging due to reduced photosynthetic capacity (Esmaili & Salehi, 2016). Numerous studies have examined the differing levels of salt tolerance among cool-season turfgrasses (Alizadeh *et al.*, 2009; Abdi *et al.*, 2010; Bizhani & Salehi, 2014; Esmaili & Salehi, 2016; Esmailpourmoghadam *et al.*, 2024). Sodium chloride is the main contributor to soil salinity, and salt-tolerant turfgrasses must adapt to its effects (Uddin *et al.*, 2012). Demand for such turfgrasses is rising due to expansion into arid regions, increased use of saline water, and road deicing practices. Plants adapted to salt stress by applying two main strategies: excluding salts from leaf cells or storing them in vacuoles to maintain low cytoplasmic sodium (Jiang *et al.*, 2019). These are known as salt-excluding and salt-accumulating plants. While salt exclusion allows survival in saline soils, it often reduces growth. Some plants avoid, evade, or tolerate salinity to varying degrees (Pessarakli & Kopec, 2009) (Table 1).

## Morphological Responses

Growth responses of plants to varying salinity stress levels have been extensively studied in turfgrass species. Tolerance to salinity highly varies among species and within a species. Productivity on saline land could be enhanced by utilizing the extensive natural genetic diversity in plants, which remains largely unexploited for agricultural purposes (Rahnama *et al.*, 2011). Reduced shoot and root dry weights are a common feature in cool-season turfgrass subjected to salinity stress, including perennial ryegrass, creeping bentgrass, Kentucky bluegrass, tall fescue, annual bluegrass, red fescue, and prairie junegrass [*Koeleria macrantha* (Ledeb.) Schult.] (Alshammary *et al.*, 2004; Dai *et al.*, 2008; Diédhiou *et al.*, 2009; Marcum & Pessarakli, 2010; Koch *et al.*, 2011; Liu *et al.*, 2011; Wang *et al.*, 2011). Salinity has been shown to differentially affect seminal root elongation rates and lateral root initiation, primarily due to the osmotic effects of salt rather than ion-specific toxicity (Rahnama *et al.*, 2011; Rahnama *et al.*, 2019). Root plasticity in response to variations in soil moisture and salinity stress can enhance soil water acquisition and mitigate the negative effects of water deficit (Rahnama *et al.*, 2019; Rahnama *et al.*, 2024a). A recent study by Fan *et al.* (2023) on tall fescue accessions revealed that total root length, particularly the contribution of lateral roots, played a greater role in water uptake than root number. In the salt-tolerant accession LS-11, lateral root length was the major contributor to total root length, with efficient water uptake linked to favorable lateral root positioning and vector, unlike the salt-sensitive PI531230.

Salt stress can be mitigated through morphological and anatomical adaptations (Wasim & Naz, 2020). Salt-tolerant species exhibit characteristics such as increased succulence in roots and stems, a thick cuticle with wax deposition, salt-secreting glands and trichomes, multilayered epidermis, and well-developed water-storage tissues. Additionally, reducing leaf area helps minimize water loss under salinity (Bizhani & Salehi, 2014). Many plants curl their leaves during drought, a process facilitated by water-containing bulliform cells that lose turgor and cause inward leaf folding (Bizhani & Salehi, 2014). Bizhani & Salehi (2014) reported that

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*Cynodon dactylon* has more bulliform cells than Kentucky bluegrass and maintains folded leaves under high salinity, whereas Kentucky bluegrass leaves deteriorate and do not fold at 15 dS $m^{-1}$ salinity. Abdi *et al.* (2010) demonstrated that saline water adversely affected TQ, total fresh weight, total dry weight, conductivity (CY), photosynthesis rate, transpiration, stomatal conductance, mesophyll efficiency, and water use efficiency in Kentucky bluegrass when compared to the control condition.

Pessarakli & Kopec (2008) observed that the detrimental impact of salinity stress was more pronounced on the aerial components compared to root development and dry matter accumulation in cool-season turfs.

## Physiological and metabolic responses

### Photosynthesis, chlorophyll, and water relations

Salinity-induced osmotic stress through the induction of ABA biosynthesis can decrease stomatal conductance, intercellular $CO_2$ levels, chlorophyll content, and Rubisco enzyme activity, along with alterations in electron transport and sucrose accumulation (Diédhiou *et al.*, 2009; Rahnama *et al.*, 2010). Excess salt in photosynthetic tissues can cause thylakoid shrinkage and increased stacking of membranes within the grana, which reduces photosynthesis efficiency. The resulting ionic imbalance reduces potassium ($K^+$) levels in chloroplasts and disrupts photosystem II (PSII). Furthermore, photosynthesis may be inhibited due to feedback suppression caused by elevated sugar concentrations in mesophyll cells, which typically occur shortly after salt stress exposure. These high sugar levels arise from impaired sugar utilization in growing tissues (Sehar *et al.*, 2019).

Wasim & Naz (2020) reported that chlorophyll loss under saline conditions might be due to oxidative stress, overproduction, and accumulation of ROS. Chlorophyll content and RWC reduced under salinity stress in Kentucky bluegrass (Abdi *et al.*, 2010). Similar results were found by (Bizhani & Salehi, 2014; Manuchehri & Salehi, 2014; Esmaeili & Salehi, 2016). Also, a lower reduction of chlorophyll content value was achieved after PBZ-treatment, which might have been the result of a delayed onset of leaf senescence (Abdi *et al.*, 2010). Kentucky bluegrass also exhibits moderate osmotic adjustment capacity but shows more rapid stomatal closure and leaf growth reduction (Zhang *et al.*, 2013).

## Biochemical responses

### Amino acids, soluble sugars, and starch accumulation

Numerous studies have indicated that halophytes exhibit adaptations to low water potential through the accumulation of organic solutes such as proline, which serves to maintain turgor pressure and overall water potential (Tada *et al.*, 2014; Yamamoto *et al.*, 2015; Siddiqui *et al.*, 2016; Tada *et al.*, 2023). Ashraf & Foolad (2007) noted that accumulation of proline, primarily in the cytosol, often occurs in plants under salinity stress, with a strong correlation between stress tolerance and proline accumulation. However, this relationship is dependent on the species and is not universal. Our previous studies showed that the accumulation of proline significantly increased at low levels of salinity in perennial ryegrass and tall fescue (Esmaeili *et al.*, 2015). Moreover, under increasing salinity, eight $C_3$ turfgrass species exhibited varying proline accumulation patterns, with proline content positively associated with salt tolerance but negatively with salt avoidance. This suggests that interspecies variation in salt response may be partly attributed to differences in proline metabolism (Soliman *et al.*, 2018). A previous study by Xu & Fujiyama (2013) reported that tall fescue exhibited lower accumulation of $Na^+$ and $Cl^-$ and higher levels of total soluble sugars compared to Kentucky bluegrass, suggesting that the accumulation of sugars, rather than proline, played a more significant role in the salt tolerance of tall fescue. A comparative analysis of salt tolerance between creeping bentgrass (*Agrostis stolonifera* 'Penncross') and rough bentgrass (*Agrostis scabra* 'NTAS') revealed that

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the salt-tolerant 'NTAS' cultivar exhibited significantly greater accumulation of soluble sugars, proline, and glycine betaine. These osmolytes collectively contributed to enhanced osmotic adjustment under saline conditions (Liu *et al*., 2019).

In tall fescue, osmotic adjustment via proline and sugar accumulation has been reported as an important adaptive mechanism to maintain turgor and cellular hydration under early salt stress (Su *et al*., 2013). According to Xu & Fujiyama (2013), sugars contribute up to 50% of the total osmotic potential in glycophytes subject to saline conditions. The buildup of soluble carbohydrates in plants is a commonly observed response to salinity or drought stress, even though the net rate of $CO_2$ assimilation often declines significantly under these conditions (Liu *et al.*, 2019). The maximum amount of soluble sugars was obtained from Kentucky bluegrass grown under 7.5 $dSm^{-1}$ of salinity (Bizhani & Salehi, 2014).

### Lipid remodeling

Exogenous choline chloride under salt stress induced significant lipid remodeling in Kentucky bluegrass, increasing several phospholipids and glycolipids while reducing phosphatidic acid (PA). Although choline content rose, glycine betaine was absent. These changes suggest choline-mediated lipid adjustments play a key role in salt tolerance and may serve as biomarkers for improving salt-sensitive grasses (Zuo *et al*., 2023).

### Ion accumulation and antioxidant activity

Salt tolerance in plants is primarily controlled by membrane proteins that selectively transport ions within cells. These proteins regulate the movement of $Na^+$ and $K^+$, ensuring proper ionic balance (Wang *et al.*, 2011). However, limited uptake and accumulation of $Na^+$ is typically linked to salt tolerance in plants, a process regulated by the management of influx and/or by active efflux from the cytoplasm to the vacuoles and/or subsequently back to the growth medium (Golldack *et al*., 2014). Amombo *et al*. (2018) reported that tall fescue accessions with higher physiological performance under salt stress accumulated significantly less $Na^+$ and $Cl^–$ in the roots. Six accessions were identified as salt-tolerant based on this trait, while six salt-sensitive accessions showed elevated ion accumulation and reduced physiological activity.

Our previous investigation into four turfgrass species under salt stress revealed that $Na^+$ accumulated significantly more in the leaves of three of them under all salinity levels. This indicates that the roots were ineffective at restricting the upward movement of $Na^+$. However, among the species studied, the cool-season turfgrass, perennial ryegrass, had the highest $Na^+$ concentrations in its roots. The application of silicon (Si) was found to reduce $Na^+$ levels in both shoots and roots of all turfgrasses under salinity stress (Esmaeili *et al.*, 2015; Esmaeili & Salehi, 2016). The improvement of root architecture and water uptake efficiency is one primary effect of Si application, which helps mitigate osmotic stress by maintaining better plant hydration (Liang *et al*., 2007). Si also contributes to ion homeostasis by limiting the uptake and translocation of toxic ions such as $Na^+$ and $Cl^–$, while promoting the uptake of $K^+$, thus maintaining a favorable $K^+/Na^+$ ratio essential for cellular function (Gao *et al*., 2006). Despite this benefit, the precise mechanism by which Si enhances $K^+$ uptake and limits $Na^+$ absorption remains unclear. Since $Na^+$ uptake in plants typically occurs passively and is influenced by transpiration rate (Golldack *et al*., 2011), the reduced $Na^+$ levels observed may partially result from Si's ability to lower transpiration (Ebeed *et al*., 2024). The shoot $K^+$ concentration significantly increased with application of Si in salinity treatment at 5 dS $m^{-1}$ in tall fescue. One possible mechanism for the stimulating effect of Si on $K^+$ uptake by plants under salt stress is the activation of $H^+$-ATPase in the membranes. Moreover, salt tolerance is associated with an increase in antioxidant enzyme activity within cool-season turfgrass systems (Hu *et al*., 2011). The SOD is considered a crucial enzyme for sustaining normal physiological functions and managing oxidative stress through the swift conversion of ROS to $H_2O_2$ (Quan *et al*., 2008). Si enhances antioxidant defense systems by upregulating key enzymes such as SOD, CAT, and

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POD, which scavenge reactive ROS induced by salt stress (Zhu *et al*., 2004; Saqib *et al*., 2008). Structural reinforcement of cell walls through Si deposition also reduces membrane permeability, thereby preventing ion leakage and oxidative damage. In perennial ryegrass, exposure to salt stress led to a notable increase in SOD and CAT activities, especially in the salt-tolerant genotype P2, indicating a more effective reactive ROS detoxification system. These physiological adaptations corresponded with observed growth trends, offering valuable insight for future investigations into the molecular basis of salt tolerance (Cao *et al*., 2024). Additionally, 24-epibrassinolide (EBR) has been shown to enhance salt tolerance in perennial ryegrass by strengthening osmotic regulation and activating the antioxidant defense system (Sun *et al*., 2015). Furthermore, Ahmadi *et al*. (2023) demonstrated that foliar application of GABA also effectively alleviated growth inhibition in perennial ryegrass under salt stress. This treatment enhanced proline accumulation, decreased the $Na^+/K^+$ ratio, and significantly elevated the activities of key antioxidant enzymes, POD and SOD, thereby contributing to improved stress resilience.

## Heat stress

### Morpho-physiological and biochemical responses to heat stress

Future climates are expected to bring increasingly frequent extreme weather events, significantly impacting both plant growth and development (Rahnama *et al*., 2024b). Heat stress by exceeding the optimal temperature of cool-season turfgrass, usually above 30 ˚C, significantly impairs their growth, often resulting in symptoms such as leaf wilting, chlorosis, and even necrosis (Veerasamy *et al*., 2007). Prolonged heat not only diminishes their aesthetic quality but also increases maintenance costs, thereby limiting their widespread use and presenting a critical challenge for turfgrass cultivation and management. Therefore, cultivation of the highest temperature-tolerant species of cool-season turfgrasses is required in such transitional zones.

Heat stress is usually defined as a period of stress when the temperature is high enough to harm plant development and function (Huang *et al*., 2014). High temperature is one of the most detrimental factors limiting plant productivity, especially in cool-season turf species in temperate regions during summer months (Sun *et al*., 2024). The optimal temperature for the growth of cool-season perennial grass species is 15–24 ◦C for shoots and 10–18 ◦C for roots. In response to warmer climes, different species display a wide range of phenological, physiological, and biochemical responses (Rahnama *et al*., 2024b). Under heat stress, turfgrasses exhibit increased respiration, which rapidly depletes carbohydrate reserves needed for growth and stress recovery. This energy drain, combined with reduced photosynthesis, limits the plant's ability to maintain cellular functions, leading to visible declines in turf quality such as leaf senescence, thinning, and chlorosis (Huang *et al*., 2014; Jespersen *et al*., 2016). Heat stress inhibition of photosynthesis in chloroplasts results in an imbalance of the electron-transfer chain and promotes production of ROS, including singlet oxygen ($O_2$), superoxide radical ($O_2^{\,-}$), and hydrogen peroxide ($H_2O_2$) (Liu *et al*., 2022).

According to Xu *et al.* (2017), heat stress promotes leaf senescence, typically characterized by a loss in TQ, and interruption in membrane stability, membrane lipid peroxidation, and limits whole-plant growth in Kentucky bluegrass and tall fescue.

Antioxidant responses in creeping bentgrass and other cool-season turfgrass species are influenced by heat stress (Merewitz & Liu, 2019; Li *et al*., 2022; Sun *et al*., 2024; Rossi & Huang, 2025). Root growth and viability can be detrimentally affected by elevated temperatures and stress durations, resulting in a decrease in TQ. Root sensitivity to elevated temperatures is a more significant factor in the detrimental effects of high soil temperature on cool-season turfgrass (Xu & Huang, 2001). The probability and duration of elevated temperatures during

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the day and/or night are the determining factors in the potential occurrence of heat stress in particular climatic zones.

Heat-avoidance or heat-tolerance mechanisms may enable grass to endure thermal stress (Xu *et al.*, 2011). Transpirational cooling, changes in leaf orientation, reflection of solar radiation, leaf shading of tissues that are sensitive to sunburn, and extensive rooting are all examples of heat avoidance, which is the capacity of plants to maintain internal temperatures below lethal stress levels (DaCosta & Huang, 2013). The capacity of a plant to develop and generate an economic yield in the presence of high temperatures is generally referred to as heat tolerance. Heat-tolerant grass species and cultivars typically demonstrate increased activity in the photosynthetic apparatus (Allakhverdiev *et al.*, 2008), higher carbon allocation, and nitrogen uptake rates when exposed to higher temperatures (Xu & Huang, 2006). Protein denaturation and aggregation, as well as an increase in the fluidity of membrane lipids, are direct injuries that are a result of high temperatures. The inactivation of chloroplast and mitochondria enzymes, inhibition of protein synthesis, protein degradation, and loss of membrane integrity are all examples of indirect or delayed heat injuries (Huang *et al.*, 2014).

Some studies have reported that high temperature stress affected antioxidant responses in creeping bentgrass and other cool-season turfgrass species (Xu *et al.*, 2006;Merewitz & Liu, 2019; Li *et al.*, 2022; Sun *et al.*, 2024; Rossi & Huang, 2025). For instance, a study on heat-acclimated versus non-acclimated cool-season turfgrass species indicated that the ability to protect against oxidative stress is an important component in determining the heat stress tolerance of a plant (Xu *et al.*, 2006).

## Morphological and anatomical changes

Heat stress is expected to worsen in the future as global temperatures rise. Temperature increases above a certain threshold can cause irreparable damage to cool-season turfgrass growth and development, as well as metabolic changes that reduce their function and yield output (Veerasamy *et al.*, 2007). Typical symptoms of heat stress injury in turfgrasses include leaf chlorosis and a reduction in shoot density (Huang *et al*., 2014; Seydavi, 2022). Heat stress results in TQ decline, which is common for grasses under various environmental stresses (Liu *et al.*, 2024). Xu *et al.* (2017) found that heat stress affected grass quality in tall fescue and Kentucky bluegrass. In another study, Xu & Huang (2001) reported that high temperatures lowered plant density, tiller density, root number, and root fresh weight in two creeping bentgrass varieties. Under high temperature and controlled circumstances, ‘L-93’ had larger plant and tiller densities, a higher root-to-tiller ratio, and more and finer roots than ‘Penncross’. The superior performance of ‘L-93’ under heat stress was mostly attributable to its morphological traits, such as tillering and root growth, and was unrelated to single-leaf photosynthetic capability. To pick heat-tolerant cultivars, look for narrow leaves, petite plants, dense tillers, a large root system, and a high root-to-shoot ratio (Xu & Huang, 2001).

As cool-season turfgrasses, tall fescue and perennial ryegrass are two major forage and turfgrass species in the world's temperate regions. Roots of cool-season grasses typically appear to be shorter and less extensive during summer compared to those in spring. Rooting decline at high temperatures is mainly due to dieback (gradual death) and a reduction in new root formation. Root growth is more sensitive to high temperatures than shoot growth (Huang *et al.*, 2014). Pote *et al.* (2006) reported that a decline in root number, length, mass, and viability often precedes visual TQ decline during high temperature exposure.

A growth chamber experiment evaluated the heat stress response of four tall fescue genotypes (Aburaihan1, Aburaihan5, Isfahan2, and a polycross sample) under four temperature conditions: 24/18 °C (control), 35/29 °C, 40/34 °C, and 46/40 °C (Seydavi, 2022). High temperatures reduced shoot and root growth, tiller number, leaf color intensity, and biomass in all genotypes. Moreover, a strong positive correlation was found between leaf color, root length, and shoot fresh weight (Seydavi, 2022).

## Physiological responses

### Photosynthesis, chlorophyll, and water relations

The ideal temperature ranges for the $C_3$ photosynthetic pathway, which is present in cool-season turfgrasses, is around 16 ◦C to 24 ◦C, according to Law *et al.* (2021). Important physiological traits used to assess heat tolerance in grass genotypes include leaf chlorophyll content, photochemical efficiency, and EL, all of which are commonly measured indicators (Huang *et al.*, 2014).

Photosynthesis under high-temperature stress can be hindered by two primary factors: stomatal limitations, which restrict $CO_2$ availability, and metabolic limitations, which involve the direct thermal sensitivity of the photosynthetic machinery, such as the Photosystem II (PSII) reaction center, electron transport systems, and the biochemical pathways responsible for carbon fixation and assimilation (Liu *et al.*, 2022). Elevated temperatures can disrupt various physiological functions, with photosynthesis being particularly vulnerable. In cool-season turfgrasses, for instance, net photosynthetic rates begin to decline when temperatures exceed approximately 30 ◦C. rate and an increase in respiration rates of both shoots and roots due to heat stress (Fry & Huang, 2004).

Tall fescue plants use transpirational cooling mechanisms toward short-term heat stress to reduce leaf temperature; however, prolonged heat stress is associated with cell dehydration and therefore increases the stomata closure (Jiang & Huang, 2001). Stomata closure under heat stress is the result of dropping cell turgor pressure or can be induced by ABA accumulation (Huang *et al.*, 2014) (Table 1).

According to Liu & Huang (2001), cool-season grass species may experience root death when exposed to high temperatures. This is likely due to a net loss of carbon, which could be caused by an increase in respiration and a decrease in carbon assimilation during photosynthesis. Dehydration, which causes the leaves to lose more water and the roots to be unable to absorb as much water, is another cause of the root death damage (Wang & Huang, 2004). Reduced electron transport and reduced power generation for metabolic processes may result if the PSII loses its oxygen evolution capacity when subjected to heat stress (Fan & Jespersen, 2022). A comparison was made between three introduced Kentucky bluegrass cultivars, 'Mid', 'Moo', and 'Blu', and three native *Poa* species, 'Hpp', 'Hpsp', and 'Hpsi', looking at physiological characteristics related to heat sensitivity and plant growth performance. As expected, the native cultivar, 'Hpp', performed similarly to introduced accessions in terms of heat resistance, TQ, growth rate, tiller numbers, and physiological responses like ROS, osmolytes, and antioxidant production. This suggests that native 'Hpp' could be a valuable new resource for improving and applying turf in heat-stress-prone climates. Because of its distinctive dark green color in the spring and fall and its capacity to recover from summer, 'Hpsp' could be utilized to restore degraded ecosystems or provide an alternate sense of seasonal verdure (Chen *et al.*, 2021) (Table 1).

A study conducted by Rutledge *et al.* (2012) found that raising the temperature from 23/15 ˚C (day/night) to 35/25 ◦C lowered the photosynthetic rate by 47% and increased dark respiration by 42% in three species of bluegrass (*P. pratensis* L., *P. trivialis* L., and *P. compressa* L.). Research has shown that tall fescue plants with higher rates of dark respiration also produce less biomass, which suggests that this process can harm growth rates when left unchecked (Rutledge *et al.*, 2012). Heat stress decreased canopy Pn, single-leaf Pn, and Rubisco activity for two creeping bentgrass cultivars, according to Xu & Huang (2001). Under heat stress, 'L-93' had a canopy Pn that was over twice as high as 'Penncross' (64 d of treatment). The deactivation of Rubisco is intimately associated with the inhibition of $C_3$ photosynthesis

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(Scafaro *et al.*, 2023). According to research by Huang *et al.* (2014), heat stress in $C_3$ grass species led to an increase in RuBP content and a decrease in 3-phosphoglycerate, fructose-6-phosphate, and glucose-6-phosphate concentrations in the leaves. This suggests that Rubisco is inhibiting the turnover of other metabolites in the CBB cycle. Su *et al.* (2007) found a positive correlation between active photosynthesis and whole-plant heat tolerance in tall fescue, hybrid bluegrass, and Kentucky bluegrass, whereas Liu and Huang (2001) found the same thing in creeping bentgrass.

In another investigation, Yang *et al.* (2013) examined four cool-season turfgrasses that were exposed to three temperature regimes in growth chambers with optimal temperature control (20/15 ◦C day/night), moderate heat stress (30/25 ◦C), and severe heat stress (40/35 ◦C). Their results vividly showed that moderate heat stress caused no significant physiological damage in any of the four cool-season grass species. Severe heat stress caused a significant decline in TQ, RWC, CAT activity, and EL, and resulted in severe membrane lipid peroxidation in all four grass species. Based on these results, they concluded that the two annual grass species were more sensitive to heat stress than the two perennial species. The maintenance of higher TQ in the two perennial grass species was associated with greater RWC and EL, as well as decreased MDA. Prolonged heat stress typically induces lipid peroxidation and membrane instability with subsequent effects on chlorophyll integrity and net photosynthetic rates in cool-season grass species, including creeping bentgrass, Kentucky bluegrass, and perennial ryegrass (Jiang & Huang, 2001; Yang *et al.*, 2014; Killi *et al.*, 2020). Annual ryegrass may be more susceptible to heat stress and have lower photosynthetic rates because of the decreased chlorophyll content, as observed by Nelson & Foster (2005) (Table 1). Summer stress adversely impacted the TQ of four creeping bentgrass cultivars (‘13M’, ‘Penncross’, ‘Seaside II’, and ‘PA-1’) in 2017-2019. Heat stress during this period affected multiple physiological processes, including reduced chlorophyll content, photosynthesis, leaf RWC, and OP, while increasing carbohydrates, proline, $H_2O_2$, MDA, and EL. ‘13M’ and ‘Penncross’ cultivars performed better, maintaining higher photosynthesis, water status, osmolyte accumulation, and cell membrane stability. These cultivars show potential for turf establishment in subtropical zones, benefiting breeding and germplasm development for heat tolerance in creeping bentgrass (Li *et al*., 2022).

## Biochemical responses

### Antioxidants activity

Plants counteract the oxidative stress caused by high temperatures through the action of antioxidant enzymes, though the effectiveness of this response varies depending on the species and the severity of the heat stress (Huang et al., 2014; Xu *et al*., 2017; Seydavi, 2022). Heat stress can lead to harmful effects such as oxidative damage and dehydration of plant tissues. The majority of reactive oxygen species, particularly superoxide radicals, are generated in the mitochondria and chloroplasts, with microbodies also playing a role. Generally, a plant’s capacity to tolerate heat stress is closely linked to the strength and efficiency of its antioxidant defense mechanisms (Huang *et al*., 2014). Xu *et al.* (2006) found that heat-acclimated cool-season turfgrass species produced less ROS due to increased ascorbate and glutathione synthesis compared to non-acclimated species. A close relationship is well established between reactive ROS scavenging and stress tolerance under temperature extremes (Sheikh-Mohamadi *et al*., 2018). Catalase (CAT) is located primarily in peroxisomes of aerobic organisms and functions as a primary antioxidant enzyme, degrading hydrogen peroxide into water and oxygen (Xu *et al*., 2017). Based on the obtained results by Yang *et al.* (2013), higher levels of lipid peroxidation in annual ryegrass and bluegrass species during severe heat stress may be associated with the pronounced decline in CAT activity compared to perennial species, but this is most likely not related to SOD activity, which increased during heat stress to similar levels for all four species. Thus, the decline in CAT activity during severe heat stress may cause hydrogen peroxide accumulation, resulting in membrane lipid peroxidation (Xu *et al.*, 2017).

Heat-induced changes in CAT activity were also reported in other turfgrass species, such as creeping bentgrass, Kentucky bluegrass, and tall fescue (Du *et al.*, 2013; Li *et al.*, 2014; Yang *et al.*, 2014; Xu *et al.*, 2018). Heat stress on SOD activity was variable. Li *et al.* (2014) examined how two Kentucky bluegrass cultivars with different heat tolerance, ‘EverGlade’ (tolerant) and ‘Kenblue’ (sensitive), respond to prolonged heat stress. Plants were exposed to either normal (20/20 ◦C) or heat stress (38/30 ◦C) conditions for 28 d. Heat stress increased leaf damage indicators (EL and MDA), but ‘EverGlade’ showed lower levels than ‘Kenblue’. Antioxidant enzyme activity (SOD, CAT, POD, APX) varied over time, with ‘EverGlade’ consistently showing higher activity and more antioxidant isozymes. Heat stress also triggered increases in the hormones abscisic acid (ABA) and indole-3-acetic acid (IAA), with ‘EverGlade’ accumulating significantly more of both (Li *et al.*, 2014).

Du *et al.* (2013) showed an increase in SOD, CAT, APZ, and POD activity in the heat-tolerant Kentucky bluegrass genotype (‘Midnight’) during heat stress conditions, while they observed the reverse results on the heat-sensitive genotype (‘Brilliant’), or no changes (Du *et al.*, 2013).

Also in 2004, Wang & Huang conducted a comparison of two Kentucky bluegrass cultivars under combined heat and drought stress. They discovered that the heat-tolerant 'Midnight' exhibited superior TQ, lower lipid peroxidation, and greater membrane stability in comparison to the heat-sensitive 'Brilliant'; this was due to increased SOD activity.

It has been asserted that increased enzymatic ROS scavenging capacity was accompanied by increased photochemical efficiency, higher chlorophyll content, and delayed leaf senescence, all of which contributed to improved overall turfgrass quality. In 2004, Alshammary *et al.* demonstrated that antioxidant compounds, including glutathione, ascorbic acid, α-tocopherol, and carotenoids, offer protection from the cytotoxic effects of ROS that are brought about by thermal stress. These compounds disrupt cellular homeostasis. The heat tolerance of turfgrass could be enhanced by increasing endogenous antioxidant levels through foliar application of antioxidants or genetic modification and overexpression of antioxidant enzymes, which would enhance the antioxidant protection capacity. Additional research employing these methodologies may demonstrate the metabolic and molecular factors that regulate antioxidant protection for heat tolerance in cool-season grass species (Huang *et al.*, 2014).

### Assimilate accumulation

High temperatures significantly affect carbohydrate metabolism, which includes both carbon fixation through photosynthesis and carbon utilization via respiration to generate energy needed for plant growth, maintenance, and other metabolic functions. In cool-season turfgrasses, especially those maintained at low mowing heights, heat stress often disrupts the balance between photosynthetic carbon gain and respiratory carbon loss, ultimately resulting in stunted growth (Jiang & Huang, 2001). This disruption can lead to a depletion of carbohydrate reserves or carbon starvation during extended periods of stress (Fry & Huang, 2004; Yang *et al.*, 2014).

Carbohydrates not only serve as vital structural components of plants but also provide essential metabolic energy, particularly important for shoot and root regrowth after defoliation or mowing (Fry & Huang, 2004). Root carbohydrate metabolism is especially critical, as roots depend entirely on carbon assimilated and transported from the leaves (Liu *et al.*, 2024).

According to Calleja-Cabrera *et al.* (2020), roots grown in soil with high temperatures have stunted growth and malfunction due to disruptions in glucose metabolism. Two creeping bentgrass cultivars, ‘L-93’ and 'Penncross,' showed a decrease in concentrations of TNCs, fructans, starch, glucose, and sucrose at 35/25 ˚C (day/night). Compared to roots, shoots had a more noticeable drop in carbohydrate content. Compared to other carbohydrates, shoot glucose and sucrose concentrations were more heat stress-sensitive. Under the same day/night temperature conditions as ‘Penncross’, ‘L-93’ kept far larger amounts of carbohydrates.

According to the results, a key physiological characteristic associated with heat-stress tolerance in creeping bentgrass (Jiang & Huang, 2001; Yang *et al.*, 2014) was increased non-structural carbohydrate availability, especially glucose and sucrose, while the plant was under stress (Table 1). Similarly, in tall fescue, the elevated levels of TSCs in the polycross and Isfahan2 genotypes suggest greater heat tolerance compared to Aburaihan1 and 5 (Seydavi, 2022). These increases, along with the accumulation of amino acids such as glycine betaine (GB) and proline, play vital roles in regulating osmotic adjustment and preserving cell integrity under extreme heat stress conditions (Seydavi, 2022).

## Heat Shock Proteins

The primary heat shock proteins are classified into five conserved classes based on their approximate molecular weight: HSP100, HSP90, HSP70, HSP60, and tiny heat shock proteins (Sun *et al.*, 2020). HSPs primarily operate as molecular chaperones, assisting other proteins in maintaining their native shape and thereby enhancing protein stability under stress (Wahid *et al.*, 2007). Low molecular weight heat shock proteins, also known as tiny HSPs, are the most abundant proteins generated by higher plants in response to heat stress (Yang *et al.*, 2014). Dimascio *et al.* (1994) discovered changes in the levels of heat-induced heat shock protein (HSP26) between two perennial ryegrass varieties, which could be attributed to variances in heat tolerance. Cool-season turfgrasses that are subjected to extreme temperature stress throughout the summer in warm climatic locations will lose quality. Heat stress-induced protein modifications, in particular HSP expression, are associated with heat stress tolerance in cool-season turfgrass species such as creeping bentgrass (Xu *et al.*, 2011). He & Huang (2007) demonstrated the synthesis of many heat-inducible proteins in the cytoplasm and membranes of Kentucky bluegrass, indicating that improved heat tolerance in specific cultivars was linked to the induction of these proteins during the early phase of heat stress. In their study, they examined genetic variation in heat tolerance among 26 fine fescue cultivars from five fescue species by analyzing physiological responses and gene expression under heat stress (38/33 ◦C, day/night). Significant differences were found in Chl content, photochemical efficiency, and EL, indicating variation in heat tolerance. Transcript levels of genes related to photosynthesis, carbohydrate metabolism, energy production, growth regulation, oxidative response, and stress protection showed positive correlations with heat-tolerant physiological traits (Xu *et al.*, 2018). According to Sun *et al.* (2020), HSP25 is genetically involved in creeping bentgrass heat tolerance. The level and type of HSP expression vary depending on the plant species and its heat tolerance. Xu & Huang (2012) found that HSP90 was up-regulated during both drought and heat stress only in 'Midnight', a heat-tolerant Kentucky bluegrass cultivar, but not in the heat-sensitive cultivar, Brilliant.

Zhang *et al.* (2016) discovered that greater heat tolerance in Kentucky bluegrass was connected with the induction of HSP in the cytoplasm and membranes during the early stages of heat stress. He *et al.* (2005) discovered that heat acclimatization caused two distinct HSPs in creeping bentgrass leaves (57 and 54 kDa) that were not present in non-acclimated plants, which has been ascribed to improved heat tolerance through acclimation in this species.

## Hormonal regulation

In turfgrass, the key hormones implicated in the response to heat stress include CKs, ethylene, and gibberellins (GA). Despite their apparent involvement, the specific roles and underlying mechanisms of hormonal regulation in developing heat tolerance in turfgrass species remain largely undefined. Each plant hormone serves a specific function, yet they often work in coordination to regulate the same physiological processes, highlighting the intricate network of interactions between hormones and plant responses (Li *et al.*, 2020). Among these, CK and ethylene have been particularly noted for their influence on heat tolerance (Chen & Huang,

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2022). Moreover, hormonal cross-talk is evident in how the synthesis of one hormone can either promote or inhibit the production of another. Consequently, the physiological outcomes are typically shaped not by the action of a single hormone but by the combined, synergistic, or antagonistic effects of multiple hormones (Yang *et al.*, 2014). CKs, which are mainly produced in the roots, play a crucial role in plant growth and development by promoting cell division, delaying leaf senescence, enhancing chlorophyll and photosynthetic protein production, and boosting the antioxidant defense system (Li *et al.,* 2020). A decline in CK levels under heat stress may result from reduced biosynthesis, increased degradation, or disrupted transport from roots to shoots.

Wang *et al.* (2013) reported that the suppression of leaf senescence or improvement in TQ under heat stress by injection of CK to the root zone of creeping bentgrass could be associated with the maintenance of more active antioxidant enzymes, such as SOD and CAT, for the alleviation of lipid peroxidation in the cell. According to research conducted by. Creeping bentgrass showed a rise in soluble protein content and an enhancement of expression of heat stress proteins (HSP; 32 and 57 kDa) when zeatin riboside was applied topically. This suggests that CKs may have a role in reducing heat injury by inducing or up-regulating HSP (Veerasamy *et al.,* 2007). During the earlier phase of heat stress (35 ˚C for 14 d) in heat-sensitive creeping bentgrass, ethylene resulted in a rapid loss in chlorophyll content and TQ compared to the heat-tolerant thermal *A. scabra* (35 ◦C for 35 d) (Xu & Huang, 2007) (Table 1).

### Membrane lipids

Phosphatidic acid is widely recognized not only as a crucial precursor in the biosynthesis of most membrane lipids but also as a key signaling molecule involved in plant responses to various abiotic stresses (Ischebeck, 2017). In a recent study, Zhang *et al*. (2023) demonstrated that 14 d of heat stress led to a significant decline in PA content in tall fescue. However, exogenous PA priming elevated endogenous PA levels and improved heat tolerance, as evidenced by increased leaf dry weight, chlorophyll content, and photochemical efficiency, alongside reduced electrolyte leakage. This enhanced tolerance was linked to the reprogramming of phospholipid and glycolipid metabolism, contributing to membrane stability under heat stress.

## Cold stress

### Morpho-physiological and biochemical responses to low-temperature stress

The ideal temperature range for the shoots of cool-season turfgrasses is around 15 to 24 ◦C, while the roots perform best at temperatures between 10 and 18 ◦C (Sun *et al.*, 2024). The level of low-temperature tolerance varies by species and cultivar, resulting in significant variation in winter survival of many plants, including temperate turfgrasses (Manuchehri *et al.*, 2014; Yang *et al.*, 2014).

In addition to low temperature, plants are susceptible to the formation of ice crystals within the cell (intracellular freezing) and between cell walls (extracellular freezing) at temperatures below water freezing. These crystals can result in dehydration, mechanical damage, and protein denaturation, among other metabolic damages (Xiang *et al.*, 2023). Intracellular and extracellular freezing have the potential to be fatal for both warm-season and cool-season turfgrass species (Fry & Huang, 2004). The period of cold acclimation that is initiated upon exposure to low, nonfreezing temperatures and brief days is a critical factor in the development of freezing tolerance (Hoffman *et al.*, 2014). During cold acclimation, plants undergo extensive changes at the molecular, cellular, and whole-plant levels. This cold acclimation process is governed by several physiological and biochemical changes. Alteration of the membrane lipid composition and the accumulation of cryoprotective proteins, sugars, and free amino acids are biochemical changes that are typically observed in cold-acclimated plants (Bocial *et al.*, 2011).

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## Morphophysiological characteristics

Cold stress suppresses shoot elongation, leaf expansion, and root growth in most turfgrasses. Cool-season species such as Kentucky bluegrass, tall fescue, and perennial ryegrass tend to exhibit better cold tolerance than warm-season grasses due to their ability to maintain growth under lower temperatures (Huang *et al.*, 2014). In Kentucky bluegrass, enhanced tillering and crown compactness during cold periods were associated with improved winter survival (Zhou *et al*., 2020). Moreover, Genotypes of tall fescue characterized by higher root-to-shoot ratios and more extensive root systems have demonstrated enhanced freezing tolerance and improved regrowth during the spring, highlighting the critical role of belowground traits in cold stress resilience (Xie *et al*., 2021).

Crown viability is critical for grass survival following freezing temperatures and offers a valuable non-destructive trait for phenotyping and improving freezing tolerance. In a study by Tamang *et al*. (2021), winter barley genotypes possessing narrower xylem vessels demonstrated greater freezing tolerance compared to those with wider vessels, suggesting a functional link between vascular anatomy and cold hardiness. At freezing temperatures, smaller xylem vessels help prevent cellular rupture. In the crown, this trait may reduce freeze-induced damage and enhance winter survival.

## Carbohydrate accumulation, photosynthesis, amino acid metabolism, and antioxidant enzyme activity

Avoidance mechanisms involve the accumulation of cryoprotective compounds such as potassium ions ($K^+$), proline, glycerol, and antifreeze proteins (AFPs). These cryoprotectants regulate intracellular solute concentrations, depress the freezing point, inhibit ice crystal formation, and help maintain plasma membrane fluidity under freezing stress. Moreover, many of these molecules exhibit antioxidant properties by scavenging ROSs, preventing protein denaturation, and thereby reducing cellular damage (Jahed *et al*., 2023). Some plant species have evolved advanced strategies to mitigate freezing injury through the production of ice-binding proteins (IBPs), which play a crucial role in cold survival. Also referred to as AFPs or ice recrystallization inhibition (IRI) proteins, IBPs are low-temperature-responsive proteins found in a range of cold-adapted organisms, including plant species such as perennial ryegrass and *Ammopiptanthus nanus* (Yu *et al*., 2021).

Tissue survival during freezing and its regrowth following freezing mostly depend upon carbohydrate reserves. Starch, fructans, and sucrose are the primary storage carbohydrates in crowns and stolons in overwintering turfgrasses (Fry & Huang, 2004). Nonstructural carbohydrates may influence turfgrass freezing tolerance by serving as osmotic buffers and food reserves (Hoffman *et al.*, 2014; Dong *et al*., 2020). Hoffman *et al.* (2014) have found that cool-season turfgrass with a higher accumulation of TNC content after cold acclimation showed a better freezing tolerance. They reported that total soluble sugars, mainly high molecular weight fructans, accumulated in each species/ecotype during cold acclimation, with higher levels measured in creeping bentgrass. Previous research has identified sucrose as a critical soluble carbohydrate involved in plant responses to abiotic stress, functioning in osmotic adjustment, membrane stabilization, and ROSs scavenging during cold acclimation (Dong *et al*., 2020). The findings by Dong *et al*. (2020) suggest that enhanced carbohydrate accumulation, particularly of sucrose and hexoses, may contribute to the superior cold tolerance observed in Kentucky bluegrass (var. anceps cv. Qinghai), probably through mechanisms involving osmoprotection, energy supply, and stabilization of cellular structures during stress. There is a gap in information on plant photosynthetic response during cold acclimation in turfgrasses, and this missing key would help to understand its connection to freezing tolerance. Cool-season forage grass (perennial ryegrass) research showed that the minimum temperatures to have a positive net photosynthesis can be as low as -4 ◦C based upon light level and exposure (Höglind

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*et al.*, 2011). Kosmala *et al.* (2009) found that Rubisco activity and photosynthetic activity contribute to the freezing tolerance of *Festuca pratensis* (meadow fescue) when exposed to low temperature conditions. Similar results were also reported by Bocian *et al.* (2011), where, under cold acclimation periods, Rubisco activase beta and chloroplastic phosphoglycerate kinase activity of perennial ryegrass as a freezing-tolerant genotype was much higher than freezing freezing-sensitive genotype.

Hoffman *et al.* (2010) found that four different perennial ryegrass accessions, after being exposed to cold acclimation at 2 ◦C for 21 d, showed a decrease in photochemical efficiency, ranging from around 0.79 to 0.67. According to Hoffman *et al.* (2014), annual bluegrass and creeping bentgrass both showed a decrease in photochemical efficiency when subjected to 2 ◦C for 14 d. Cold acclimation in creeping bentgrass, perennial ryegrass, and Kentucky bluegrass likewise showed a drop in photochemical efficiency (Sarkar *et al.*, 2009).

Cold acclimation led to an increase in amino acid content within the stolons and crowns of three *Poa annua* (annual bluegrass) ecotypes (Dionne *et al.*, 2010). While total and individual amino acid levels rose significantly in response to low temperatures, these changes did not correlate with differences in freezing tolerance among the ecotypes. In perennial turfgrasses, amino acids play two essential roles under mild stress conditions: they help protect cellular structures from chilling injury and act as nitrogen reserves that support regrowth during spring (Höglind *et al.*, 2011) (Table 1).

Proline is one of the amino acids that has been extensively investigated and has been reported to be involved in plant abiotic stress responses, including freezing tolerance. Proline, a hydrophilic compound, may contribute to the preservation of membrane stability in response to conditions associated with cellular desiccation by forming hydration barriers around proteins, nucleic acids, and cell membranes (Huang *et al.*, 2014). Proline has been estimated to play a regulatory role in the stimulation of the pentose phosphate pathway, which can result in the production of phenolic compounds, including antioxidants (Bocian *et al.*, 2011). Throughout the cold acclimation process, cool-season turfgrasses maintain high levels of proline (Sarkar *et al.*, 2009; Hoffman *et al.*, 2010). However, no correlation was found between proline content and intraspecific differences in freezing tolerance for perennial ryegrass (Hoffman *et al.*, 2010) or annual bluegrass ecotypes (Dionne *et al.*, 2010) during cold acclimation. Similarly, cold acclimation led to a notable increase in proline accumulation in both cold-tolerant and cold-sensitive perennial ryegrass genotypes compared to non-acclimated plants. However, the extent of proline accumulation differed significantly between the two groups, with cold-tolerant varieties exhibiting higher levels, suggesting a stronger osmoprotective response associated with cold tolerance (Chang *et al*., 2017).

As temperatures decrease below optimal thresholds, energy imbalances may arise within key metabolic pathways, while the production of ROSs can lead to damage in lipids, nucleic acids, and proteins (Huang *et al.*, 2014). Reactive oxygen species induce both enzymatic and non-enzymatic antioxidants, which play a crucial role in mitigating oxidative stress damage within plant tissues. The enhancement of antioxidant scavenging activity contributed to improved survival rates in certain plant species under low-temperature conditions (Chen *et al.*, 2021).

Pyruvic acid functions as a critical metabolic intermediate that bridges glycolysis and the tricarboxylic acid (TCA) cycle. In the study by Dong *et al*. (2020), cold stress significantly increased pyruvate accumulation in the cold-tolerant Kentucky bluegrass cultivar Qinghai, potentially enhancing substrate availability for the TCA cycle and maintaining cellular energy production under low-temperature conditions. Conversely, in the cold-sensitive cultivar PB, cold stress markedly reduced the activities of key TCA cycle enzymes, including malate dehydrogenase (MDH), succinate dehydrogenase (SDH), and isocitrate dehydrogenase (IDH), suggesting impaired respiratory metabolism under stress.

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## Shade stress

### Morpho-physiological and biochemical responses to shade stress

Shade stress is a limiting factor in the landscape for turfgrass species. Establishing turfgrass under shade conditions has many obstacles, so a low light regime would finally affect turfgrass growth and responses to management techniques. Turfgrass management under shade conditions is challenging for golf course managers and gardeners. Applying turfgrass for indoor sports facilities has accelerated, and this has developed strategies for turfgrass management when we are faced with reduced irradiance (Malik *et al.*, 2014). Low light can significantly reduce the quality of the turfgrass and cause a serious delay in the growth and development of plants (Dong *et al.*, 2022).

Cool-season grasses are generally more shade-tolerant than warm-season grasses. Tall fescue is relatively heat and drought-tolerant and has a good shade tolerance, as well. Previous studies on the effect of shade stress have been reported on some turfgrass species, including perennial ryegrass, red fescue, Kentucky bluegrass, tall fescue, sheep fescue, and creeping bentgrass (Dąbrowski *et al.*, 2015; Esmailpourmoghadam & Salehi, 2021). Jespersen *et al.* (2025) evaluated the shade responses of several turfgrass species, including cool-season grasses, hybrid bluegrass (*Poa arachnifera* × *Poa pratensis*), and tall fescue, and some warm-season grasses. Cool-season species showed the highest shade tolerance, followed by warm-season turfgrasses, which are shade-sensitive. Chlorophyll fluorescence analysis indicated that a plant’s ability to capture electrons during the initial steps of photosynthesis is more critical for shade tolerance than intersystem electron transport (Jespersen *et al.*, 2025).

Other studies showed that the suitable nitrogen to carbon assimilation in plants is crucial to overcome stress signals (Wen *et al.*, 2022; Li *et al.*, 2024). Under low-light conditions, tall fescue plants exhibited significant declines in growth parameters, chlorophyll content, photosynthetic efficiency, and carbon and nitrogen content in both leaves and roots (Wen *et al.*, 2022). However, reducing nitrogen input alleviated these negative effects by enhancing tiller production, root development, sugar accumulation, and key enzymatic activities involved in carbon and nitrogen metabolism. Metabolomic analysis further revealed that low nitrogen treatment under low light conditions altered key metabolic pathways, including the TCA cycle and amino acid metabolism, contributing to improved carbon-nitrogen balance and photosynthetic performance (Wen *et al.*, 2022). These findings suggest that adjusting nitrogen levels may be an effective strategy to improve shade tolerance in turfgrass by optimizing the interplay between carbon and nitrogen metabolism.

### Turf quality, morphological, and anatomical characteristics

When plants receive a limited quantity of light quantum, which is lower than what they need for normal growth, changes take place in their internal anatomy, physiological and biochemical properties, as well as their visible phenotype (Lazowski *et al.*, 2020).

Li *et al.* (2016) have presented a novel two-step methodology for the screening of shade-tolerant mutant perennial ryegrass characterized by dwarfism. They isolated shadow-1, which exhibits partial GA insensitivity and demonstrates a significantly higher tolerance to high-intensity and prolonged shade in comparison with its wild-type counterpart. Mutation breeding, as a conventional method of plant breeding, can effectively generate novel plant traits while mitigating concerns related to gene flow. This approach may prove beneficial in the development of shade-tolerant cultivars (Shu, 2012). In a study, Pease *et al*. (2018) compared velvet and creeping bentgrass shade tolerance under different rates of nitrogen and trinexapac-ethyl. Their results demonstrated that low nitrogen rates led to better turf survival under shade stress when compared to high nitrogen rates in both turfgrasses. However, both species showed equivalent responses to shade and trinexapac-ethyl. In the turf industry, the significance of shade tolerance becomes most pronounced during the mature stages; consequently, it is

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advisable to evaluate mature, mutagenized plant populations for their shade tolerance. Nonetheless, the process of directly screening for shade tolerance in mature turf can be quite labor-intensive due to the significant time and spatial resources it necessitates. Esmailpourmoghadam & Salehi (2021) investigated different levels of constant and temporal shade conditions in the morning and the afternoon (60% and 80%) and full sunlight on five cool-season turfgrass species: tall fescue, red fescue, perennial ryegrass, Kentucky bluegrass, and sheep fescue. Results of this study showed that the tall fescue genotype in the high levels of shade stress (80% constant shade) has the highest quality in terms of morpho-physiological characteristics and was not significantly different from sheep fescue. Perennial ryegrass and Kentucky bluegrass showed weak tolerance to stress conditions. The 80% constant shade had the greatest influence on turfgrass, but there was no significant difference between the temporal shades and the control treatment. Similar results were found by Seydavi (2022) on tall fescue genotypes. In 60% shade, leaf width in the polycross decreased by 29.16%, while this amount increased by 2.63% in the Aburaihan1. In 80% shade, the polycross also showed a 25.31% decrease in leaf width, while this amount was unchanged in the Aburaihan1 and Isfahan2 genotypes compared to full sunlight. Shade stress also impacts chloroplast ultrastructure. Wherley *et al.* (2005) reported a reduction in both the number and volume of chloroplasts under low light. However, this was accompanied by an increase in the number of grana and grana lamellae. For example, in tall fescue, the number of grana per chloroplast increased sharply after plants were transferred from full sun to shaded conditions. In a study, shading significantly reduced leaf thickness, as well as the thickness and length of epidermal cells, and decreased the size of the leaf midrib. These anatomical modifications, including the development of larger and thinner leaves, enhance light interception efficiency and are considered adaptive strategies to optimize photosynthetic performance under low-light environments (Xie *et al.*, 2020). Moreover, in tall fescue exposed to ~30 % light, chloroplasts adopt a spindle shape and align tightly along periclinal cell walls, optimizing light absorption without altering granum number or size (He & Li, 2021).

## Physiological changes: Chlorophyll content and photosynthesis

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Shade stress significantly alters the chlorophyll content and photosynthetic characteristics of various turfgrass species. In creeping bentgrass (*Agrostis palustris* Huds.), Dong *et al.* (2022) observed notable pigment reductions under continual shade compared to full sun: chlorophyll a decreased by 46%, chlorophyll b by 50%, neoxanthin by 31%, violaxanthin by 44%, and lutein by 34%. In studies on cool-season grasses, perennial ryegrass showed a remarkable increase in chlorophyll content when exposed to shade, whereas levels decreased in Kentucky bluegrass and prairie junegrass, and remained unchanged in red fescue. Notably, *L. perenne* also exhibited the highest net photosynthesis rates under these conditions (Van Huylenbroeck & Van Bockstaele, 2001). Conversely, Kentucky bluegrass experienced a significant reduction in maximal photosynthetic capacity under low light, while red fescue reached higher net $CO_2$ gas exchange rates. For other species, no significant differences were detected in light response curves (when expressed on a dry weight basis) between shaded and non-shaded conditions. In tall fescue, shade increases chlorophyll content per unit leaf mass and decreases the chlorophyll a/b ratio, enhancing light-harvesting efficiency under low-light conditions (He & Le, 2021). Further physiological responses include shade-related changes in stomatal conductance. Dabrowski *et al.* (2015) noted that while stomatal conductance itself was not significantly altered, the light threshold requirements varied across different perennial ryegrass cultivars, indicating genotype-specific adaptations to shading. Dong *et al.* (2022) compared shade tolerance in two cool-season turfgrasses, ‘SupraNova’ (supine bluegrass) and ‘Lark’ (perennial ryegrass), under increasing shade levels. ‘SupraNova’ maintained better turf quality, photosynthetic efficiency, and antioxidant activity than ‘Lark’ under shade. While ‘Lark’ showed reduced root growth and more pronounced physiological stress, ‘SupraNova’ showed better adaptability, making it more suitable for shaded environments.

### Photochemical efficiency

Photochemical efficiency (Fv/Fm) is an indicator of the maximum quantum efficiency of photosystem II photochemistry (Trinh & Masuda, 2022). Effects of shade condition on photochemical efficiency were investigated in some species of turfgrasses, including perennial ryegrass (Jiang *et al.*, 2005; Li *et al.*, 2016). Dabrowski *et al.* (2015) explored the differences between perennial ryegrass varieties in terms of their photosynthetic apparatus adaptation to light conditions. They found that the significance of the impact of the shading level depended on the cultivar and the season. The increase in the minimal fluorescence ($F_0$) parameter under shade stress is explained by the loss of PSII reaction centers and their inactivation. Fv/Fm value is also correlated with chlorophyll content in the shade (Guo *et al.*, 2022).

Dabrowski *et al.* (2015) evaluated the ability of chlorophyll a fluorescence (OJIP test) to detect shade-induced stress in three perennial ryegrass varieties under different light conditions. Significant differences were found among the varieties in their photosynthetic adaptation to shade, among which ‘Taya’ was distinguished by particularly large differences in the $F_0$ parameter. ‘Taya’ showed the most pronounced changes, but a decline in efficiency over longer shade stress. The values were 30–70% higher in the shade than in the sun and 8–27% higher than in the half shade. The maximal fluorescence (Fm) may be detected when all centers are closed (QA fully reduced). Fm values in ‘Nira’ were significantly higher in the shade than in the half shade and in the sun (34%) in May and June, but they were lower than in the half shade and in the sun in July (14%) (Dabrowski *et al.*, 2015).

## Biochemical responses

### Carbohydrate content

Turfgrass grown under low light conditions will experience lower amounts of carbohydrates due to photosynthesis reduction. Additionally, turfgrass does not have enough energy for leaf regeneration when they are frequently mowed under low light conditions. Therefore, nonstructural carbohydrates and photosynthetic efficiency of the turfgrass greatly dropped in the low light conditions (Jespersen *et al.*, 2025). The photosynthetic-respiratory balance (Pn: Rd) is a critical factor in shade tolerance, and positive $CO_2$ balance contributes to shade adaptation in red fescue (Jespersen *et al.*, 2022). A low ratio of Pn: Pd in response to stress conditions may result in reduced total non-structural carbohydrate content and reduce the plant's ability to grow or recover from stress injuries. Similar results were observed by Esmailpourmoghadam & Salehi (2021) under 80% shade in *F. arundinacea* (Table 1). However, proline accumulated in tall fescue leaves and roots under low light, and the content of proline was further enhanced by $Ca^{2+}$ application, suggesting that exogenous $Ca^{2+}$ promoted the ability of tall fescue to cope with low light stress by restoring various physiological mechanisms, including increases in proline content (Yang *et al.*, 2014).

Carotenoid-derived plant hormone strigolactone (SL) can substantially reduce the adverse effects of low-light conditions on plant growth. SL regulates morphological traits, enhances photosynthesis parameters (photosynthetic pigments, Fv/Fm, $\Phi_{PSII}$, qP, and NPQ), and increases antioxidant activity (CAT, POD, ASA[1], GSH[2], and SOD) in plants when light intensity is low. Gong *et al.* (2024) explored how SLs affect tall fescue's growth, photosynthesis, antioxidant responses, and internal SL levels when grown under shaded conditions. Application of GR24, a synthetic SL analog, improved growth traits such as height, leaf width, and biomass, though it reduced tiller number. It also enhanced photosynthetic performance by boosting chlorophyll fluorescence and gas exchange, while reducing cellular damage and promoting antioxidant activity through increased enzyme and compound levels. Additionally, GR24 elevated SL concentrations and upregulated related gene expression. Due to limitations in genetic modification techniques in tall fescue, some aspects were validated using *Arabidopsis*. Overall, the results suggest that SLs are essential for tall fescue to cope with shade by improving physiological resilience, potentially through pathways involving the *FaD14* gene (Gong *et al.* 2024).

## Combined stresses

### Morpho-physiological and biochemical responses to combined stresses

In natural environments, plants are rarely subjected to a single stress factor; instead, they are continually exposed to combinations of abiotic stresses, such as drought and heat, salinity and alkalinity, freezing and drought, or shade and drought. These combined stressors often interact, eliciting plant responses that are distinct from those triggered by individual stresses alone. However, translating findings from controlled-environment studies to complex and variable field conditions remains challenging, as interactions among multiple stress factors in the field are often nonlinear, unpredictable, and influenced by additional environmental and soil variables. The plant’s adaptive behavior is governed by an integrated signaling network that responds specifically to these stress combinations, rather than to isolated stress events (Martin *et al.,* 2021). Consequently, to develop plant lines that are resilient under real-world conditions, it is crucial to investigate plant responses under actual combined stress scenarios (Esmailpourmoghadam & Salehi, 2021; Esmailpourmoghadam *et al.*, 2024).

### Salinity and drought stress

Esmailpourmoghadam *et al.* (2023) investigated the physiological, biochemical, and molecular responses of tall fescue under combined salinity and drought stress conditions. The researchers observed that the combination of these stresses led to increased levels of ROSs, electrolyte leakage, and antioxidant enzyme activities (such as catalase and superoxide dismutase), along with elevated concentrations of proline and soluble sugars. These changes were accompanied

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[1]. Ascorbic acid 2. Glutathione

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by decreased relative water content, total chlorophyll, and membrane stability index (Esmailpourmoghadam *et al.*, 2023) (Figure 1). Pessarakli & Kopec (2008) evaluated and compared the growth responses of three cool-season turfgrass species encompassing creeping bentgrass, rough bluegrass, and perennial ryegrass under controlled salinity and drought stress conditions using a hydroponic system. Results showed that drought stress had a more severe impact on turfgrass growth than salinity, and among the three species, Rough bluegrass was the most sensitive to both stresses, while Creeping bentgrass demonstrated the highest tolerance. The findings highlight species-specific differences in stress responses (Pessarakli & Kopec, 2008).

## Heat and drought stress

The decline in quality of cool-season turfgrasses due to drought, heat, or their combination is expected to become increasingly common. Gaining insight into how these grasses respond to such stresses can support the development and selection of more tolerant varieties. Plants mitigate heat stress by cooling through transpiration, a process that necessitates stomatal opening. However, under combined heat and drought stress, stomatal closure to conserve water results in reduced transpiration and consequently higher leaf temperatures (Rahman *et al.*, 2021).

Cell membrane stability declined rapidly in Kentucky bluegrass exposed to combined drought and heat stresses (Wang & Huang, 2004). Moreover, the combination of drought and heat stress on *Lolium temulentum* (Darnel ryegrass) caused a unique response compared to single drought and salt stress. Significantly increased metabolites following heat and drought stress treatments revealed a predominance of genes associated with gibberellic acid (GA), CK, ABA, and auxin (AUX). Also, auxin influx and efflux carriers, auxin-binding proteins, and auxin-responsive factors exhibited significant expression. In contrast, genes related to JA and BS were expressed at lower levels. However, HSFs consistently showed upregulation in response to both heat and drought stress (Martin *et al.*, 2021). Protein phosphorylation is altered due to exogenous signals like drought, cold, and thermal stress. In their study, Zhang *et al.* (2020) investigated how protein phosphorylation contributes to drought priming-enhanced heat tolerance in tall fescue, a temperate grass species. While phosphorylation is known to play roles in plant responses to individual stresses, its involvement in cross-stress tolerance is less understood. Bi *et al.* (2016) in their study compared two tall fescue genotypes, 'PI 578718' (heat-tolerant) and 'PI 234881' (heat-sensitive), to evaluate their antioxidant defense systems and PSII photochemical performance under heat, drought, and combined stress conditions. Significant differences were observed between the two genotypes: the heat-tolerant genotype maintained higher leaf water content and showed less membrane damage and lipid peroxidation than the heat-sensitive genotype. The greater susceptibility of the heat-sensitive genotype under combined stresses was linked to lower activity of antioxidant enzymes like SOD and higher $H_2O_2$ accumulation. Antioxidant enzyme activity generally correlated positively with chlorophyll content and negatively with membrane injury. JIP-test results demonstrated that the heat-tolerant genotype maintained higher values in key PSII photochemistry parameters (e.g., ABS/RC, TR0/RC, RE0/RC), suggesting stronger protection of PSII under stress. In contrast, the heat-sensitive genotype exhibited greater PSII damage (Table 1). Recent work on creeping bentgrass found foliar Ortho-silicic acid applications (0.32 mL $m^{-2}$) enhanced antioxidant enzyme activity and boosted root biomass by ~53% and viability by ~89% under drought and heat stress (Zhang *et al.*, 2024).

## Cold and drought stress

Abiotic stresses like cold and drought limit turfgrass establishment. Li *et al.* (2024) assessed how 16 wild annual bluegrass germplasms respond to the combined effects of extreme cold and

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drought by examining their morphological, physiological, photosynthetic, and biochemical traits. The results showed that combined stress negatively impacted growth traits, photosynthesis, water-use efficiency, pigment content, and stress markers like proline and MDA. However, antioxidant enzyme activities such as SOD, POD, CAT, APX, and GR increased under stress. Multivariate analyses showed 'HZ' genotype had strong stress tolerance, and is recommended for cold, drought-prone areas (Li *et al.*, 2024) (Figure 1).

### Shade and drought stress

In a study by Esmailpourmoghadam & Salehi (2021), it was demonstrated that the simultaneous application of shade and drought stress on tall fescue resulted in a mitigation of damage typically caused by each stress. Their findings suggest that shade can alleviate some of the adverse effects of drought, possibly through reduced evapotranspiration and enhanced biochemical adaptations. These findings emphasize that, under certain conditions, the combination of stress factors may be beneficial to plants and can be strategically utilized to improve plant resilience (Esmailpourmoghadam & Salehi, 2021). Since tree shade has a stronger cooling effect than building shade by significantly lowering surface and air temperatures, it can effectively mitigate heat in urban landscapes and also reduce evapotranspiration stress on the underlying grass (Rahman *et al.*, 2021) (Figure 1).

## Conclusions

Over the past three decades, a large body of research has examined the morphological, physiological, and biochemical responses of various cool-season turfgrass species against major abiotic stresses, including drought, salinity, heat, cold, and shade. These studies reveal that cool-season turfgrass responses are highly species-dependent and that tolerance mechanisms, such as osmotic adjustment, antioxidant defense, root-shoot allocation, and chlorophyll retention, are differentially activated depending on the type, length, and severity of stress. While most existing studies have focused on individual stress factors, real-world field conditions often involve combinations of stresses, which can lead to synergistic or antagonistic effects. Therefore, future research should adopt integrated, multi-stress approaches to better reflect natural environments and to identify underlying mechanisms of cross-tolerance. In this review, by compiling and synthesizing fragmented data across decades, we aimed to provide a clearer foundation for species-specific turfgrass management and to support breeding strategies that align with the challenges of modern turfgrass cultivation. Cool-season turfgrasses exhibit a wide array of physiological, biochemical, and morphological adaptation strategies to cope with diverse abiotic stresses, including drought, salinity, heat, low temperature, and shade. Under drought stress, key strategies include osmotic adjustment through proline and sugar accumulation, and the development of deeper root systems to improve water uptake. In salinity stress, cool-season turfgrasses maintain ion balance by regulating $Na^+$ and $K^+$ levels and activating antioxidant defenses to reduce oxidative damage. In response to cold stress, cool turfgrasses accumulate compatible solutes like proline and sugars and adjust membrane composition to preserve fluidity, supporting continued function at low temperatures. During heat stress, turfgrasses rely on antioxidant enzymes, heat shock proteins, and deep rooting to maintain photosynthesis and water uptake. Under shade stress, morphological adaptations such as broader, thinner leaves enhance light capture, while physiological adjustments like optimizing the photosynthesis-to-respiration ratio support energy efficiency. While most studies focus on individual stresses, real-world turf environments often involve multiple overlapping stresses. This makes translating lab findings to the field complex, underscoring the need for integrated research approaches that reflect natural conditions and support cross-tolerance breeding and management strategies.

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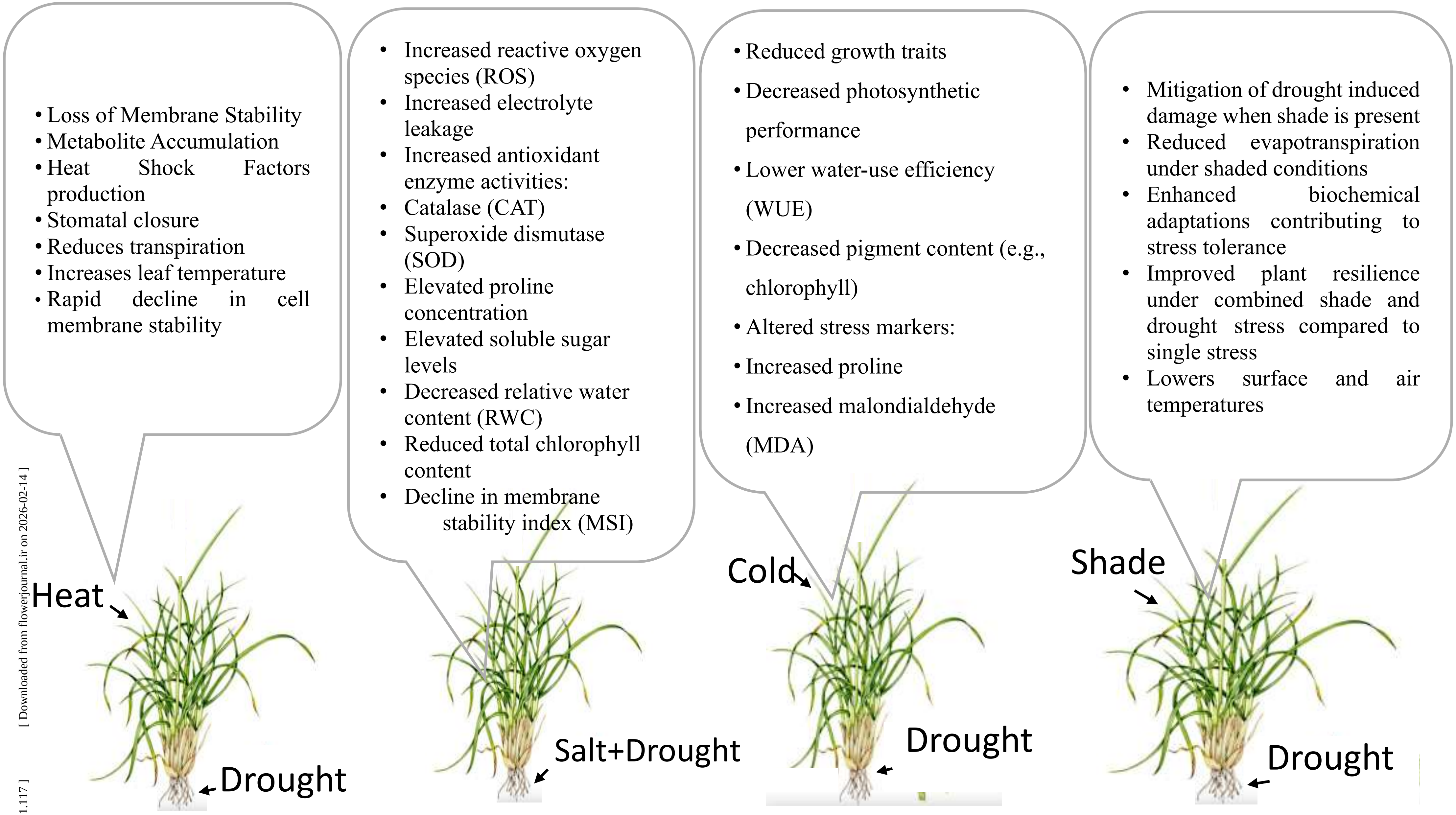

- Loss of Membrane Stability
- Metabolite Accumulation
- Heat Shock Factors production
- Stomatal closure
- Reduces transpiration
- Increases leaf temperature
- Rapid decline in cell membrane stability

- Increased reactive oxygen species (ROS)
- Increased electrolyte leakage
- Increased antioxidant enzyme activities:
- Catalase (CAT)
- Superoxide dismutase (SOD)
- Elevated proline concentration
- Elevated soluble sugar levels
- Decreased relative water content (RWC)
- Reduced total chlorophyll content
- Decline in membrane stability index (MSI)

- Reduced growth traits
- Decreased photosynthetic performance
- Lower water-use efficiency (WUE)
- Decreased pigment content (e.g., chlorophyll)
- Altered stress markers:
- Increased proline
- Increased malondialdehyde (MDA)

- Mitigation of drought induced damage when shade is present
- Reduced evapotranspiration under shaded conditions
- Enhanced biochemical adaptations contributing to stress tolerance
- Improved plant resilience under combined shade and drought stress compared to single stress
- Lowers surface and air temperatures

**Figure 1. Turfgrass response to combined abiotic stress conditions.**

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