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Review article

Turfgrass response to environmental stress: II. Warm-season turfgrasses

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Abstract

As climate change intensifies, warm-season turfgrasses are widely used in urban green spaces and sports landscapes. The quality of these turfgrasses is affected by abiotic stresses, specifically drought, salinity, heat, cold, and shade. To provide a comprehensive overview of adaptation strategies to abiotic stresses, this article reviews known morpho-physiological and biochemical responses of different warm-season turfgrass species over the past three decades. Certain abiotic stresses increase soluble salt concentrations in the soil solution, reducing water availability to plant roots. The resulting increase in rhizosphere osmotic pressure restricts root development and consequently diminishes turfgrass tolerance to stress. Physiological responses to one or more stress factors include reductions in leaf osmotic potential, leaf water potential, and relative water content, as well as nutritional imbalances. Biochemical alterations, including changes in the accumulation of secondary metabolites and osmoprotective compounds such as glycine betaine, proline, malondialdehyde (MDA), and abscisic acid (ABA), disrupt the plant's source–sink relationship. Under stressful conditions, one or more of these physiological and biochemical changes ultimately exacerbate damage to turfgrass. Moreover, emerging evidence suggests that combined stress conditions can sometimes produce unexpected synergistic and/or antagonistic effects, affecting plant responses differently than a single stress exposure. Understanding these complex responses is critical for breeding programs, especially considering the anatomical limitations of turfgrass species and the need for genetic compatibility in gene transfer. This review highlights the importance of species-specific knowledge in turfgrass science and sets the stage for future research on sustainable warm-season grass management.

Keywords: Abiotic stress, C_4 photosynthesis, Turfgrass, Warm season.

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; P_n, net photosynthetic rate; g_s, gaseous exchange; MDA, Malondialdehyde; MHAR, monodehydroascorbate; reductase; PN, potassium nitrite; PBZ, Paclobutrazol; POD, Peroxidase; ROSs, reactive oxygen species; RWC, relative water content; SDL, short day length; SNP, sodium nitroprusside; SOD, superoxide dismutase; SRL, specific root length; TNC, total nonstructural carbohydrates, TQ, turf quality; WSC, water-soluble carbohydrates; WUE, water-use efficiency.

Introduction

Turfgrasses are grass species that form a relatively continuous ground cover and can maintain their growth and function under regular mowing and traffic (Turgeon, 2008). Based on this definition, fewer than 50 grass species are generally recognized as turfgrasses (Chawla *et al*., 2018). Turfgrasses

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indisputably affect our daily lives by providing ground cover in parks, home lawns, sports fields, and golf courses (Esmaeili *et al*., 2025). Turfgrasses are also used in low-input and/or low-maintenance settings, such as on roadsides, along waterways, or on preserved land, where they may serve as barriers to reduce pollution, water runoff, and wind erosion of the underlying soil (Zhou & Abaraha, 2007).

Based on their ability to adapt to specific temperature and precipitation ranges, which are primarily determined by latitude and altitude, turfgrasses are typically divided into cool- and warm-season groups (Turgeon, 2008). Warm-season turfgrasses, known as sod-forming turfs, use a C4 photosynthetic pathway. Because C4 photosynthesis maximizes at higher temperatures (30–35 °C), warm-season turfgrass growth is optimized in summer. For warm-season perennial grasses, optimum temperature ranges from 27 to 35 °C for shoot growth and 24 to 29 °C for root growth, which is mainly affected by low-temperature stress (chilling and freezing temperatures) (Beard, 1973; Turgeon, 2008). Commonly used C_4 turfgrass species include buffalograss [*Buchloe dactyloides* (Nutt.) Engelm], zoysiagrasses [*Zoysia japonica* Steud., *Zoysia matrella* (L.) Merr], bermudagrass [(*Cynodon dactylon* (L.) Pers.)], centipedegrass [(*Eremochloa ophiuroides* (Munro) Hack.)], seashore paspalum (*Paspalum vaginatum* Sw.), and St. Augustinegrass [*Stenotaphrum secundatum* (Walt.) Kuntze] (Huang *et al*., 2014).

Key challenges in warm-season turfgrass management, particularly in urban, non-irrigated areas, include maintaining adequate soil moisture and managing shade stress (Zhou & Abaraha, 2007). Because of global warming, rising air and soil temperatures are expected to push even warm-season grasses beyond their optimal temperature range (Hatfield, 2017). However, research has indicated that genotypic variation influences water-use efficiency, root growth capacity, and photosynthetic efficiency. A deeper understanding of these differences could improve the sustainability of turfgrass systems. Under changing climate conditions, a major priority will be to assess the impact of abiotic stresses and to characterize how different genotypes respond to these environmental challenges. Therefore, this review examines previous research on the morphological, physiological, and biochemical responses of warm-season turfgrasses, with a particular focus on studies conducted under Iran's microclimatic conditions.

Drought Stress

The water-use efficiency (WUE) of C_4 grasses is greater than that of C_3 species due to higher photosynthetic rates at high levels of temperature and light intensity and lower transpiration rates at low light intensity (Xuan *et al*., 2013) (Fig. 1). So far, many studies have tried to evaluate warm-season turfgrass responses to water deficit conditions (Hu *et al*., 2010; Lu *et al*., 2009; Manuchehri & Salehi, 2014; Adamipour *et al*., 2016). Notably, the most drought-tolerant species/genotypes identified include *Paspalum vaginatum***,** *Cynodon dactylon* (some accessions), and *Zoysia* spp., which exhibit various combinations of drought avoidance, tolerance, and escape mechanisms (Table 1).

Morphological responses

Growth of ‘Emerald’ zoysiagrass, Common bermudagrass, and Adalayd paspalum declined as moisture content in the upper 20- and 40-cm soil layers decreased. Conversely, root growth in ‘PI 299042’, ‘AP14’, and ‘PI 509018’ paspalums, as well as ‘TifBlair’ centipedegrass, declined only when the upper 40 cm of soil dried out. Root dry weight returned to control levels promptly after re-watering for ‘TifBlair’ centipedegrass and the three paspalum accessions; however, it recovered only partially for ‘Adalayd’ paspalum, Common bermudagrass, and ‘Emerald’ zoysiagrass. These morphological responses, including reduced shoot growth and leaf area, increased root depth and density, leaf rolling and folding, and reduced tillering, are key indicators of drought stress adaptation (Table 1). The enhanced drought resistance observed in ‘PI 509018’ paspalum and ‘TifBlair’ centipedegrass can be attributed to improved root development and increased water absorption in deeper soil strata. This capability further helps preserve root viability and facilitates rapid root regeneration after rewatering. Variations in drought-avoidance traits among turfgrasses may provide a basis for selecting a diverse

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range of turf species, ultimately enhancing drought resistance in commercial cultivars (Huang *et al*., 1997).

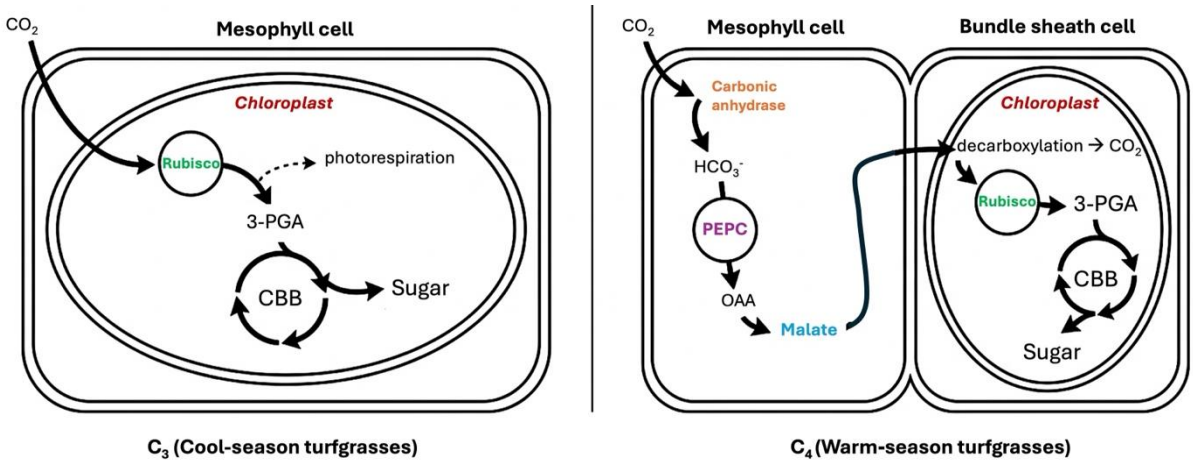

Figure 1. Schematic figure illustrating the C_3 and C_4 photosynthetic pathways of cool-season and warm-season turfgrasses. Abbreviations: CBB, Calvin-Benson-Bassham; PEPC, Phosphoenolpyruvate carboxylase; 3-PGA, 3-Phosphoglyceric acid; OAA, Oxaloacetic acid; Rubisco, Ribulose-1,5-bisphosphate carboxylase/oxygenase.

Table 1. Overview of morpho-physiological and biochemical responses of warm-season turfgrasses to major abiotic stresses.

Stress type	Key morphological responses	Key physiological responses	Key biochemical responses	Primary tolerance mechanisms	Most tolerant species/genotypes
Drought	– Reduced shoot growth and leaf area – Increased root depth and density – Leaf rolling and folding – Reduced tillering	– Stomatal closure – Reduced photosynthesis – Decreased RWC and water potential – Reduced transpiration rate	– Osmolyte accumulation (proline, glycine betaine, soluble sugars) – Increased antioxidant enzyme activity (SOD, CAT, POD) – ABA accumulation – Membrane stabilization	– Drought avoidance (deep roots, reduced leaf area) – Drought tolerance (osmotic adjustment, antioxidant defense) – Dormancy escape	– *Paspalum vaginatum* – *Cynodon dactylon* (some accessions) – *Zoysia* spp.
Salinity	– Reduced shoot and root growth – Leaf firing and chlorosis – Thickened cuticle and epidermis – Salt gland development (in some species) – Leaf curling (bulliform cells)	– Reduced photosynthesis – Stomatal closure – Decreased chlorophyll content – Reduced RWC – Ion imbalance (Na^+ accumulation, K^+/Na^+ ratio decline)	– Proline and glycine betaine accumulation – Increased antioxidant enzyme activity – Ion compartmentalization (vacuoles) – ABA accumulation – Synthesis of osmoprotectants	– Salt exclusion (root level) – Salt secretion (glands) – Ion compartmentalization – Osmotic adjustment	– *Paspalum vaginatum* – *Zoysia matrella* – *Zoysia japonica* – *Distichlis spicata*
Heat	– Reduced shoot density – Leaf chlorosis and senescence – Root growth inhibition – Altered leaf angles (heat avoidance)	– Reduced photosynthesis (stomatal and non-stomatal) – PSII damage – Increased EL – Reduced chlorophyll content – Increased respiration	– Heat shock protein (HSP) accumulation – Increased antioxidant enzyme activity – Carbohydrate metabolism changes – CK and ethylene signaling – Membrane lipid adjustments	– Heat avoidance (transpirational cooling, reflective leaf angles) – Heat tolerance (HSPs, antioxidant defense, membrane stability)	– *Cynodon dactylon* (some accessions) – *Zoysia japonica* – *Paspalum vaginatum*

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Cold/ Freezing	– Growth cessation – Leaf chlorosis (chilling) – Reduced tillering – Dormancy (winter) – Crown protection (morphological)	– Reduced photosynthesis – Decreased chlorophyll content – Reduced RWC – Increased EL (membrane damage) – Reduced photochemical efficiency	– Proline accumulation – Soluble sugar accumulation (sucrose, fructans) – Increased antioxidant enzyme activity – Dehydrins and antifreeze proteins – Starch to sugar conversion	– Cold acclimation (membrane modifications, sugar accumulation) – Freezing tolerance (antifreeze proteins, osmotic adjustment) – Dormancy	– *Zoysia japonica* (some cultivars) – *Cynodon dactylon* (cold-tolerant accessions) – *Buchloe dactyloides*
Shade	– Reduced root and tiller numbers – Thinner, elongated stems – Longer internodes – Wider, thinner leaves (anatomical) – Reduced lateral spread	– Reduced photosynthesis – Lower chlorophyll a/b ratio – Decreased carbohydrate reserves – Increased photochemical efficiency (compensatory) – Reduced Pn: Rd ratio	– Decreased chlorophyll content – Altered carbohydrate partitioning – Reduced soluble sugars – Reduced antioxidant enzyme activity	– Shade avoidance (elongation) – Shade tolerance (maintaining photosynthesis, efficient light capture) – Biomass allocation changes	– *Stenotaphrum secundatum* – *Zoysia matrella* – Some *Zoysia japonica* cultivars

Roots are usually less sensitive to water deficits than shoots and are more important for plant adaptation to soil-water deficits by maintaining water uptake under dry conditions (Colmer & Barton, 2017). In addition, broad root systems facilitate greater water uptake and, as such, increase plants' drought tolerance. Water stress notably reduced root length within the upper 40 cm of soil in 'Emerald' zoysia, whereas no such effect was observed in 'PI 509018' paspalum. Variation among species in their ability to establish and sustain a robust root system at different soil depths is crucial for genetically enhancing drought resistance (Duncan, 1994). Root length increased significantly after rewatering in both 'Emerald' zoysia and 'PI 509018' paspalum, particularly in the 20 cm soil layer (Huang *et al*., 1997). Bahrani *et al*. (2010) report that different desert wheatgrass species subjected to short-term water scarcity showed that drought decreased plant height, leaf area, and root dry weight. In the drought-stress experiment, the limited pot space (2.5 kg of soil) may have limited root mass. During 21days of drought stress, the 'PennA-4' cultivar of creeping bentgrass exhibited higher TQ at high N levels compared to low N (Chang *et al*., 2016). However, exogenous CK improved TQ and delayed leaf wilting under drought stress, especially at high N levels.

Physiological responses

Photosynthesis, chlorophyll, and water relations

Photosynthesis plays a central role in plant metabolism, regulating how plants respond to drought stress and how they recover after rewatering (Lawlor & Cornic, 2002; Chaves *et al*., 2003; Flexas *et al*., 2004a; Chaves *et al*., 2009). This process relies on photochemical reactions that drive energy production, carbon dioxide (CO_2) uptake, and carbon fixation. Drought stress commonly suppresses photosynthesis by reducing CO_2 availability, either through diffusion limitations in stomata and mesophyll tissues (Flexas et al., 2004b) or through disruptions in carbon assimilation metabolism (Lawlor, 2002a, b; Lawlor & Cornic, 2002). Key physiological responses to drought include stomatal closure, reduced photosynthesis, decreased relative water content (RWC) and water potential, and reduced transpiration rate (Table 1). The sensitivity of photosynthetic processes to drought varies by plant species, cultivar, and stress severity (Chaves *et al*., 2009; Sarmast *et al*., 2015). In mild or early drought conditions, the decline in photosynthesis is primarily attributed to stomatal closure, while under more severe drought stress, metabolic and biochemical limitations become the dominant factors (Yordanov *et al*., 2000; Flexas & Medrano, 2002).

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Eight days after the start of the water stress experiment at a salinity level of 9 dS m^{-1}, photosynthetic rate, chlorophyll content, and RWC diminished to their lowest levels during the course of drought and salinity stress in common Bermudagrass (Manuchehri & Salehi, 2014). In another study by Bahrani *et al*. (2010), total water use by plants decreased under drought stress in all grass species. In addition, leaf water potential and water-use efficiency tend to decrease in most species.

Cell Membrane Stability

Maintaining cellular membrane integrity is essential for plant survival under dehydration stress (Xu *et al*., 2011). Membrane stabilization is a primary tolerance mechanism identified in drought-resistant species (Table 1). Among various physiological indicators, electrolyte leakage (EL) is commonly used to assess membrane damage, particularly under drought conditions, because it reliably reflects stress-induced cellular injury (Blum & Ebercon, 1981; Rachmilevitch *et al*., 2006). Manuchehri & Salehi's (2014) study showed that common bermudagrass species that received water at 8-day intervals and at the highest salinity level experienced the highest EL percentage.

Root viability is another important root characteristic that can substantially influence water uptake and drought resistance in turfgrasses. Huang *et al*. (1997) reported that soil surface drying induced dramatic electrolyte leakage from roots grown 20 cm below the soil surface. Roots in deeper, wetter soil layers showed much less leakage. Roots of 'TifBlair' centipedegrass and 'PI 509018' *Paspalum* had much less EL (20-30%) in the upper 20 cm of the soil layer than the others (30-60%). Restoration of membrane integrity is also a major factor in dehydration tolerance capacity (Georgieva *et al.*, 2022). Under low N conditions and drought stress, EL was raised; the application of CK, to some extent, mitigated the damage as compared to the control (Chang *et al*., 2016).

Biochemical responses

Antioxidant enzyme activity

Plants have evolved a wide range of defense systems to survive under drought stress (Bandurska, 2022). Key biochemical responses include osmolyte accumulation (proline, glycine betaine, soluble sugars), increased antioxidant enzyme activity, and ABA accumulation (Table 1). One of the earliest plant responses to stresses such as water deficiency is the accumulation of reactive oxygen species (ROS), including superoxide, hydroxyl radicals, hydrogen peroxide, and singlet oxygen, which can damage plant cells (Sultan *et al*., 2025). ROS 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 (Foyer & Hanke, 2022). In the recent study by Chang *et al*. (2016), ROS activity was relatively stable in well-watered creeping bentgrass plants but increased significantly under water stress; as such, H_2O_2 and O_2^- contents increased 3-fold and 2-fold, respectively, on the last day of the stress period. However, plants can generally 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 and are 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, increase in plant cells in response to drought stress, serving a crucial role in defense against oxidative stress.

Effects of sodium nitroprusside (SNP) in three turfgrass species indicated that the maximum activity of CAT, POD, SOD, and APX was obtained with the application of 200 µM SNP or potassium nitrate (PN). Nitric oxide donors led to a greater increase in antioxidant enzyme activities in plants subjected to 7 or 9 days of drought stress. Among different turfgrasses tested under water stress, *C. dactylon* showed the highest activity for antioxidant enzymes, which is consistent with its identification as one of the most tolerant species/genotypes (Boogar *et al*., 2014). (Table 1).

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Amino acid, amid, and carbon metabolism

Soil water deficit causes osmotic stress in plant cells, in which osmolytes play a pivotal role in maintaining water homeostasis across plant developmental stages. These compounds encompass a broad range of molecules, including non-protein amino acids, quaternary ammonium compounds, soluble sugars, sugar alcohols, organic acids, and inorganic ions (Zhang *et al*., 2011). Osmolyte accumulation (proline, glycine betaine, soluble sugars) serves as a primary biochemical response and tolerance mechanism (Table 1).

Proline and glycine betaine fall into this category and support osmotic adjustment under stress by promoting water influx into cells, helping maintain intracellular osmotic equilibrium, and regulating signal transduction cascades. Glycine betaine also, by accumulating in the chloroplast, leads to better function of the thylakoid membrane under stress conditions (Tian *et al*., 2017).

The most frequent nonstructural polysaccharides in C_4 grass species are fructans. These are important energy reserves, especially under drought stress when photosynthesis for the synthesis of water-soluble carbohydrates (WSC) (fructose, glucose, and sucrose) is restricted (Undersander & Sharpe, 2025). Different types of carbohydrates serve a variety of functions. While sucrose, fructose, and glucose are solutes that help maintain cell turgor and may also stabilize proteins and membranes during stress-induced damage, starch and fructans, for instance, are important sources of energy reserves (Sharma *et al*., 2023). Drought stress alters the buildup of WSC and storage carbohydrates (fructans and starch) (George *et al*., 2025). Different plant species, carbohydrate types, and the duration or intensity of drought stress all affect the plant response. Short-term drought stress decreases sucrose and starch content, whereas longer-term drought stress increases them in C4 grasses such as *Setaria sphacelata* (Da Silva & Arrabaca, 2004).

ABA and cytokinin (CK)

Drought stress causes a cascade of responses within plant cells, including changes in phytohormone metabolism (Iqbal *et al*., 2022). Abscisic acid (ABA) is a growth inhibitor and is produced under a wide variety of environmental stresses, including drought. ABA accumulation is a key biochemical response and contributes to primary tolerance mechanisms (Table 1). All plants respond to drought and many other stresses by accumulating abscisic acid. ABA is ubiquitous in all flowering plants and is generally recognized as a stress hormone that regulates gene expression and signals the initiation of processes involved in adaptation to drought and other environmental stresses (Da Silva & Arrabaca, 2004). ABA and CK have antagonistic roles in drought stress. Higher abscisic acid and lower CK levels favor stomatal closure and limit water loss through transpiration under water stress (Kurepa & Smalle, 2022). The beneficial effects of ABA on drought resistance have been linked to increased antioxidant enzyme activity in bermudagrass (Noor *et al*., 2024). Ethylene has long been considered a growth-inhibitory hormone, although it is involved in environmentally driven growth inhibition and stimulation (Gu *et al*., 2022). Water stress in Arabidopsis is linked to two main signal transduction pathways: ABA-dependent and ABA-independent (Shan *et al*., 2022). Some endophytic fungi increase drought- and heat tolerance in turfgrasses by altering antioxidant enzyme activities (Xu *et al*., 2017).

CK synthesis, a hormone that promotes growth by regulating cell division and other developmental processes, generally decreases under drought stress (Kudoyarova *et al*., 2006). ABA's role as a metabolic factor in regulating plant tolerance to various stresses has garnered considerable attention in other species; however, information on the relationship between ABA signaling and drought tolerance in turfgrass species remains limited. Poaceae respond to drought with reduced leaf function and early senescence in mature leaves. Nonetheless, the direct impacts of heightened endogenous CK production on enhanced stomatal conductance during drought stress were not evident in transgenic creeping bentgrass possessing the isopentenyl transferase ipt gene that regulates CK synthesis (Merewitz *et al*., 2010). CK content diminishes under drought stress, potentially enhancing stomatal responses to elevated ABA levels (Huang *et al*., 2014).

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Salinity Stress

Morpho-physiological and biochemical responses

For plants to thrive in saline media, osmotic equilibrium is necessary; when this equilibrium is disrupted, cells lose turgidity, dehydrate, and eventually die (Tada *et al*., 2014). One of the main stresses that can significantly reduce crop productivity, particularly in arid and semi-arid areas, is soil or water salinity. Low osmotic potential of the soil solution (Yang et al., 2022), nutritional imbalance, specific ion effects (salt stress), or a combination of these factors (Bizhani & Salehi, 2014) are linked to salinity's detrimental effects on plant growth. Depending on its duration and intensity, salinity stress can cause various issues in plant cells, such as ion imbalance, physiological drought, and ion toxicity (Amombo *et al*., 2018; Esmailpourmoghadam *et al*., 2023). The key morphological responses to salinity include reduced shoot and root growth, leaf firing and chlorosis, thickened cuticle and epidermis, salt gland development (in some species), and leaf curling via bulliform cells. Primary physiological responses include reduced photosynthesis, stomatal closure, decreased chlorophyll content, reduced RWC, and ionic imbalances (Na^+ accumulation, declining K^+/Na^+ ratio). Biochemically, salinity triggers proline and glycine betaine accumulation, increased antioxidant enzyme activity, ABA accumulation, and osmoprotectant synthesis. The primary tolerance mechanisms include salt exclusion at the root level, salt secretion via glands, ion compartmentalization in vacuoles, and osmotic adjustment. The most tolerant species/genotypes identified are *Paspalum vaginatum***,** *Zoysia matrella*, *Zoysia japonica*, and *Distichlis spicata* (Table 1).

Salt stress can generate osmotic and ionic stresses that, at the physiological and biochemical levels, have detrimental, pleiotropic effects on plant growth and development (Abdi *et al*., 2010). Because of osmotic effects, salinity can inhibit cell growth in the short term. Excessive salt absorption can have long-term consequences, such as ionic stress and premature leaf aging, when the accessible photosynthetic area available to sustain development is reduced (Yang *et al*., 2022). Numerous studies have examined salt tolerance in warm-season turfgrasses (Hu *et al*., 2012; Zhou *et al*., 2013; Bizhani & Salehi, 2014; Manuchehri & Salehi, 2014). Sodium chloride (NaCl) is the primary cause of soil salinity, and any turfgrass that can withstand salt must deal with this issue (Uddin *et al*., 2012). The need for a superior turfgrass that can tolerate salinity has increased due to the expansion of turfgrass use in dry and semi-arid locations, the growing use of saline and non-potable water, and the use of salt to de-ice roads.

Plants have evolved two distinct strategies in adapting to high levels of sodium salts in their environment. One strategy is to exclude salts from the interior of leaf cells, and the other is to compartmentalize them within cell vacuoles (Gu *et al*., 2019). In both cases, this results in a relatively low cytoplasmic sodium concentration. These two broad categories of plants are called salt-secreting and salt-accumulating (Jiang *et al*., 2019). Those that exclude salts from leaf cells can tolerate high salt levels in the root environment, but at the expense of reduced growth. Most avoid salinity, some evade it, and a few tolerate it (Pessarakli & Kopec, 2009). Certain warm-season turfgrasses show notable salinity tolerance, with some classified as halophytes, including *Z. matrella* (L.) Merr., *Z. japonica* Steud., and *Paspalum vaginatum* Sw. Various turfgrasses are recognized as primary selections for saline soils; however, salinity tolerance varies significantly among these grasses, their cultivars, and genotypes. In another study conducted by our research group, *P. vaginatum* Sw. demonstrated greater tolerance to salinity stress than *C. dactylon* (L.) Pers. and *Pennisetum clandestinum* Hochst. ex Chiov (Bizhani & Salehi, 2014).

Chavarria *et al*. (2024) provided novel anatomical insights into salinity tolerance mechanisms using SEM-EDS [1]. The species-specific responses were characterized: St. Augustinegrass showed no anatomical changes; bermudagrass developed salt glands only under high salinity; zoysiagrass had constitutively present salt glands that increased in density under stress; and seashore paspalum

1. Scanning electron microscopy coupled with energy-dispersive X-ray spectroscopy

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accumulated Na^+ in bladder-like structures (Chavarria *et al*., 2024). This information is valuable for breeders and physiologists.

Morphological responses

Researchers have extensively studied plant growth responses to varying levels of salinity stress in turfgrass species. Salinity tolerance varies widely among species and within species.

Salt stress can influence turf quality (TQ). Tropical turf quality decreased severely in *Axonopus affinis* and *A. compressus,* while *P. vaginatum* and *Z. matrella* exhibited the highest TQ among the species at all salinity levels (Uddin *et al*., 2009). Based on growth parameters, the salinity tolerance ranking of selected grasses, from most to least tolerant, was *P. vaginatum* Sw., *Z. matrella* L., *P. vaginatum* Sw. (local), *C. dactylon* (L.) Pers., *Cynodon dactylon* × *Cynodon transvaalensis*, *E. ophiuroides* (Munro) Hack., *A. affinis* Chase. and *A. compressus* (Sw) P. Beauv.

Uddin *et al.* (2012) showed that a salinity level of 21 dS m^{-1} reduces shoot growth in C. dactylon by 50%. In a separate investigation, Marcum & Murdoch (1994) demonstrated that in salinity-tolerant species such as *Paspalum*, increased salinity levels correlate with elevated growth rates. Salt stress at high concentrations (20 dS m^{-1}) significantly reduced both root and shoot fresh weight in *C. dactylon*. However, root fresh weight increased to some extent at low salinity (5 dS m^{-1}). Shoot length significantly decreased with increasing salinity level, but these parameters were less affected in the salinity-tolerant turfgrasses compared to those of sensitive turfgrass species (Bizhani & Salehi, 2014; Esmaeili *et al*., 2015; Esmaeili & Salehi, 2016).

Growth stunting in both shoot and root is a common feature in warm-season turfgrass subjected to salinity stress, including weeping alkaligrass [*Puccinellia distans* (Jacq.) Parl.], saltgrass [*Distichlis spicata* (L.) Greene], bermudagrass, centipedegrass, St. Augustinegrass, seashore paspalum, and zoysiagrass (Dudeck *et al*., 1983; Lee *et al*., 2004 a,b; Marcum & Pessarakli, 2006; Dai *et al*., 2008; Uddin *et al*., 2012; Bizhani & Salehi, 2014; Esmaeili *et al*, 2015; Esmaeili & Salehi, 2016). Morphological and anatomical adaptations may alleviate the adverse effects of salt stress (Wasim & Naz, 2020). Salt-tolerant turfgrasses have developed a variety of anatomical adaptations, including increased succulence in both roots and stems, a thick cuticle with wax deposition, salt-secretory trichomes and glands, a thick, multilayered epidermis, and well-developed water-storing tissues within the cortex (Table 1). Additionally, researchers reported a widened Casparian band and enhanced root endodermis development (Wahid, 2003). *P. vaginatum* exhibits considerable variation in salinity tolerance among genotypes, with some genotypes capable of maintaining growth under high salinity conditions (Lee *et al*., 2004a, b). Early studies highlighted its potential for use in saline environments (Duncan, 1996a, b). At the same time, more recent research has further characterized genotypic variation in salinity responses and developed approaches for evaluating salt tolerance in *P. vaginatum* (Liu *et al*., 2024).

Many plant leaves curl in response to arid conditions and subsequently unfurl once water stress is alleviated. They possess specialized, thin-walled cells that contain water, facilitating these movements. Under water deficit, bulliform cells lose turgor and ultimately fold inward from edge to edge (Bizhani & Salehi, 2014). This bulliform-cell-mediated leaf curling is a key morphological response to salinity (Table 1). Bizhani & Salehi (2014) found that bulliform cells are more prevalent in *C. dactylon* than in *Poa pratensis*. Under elevated salinity, C. dactylon maintained a folded leaf structure; conversely, P. pratensis exhibited significant deterioration in leaf architecture, with no folded leaves observed at 15 dS m^{-1}.

Physiological and metabolic responses

Photosynthesis, chlorophyll, and water relations

The osmotic effect of salinity induces ABA accumulation, which can reduce stomatal conductance, intercellular CO_2 concentration, chlorophyll content, and Rubisco activity, and alter electron transport and sucrose accumulation (Liang *et al*., 2024). Excess salt in photosynthetic tissues can cause thylakoid

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shrinkage and stacking of adjacent membranes within grana. Ionic imbalance reduces chloroplast K^+ and disrupts Photosystem II (PSII). In addition, high sugar concentrations in mesophyll cells may feedback-inhibit photosynthesis, a phenomenon usually observed in leaves soon after plants are exposed to salt stress. These high sugar concentrations result from impaired normal sugar utilization in growing tissues (Hameed *et al*., 2021). Inhibition of photosynthesis to a greater extent was reported in centipedegrass than in seashore paspalum when the aforementioned species were exposed to 300 mM NaCl, and the inhibition of photosynthesis in seashore paspalum was mainly associated with metabolic or biochemical factors, while in centipedegrass, both stomatal closure and metabolic factors were involved in the decline in photosynthesis. In addition, the abundance of the Rubisco large subunit was not affected in seashore Paspalum but decreased in centipedegrass under salinity stress (Liu *et al*., 2011). In seashore paspalum, the tolerant ecotypes 'SI 93-2' and 'HI 101' showed markedly higher chlorophyll fluorescence than the less tolerant ecotypes (Lee *et al*., 2004a). These studies suggest that superior salinity tolerance in turfgrass species is related to maintaining active photochemical reactions and carboxylation.

Water loss from leaves and roots due to osmotic stress is a typical response to salinity stress. Leaf RWC and root osmotic potential declined when centipedegrass and seashore paspalum were exposed to 300 mM NaCl, but this reduction was more prominent in centipedegrass than in seashore Paspalum (Liu *et al*., 2012).

High salinity levels (20 dS m^{-1}) applied to *C. dactylon*, *F. arundinacea*, and *L. perenne* significantly reduced RWC. This significant reduction was attenuated soon after silicon (Si) treatment, suggesting the role of Si in the prevention of excessive leaf transpiration (Esmaeili *et al*., 2015). Higher RWC has been reported to improve gaseous exchange (gs) and net photosynthesis (Pn) under NaCl stress, thereby increasing dry mass production (Tisarum *et al*., 2022). A study on *Cynodon dactylon*, *Zoysia matrella*, and other warm-season species demonstrated that while RWC generally decreased with increasing salinity, the most salt-tolerant species, such as *Stenotaphrum secundatum* and *Z. matrella*, maintained significantly higher RWC than more sensitive species like *Paspalum notatum*. This variation in water retention shows that species differ in their ability to adjust osmotically and achieve this adjustment through multiple mechanisms beyond simple solute accumulation (Singh *et al*., 2019). Other research has emphasized these mechanistic differences. For example, *Paspalum vaginatum*'s superior salt tolerance is linked to its ability to maintain high RWC and a high Fv/Fm ratio by adjusting stomatal opening. In contrast, *Cynodon* and *Zoysia* use opposing strategies, with the latter showing significant proline accumulation (Liu *et al*., 2011).

Bizhani & Salehi (2014) noted that as salinity levels increased, chlorophyll content gradually decreased, with plants subjected to 15 dS m^{-1} salinity exhibiting the lowest levels. Noor *et al*. (2024) assessed drought tolerance in thirteen bermudagrass genotypes from across China, identifying 'Tianshui' and 'Linxiang' as highly tolerant and 'Zhengzhou' and 'Cixian'as sensitive under water-deficit conditions. Tolerant genotypes demonstrated enhanced biochemical and physiological adjustments, including increased antioxidant activities that minimized membrane damage and preserved cell permeability. They also accumulated higher levels of proline, an organic osmolyte that helped maintain osmotic water potential and supported efficient stomatal regulation, thereby sustaining transpiration rates and CO_2 assimilation. These processes preserved higher chlorophyll content, which was essential for maintaining photosynthetic activity under stress. In addition, tolerant plants showed structural improvements, including elongated leaf mesophyll, palisade, and spongy cells, resulting in greater leaf length, longer stolons and internodes, increased plant height, and deeper root systems. The study concludes that while morphological modifications are the initial response to drought, the overall tolerance relies on an integrated physiological and biochemical strategy, and the identified tolerant germplasm provides valuable material for future breeding and physiological research (Noor *et al*., 2024).

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Osmoregulation in salt-tolerant plants involves inorganic ions and various organic osmolytes to balance external osmotic stresses. Among organic osmolytes, sugars account for half of the total osmotic adjustment in salt-tolerant plants under saline conditions (Xu & Fujiyama, 2013). The accumulation of soluble carbohydrates in plants has been widely reported as a response to salinity or drought, despite a significant decrease in net CO_2 assimilation rate (Liu & Pessarakli, 2024). Common bermudagrass had significantly higher starch content under salinity stress (Bizhani & Salehi, 2014).

Previous research indicates that plants must maintain turgor and osmotic balance to survive. Consequently, one effective strategy is to convert starch into simpler sugars (Parvaiz & Satyawati, 2008). Comparable findings were obtained on *C. dactylon*, *P. vaginatum*, and *P. clandestinum* as reported by Mandegar & Salehi (Data not published). The reduction in sugar content was significantly greater at 20 dS m^{-1} compared with the control treatment across all turfgrasses. Increased salinity reduces starch content. According to Parvaiz & Satyawati (2008), under moderate salinity conditions, plants produce compatible solutes such as soluble sugars to maintain turgor and the integrity of chlorophyll and other cellular structures. However, under severe salinity, insufficient energy and carbon skeletons reduce soluble sugar concentration.

Biochemical responses

Amino acid and amide

Numerous studies indicate that halophytes adapt to low water potential by accumulating organic solutes such as proline, which helps maintain turgor pressure and overall water potential (Tada *et al*., 2014). Ashraf & Foolad (2007) noted that proline accumulation, 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. Moreover, recent studies have moved beyond the traditional view of proline as simply an osmolyte for osmotic adjustment. Chapman *et al*. (2022) and Jiang *et al*. (2023) reported other roles proposed for proline besides osmotic adjustment in stressed plants, namely acting as a hydroxyl scavenger, stabilizing membrane and protein structure, as a sink for carbon and nitrogen (N) for stress recovery, and buffering cellular redox potential under stress. These functions align with osmoprotectant synthesis as a biochemical response and osmotic adjustment as a primary tolerance mechanism (Table 1).

Tada *et al*. (2014) isolated a specific genotype of *Sporobolus virginicus* from a coastal area in Japan. Their main objective was to investigate and define this genotype's exceptional salinity tolerance, which thrives in environments with salt concentrations up to 1.5 M NaCl. The high accumulation of K^+ ions relative to Na^+ ions, along with elevated proline levels, is closely associated with its salt tolerance. Yamamoto *et al*. (2015) explained the impressive salt tolerance and adaptation mechanisms of *S. virginicus*, including the simultaneous activation of various biological processes, such as transporters and metabolism related to amino acids, 2-oxoacids, and phospholipids, which likely contribute to the plant's response to salinity (Yamamoto *et al*., 2015). In bermudagrass and other warm-season turfgrass species, proline and glycine betaine levels increased as salinity increased (Chavarria *et al*., 2021).

Ion Accumulation

Salt tolerance regulation in plants largely depends on selective ion transport and compartmentalization mediated by membrane proteins (Joshi *et al*., 2022; Banik & Dutta, 2023). Key components include plasma membrane H^+-ATPases, plasma membrane and tonoplast Na^+/H^+ antiporters, and K^+-selective channels. These proteins collectively contribute to Na^+ exclusion, vacuolar Na^+ sequestration, and maintenance of cellular K^+ homeostasis (Amombo *et al*., 2018). These mechanisms underlie two primary salinity tolerance strategies, e.g., Na^+ exclusion at the root level and ion compartmentalization in vacuoles (Table 1).

In general, extreme Na^+ accumulation can disrupt cellular ion homeostasis and impair plant metabolism; however, maintaining K^+ uptake and a high K^+/Na^+ ratio helps maintain osmotic and ionic balance (Naz *et al*., 2023). Accordingly, several warm-season turfgrasses, including bermudagrass, zoysiagrass, and

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seashore paspalum, have shown changes in Na^+ and K^+ accumulation and in the K^+/Na^+ ratio (Chavarria *et al*., 2021; Noor *et al*., 2024; Tada *et al*., 2023; Chen *et al*., 2019). Comparative studies have further demonstrated interspecific and genotypic variation in these ionic responses, as summarised in Table 2.
Among warm-season turfgrasses, Paspalum vaginatum has generally exhibited a high degree of salinity tolerance. Uddin *et al*. (2012) reported that *P. vaginatum* maintained relatively low Na^+ accumulation and a higher K^+/Na^+ ratio than the other turfgrass species evaluated under increasing seawater salinity. These characteristics were associated with its superior growth and overall salt tolerance. Similarly, differences in Na^+ retention, K^+ selectivity, and salt secretion have been associated with variation in salinity tolerance among zoysiagrass cultivars (Chen *et al*., 2009). In bermudagrass, salt-tolerant ecotypes have been characterized by limited Na^+ absorption and enhanced uptake of K^+ and Ca^{2+} (Hameed & Ashraf, 2008). Another study on bermudagrass confirmed a positive relationship between a high K^+/Na^+ ratio and salinity tolerance (Hu *et al*., 2012). These findings collectively indicate that limiting Na^+ accumulation while maintaining K^+ homeostasis is a common ionic feature of salinity tolerance in warm-season turfgrasses. However, the relative contributions of individual mechanisms vary among species and genotypes.
Exogenous treatments may further modify ionic homeostasis under salinity stress. For example, Esmaeili *et al*. (2015) reported that silicon application reduced Na^+ accumulation in the shoots and roots of several turfgrass species exposed to salinity, suggesting that Si mitigates Na^+ concentration and improves salt tolerance (Esmaeili *et al*., 2015). However, the mechanism underlying silicon's effects on ion transport remains poorly understood. Na^+ uptake is passive and is affected by the transpiration rate (Akhter *et al*., 2022). This suggests that reductions in Na^+ accumulation may be partly due to Si's inhibitory effect on transpiration rate (Cooke & Carey, 2023). In contrast, K^+ uptake and transport are active processes associated with the ATP-driven H^+-ATPase in the plasma membrane and the proton electrochemical gradient (Gu *et al*., 2019). Therefore, H^+-ATPase activation may be a mechanism by which Si enhances K^+ uptake under salt stress (Maryam & Gul, 2022). Silicon remarkably enhanced root K^+ concentration under salt stress in *C. dactylon*.

Table 2. Summary of studies relevant to ion accumulation.

Authors	Species/cultivar	Key ionic responses/findings
Uddin *et al.* (2012)	*P. vaginatum, Z. japonica, Z. matrella, D. didactyla, C. dactylon*	Increasing salinity increased Na^+ accumulation and reduced K^+, Ca^{2+}, Mg^{2+}, and the K^+/Na^+ ratio. *P. vaginatum* accumulated the least Na^+ and maintained the highest K^+/Na^+ ratio.
Chen *et al*. (2009)	*Z. japonica* cultivars and *P. vaginatum* 'Adalayd'	Salt secretion and shoot density contributed to tolerance in 'Diamond', whereas root Na^+ accumulation and greater K^+/Na^+ selectivity were associated with tolerance in 'Adalayd'.
Hameed & Ashraf (2008)	*C. dactylon* ecotypes	Salt-tolerant ecotypes exhibited restricted Na^+ uptake and greater accumulation of K^+ and Ca^{2+} in roots and shoots.
Hu *et al*. (2012)	*C. dactylon*	A positive association was observed between K^+/Na^+ ratio and salinity tolerance.
Esmaeili *et al*. (2015)	*C. dactylon, F. arundinacea. L. perenne*	Silicon reduced Na^+ concentrations in both shoots and roots under salinity stress.
Gu *et al*. (2019)	*C. dactylon*	K^+ uptake and transport were associated with ATP-dependent H^+ pumping across the plasma membrane.

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Antioxidant metabolism

The activity of catalase and superoxide dismutase, radical-scavenging enzymes, was significantly increased under conditions of moderate salinity stress in *C. dactylon* [L.] Pers. and *P. pratensis* (Bizhani & Salehi, 2014). This increased antioxidant enzyme activity is a key biochemical response to salinity (Table 1). In the same study, CAT, SOD, and APX activities increased in *P. vaginatum* Sw., *C. dactylon* [L.] Pers., and *P. clandestinum* (Mandegar & Salehi, Unpublished data). Another study investigated the salt stress response of *Aeluropus littoralis*, a halophytic grass, highlighting its physiological and molecular adaptations. Under salt stress, shoot sodium levels rose while potassium, calcium, and magnesium decreased (except in roots), with all returning toward normal during recovery. Chlorophyll a, total chlorophyll, and carotenoids increased, whereas chlorophyll b declined. Proline, a stress-associated amino acid, accumulated under salinity. Antioxidant enzymes (APX, POD, SOD) exhibited high activity in stressed roots. Still, they decreased during recovery, aligning with gene expression patterns showing upregulation of antioxidant genes under stress and downregulation during recovery (Hashemipetroudi *et al*., 2022).

Hu *et al*. (2012) reported notable upregulation of genes involved in APX, SOD, and CAT synthesis in two *C. dactylon* genotypes under these conditions. These enzymes protect cellular structures and membranes from free-radical damage. Salt tolerance in plants is often linked to increased antioxidant enzyme activity (Shalata *et al*., 2001). These enzymes play a key role in mitigating salinity-induced oxidative stress, as observed in bermudagrass (Mane *et al*., 2011). Among them, superoxide dismutase (SOD) is particularly important for maintaining physiological balance by rapidly converting reactive oxygen species (ROS) into hydrogen peroxide (ul Islam *et al*., 2023). Salt stress increased SOD activity in bermudagrass leaves at 3 dS m^{-1} but declined under prolonged stress. These results suggested that ROS can induce SOD activity under short-term salinity stress and that the salt-tolerant genotype has a better O_2^- radical scavenging ability (Manuchehri & Salehi, 2014).

Hormonal regulations

Phytohormones can reprogram a plant's transcript profile and, therefore, its metabolism (Zhau *et al*., 2013). ABA accumulation is a key biochemical response to salinity (Table 1). Salt stress can hinder plant root development by reducing root length and branching (Xu *et al*., 2010). However, halophytes and salt-tolerant plant species, such as bermudagrass, can stimulate root growth in response to salinity (Sadeghi *et al*., 2024; Esmaeili *et al*., 2015). Plants dynamically adjust their root system architecture to sustain growth and improve salt tolerance. These changes include restricting root growth rates, redirecting growth, and reducing lateral root initiation. The salt stress-induced increase in root/shoot ratio may restore functional equilibrium between below- and above-ground organs. Salinity in C43 salt-tolerant bermudagrass cultivars induced IAA and trans-zeatin riboside (tZR) biosynthesis genes (*TAA/YUCCA*, *CYP735A*), which coincided with increases in auxin (IAA) and cytokinin (DHZR, tZR) in the root of C43 (Yang *et al*. 2022).

Heat Stress

Morpho-physiological and biochemical responses to heat stress

Heat stress refers to a period during which elevated temperatures negatively affect plant growth and physiological processes (DaCosta & Huang, 2013). The probability and duration of elevated daytime and/or nighttime temperatures determine the likelihood and severity of heat stress in particular climatic zones. Heat-avoidance or heat-tolerance mechanisms may enable grass to endure thermal stress (Huang *et al*., 2014). The primary heat tolerance mechanisms identified include heat avoidance (transpirational cooling, reflective leaf angles) and heat tolerance (HSPs, antioxidant defense, membrane stability), with the most tolerant species/genotypes being *Cynodon dactylon* (some accessions), *Zoysia japonica*, and *Paspalum vaginatum* (Table 1). According to He & Huang (2010), heat stress limits whole-plant growth and promotes leaf senescence, typically characterized by reduced TQ, disrupted membrane stability,

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and membrane lipid peroxidation. Many studies have explored the varying degrees of heat tolerance in warm-season turfgrasses (Amini *et al*., 2023; Xiang *et al*., 2023).

Plants employ various strategies to prevent their internal temperatures from reaching harmful levels, a phenomenon known as heat avoidance. These strategies include transpirational cooling, altering leaf angles, reflecting sunlight, shading vulnerable tissues to protect them from sun damage, and developing deep or widespread root systems (DaCosta & Huang, 2013). Heat tolerance, by contrast, refers to a plant's ability to continue growing and producing a viable yield despite exposure to elevated temperatures. More heat-tolerant grasses often maintain more robust photosynthetic activity (Allakhverdiev *et al*., 2008) and demonstrate enhanced carbon allocation and N absorption under thermal stress (Xu & Huang, 2006). Heat stress can cause direct cellular damage, including protein denaturation, protein clumping, and increased membrane lipid fluidity (Tang *et al*., 2007). It can also lead to secondary effects, including disruption of enzyme activity in chloroplasts and mitochondria, suppression of protein synthesis, accelerated protein breakdown, and deterioration of membrane structures (Huang *et al*., 2014).

Morphological responses

Heat stress is expected to worsen as global temperatures rise. Temperatures above a certain threshold can cause irreparable damage to plant function and development, as well as metabolic changes that reduce growth and yield (Porter, 2005). Typical symptoms of heat stress injury in turfgrasses include leaf chlorosis and reduced shoot density (Amini *et al*., 2023). These symptoms- reduced shoot density, leaf chlorosis, and senescence- are key morphological responses to heat stress (Table 1). Heat stress results in TQ decline, which is common for grasses under various environmental stresses (Liu *et al*., 2022). Root growth inhibition is another key morphological response (Table 1).

Physiological responses

Photosynthesis, chlorophyll, and water relations

The ideal temperature range for the C_4 photosynthetic pathway, which is present in warm-season turfgrasses, is approximately 27-35 °C, according to Xie *et al*. (2020). Key physiological responses to heat stress include reduced photosynthesis (stomatal and non-stomatal), PSII damage, increased electrolyte leakage (EL), reduced chlorophyll content, and increased respiration (Table 1). Key physiological factors affecting photosynthesis include leaf chlorophyll concentration, photochemical efficiency, and EL, which are routinely used to evaluate genetic variants in heat-tolerant turfgrass (Huang *et al*., 2014). During hot weather, warm-season turfgrasses can maintain high photosynthetic rates because they have unique leaf anatomy and additional enzymes, such as PEP carboxylase, that reduce photorespiration and make CO_2 capture and fixation more efficient (Liu & Pessarakli, 2024). Stomatal constraints, or a lack of available CO_2, and metabolic constraints, or the direct heat sensitivity of the photosynthetic apparatus, including the Photosystem II (PS II) reaction center, electron transport capacity, and biochemical reactions for carbon fixation and assimilation, are both thought to contribute to the inhibition of photosynthesis at high temperatures (Law *et al*., 2021). These stomatal and non-stomatal limitations correspond to the reduced photosynthesis (stomatal and non-stomatal) response (Table 1).

Biochemical responses

Antioxidants activity

Antioxidant enzymes can mitigate heat-induced oxidative stress, with activity varying by species and heat stress level (Liu & Pessarakli, 2024). Increased antioxidant enzyme activity is a key biochemical response and heat tolerance mechanism (Table 1). Oxidative damage and tissue dehydration are two potential outcomes of heat stress. Most superoxide radical production occurs in mitochondria and chloroplasts, but microbodies also contribute. A plant's ability to withstand heat stress depends on its defenses against oxidative stress. Catalase (CAT) is a key antioxidant enzyme predominantly found in

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the peroxisomes of aerobic organisms, where it breaks down hydrogen peroxide into water and oxygen, protecting cells from oxidative damage (Law *et al.*, 2021).

Assimilate accumulation

High temperatures influence carbohydrate metabolism, including carbon production through photosynthesis and carbon utilization in respiration for energy production to support growth, maintenance processes, and metabolic activities (Fry & Huang, 2004). Changes in carbohydrate metabolism are key biochemical responses to heat stress (Table 1). Carbohydrates make up the skeleton or structure of plants and are a source of metabolic energy, which is particularly important for the regrowth of shoots and roots following defoliation or mowing (Fry & Huang, 2004). Carbohydrate metabolism in roots is crucial because roots rely solely on carbon assimilates supplied by leaves (Liu *et al*., 2022).

Heat shock proteins

Heat shock proteins (HSPs) act as molecular chaperones that help stabilize and refold damaged proteins under stress. HSPs were initially identified in relation to heat stress; however, they now respond to a range of other abiotic stresses (Rossi & Huang, 2025). These proteins are located in various cellular organelles and are categorized by molecular weight, with some classified as high-molecular-weight HSPs and others as low-molecular-weight HSPs (Xu *et al*., 2021).

Hormonal regulation

Each hormone has a distinct purpose, yet in most cases they interact to regulate the same physiological events or processes, demonstrating a complex interplay between plant hormones and physiological responses (Gray, 2004). Hormonal interaction is also evident in the fact that one hormone's production can stimulate or inhibit another's. As a result, hormone output often depends on synergistic or antagonistic interactions among multiple hormones rather than on their individual activities (Weiss & Ori, 2007). HSP accumulation is a key biochemical response and heat-tolerance mechanism (Table 1). The primary hormones involved in turfgrass response to heat stress are CK, ethylene, and GA. However, the roles and mechanisms of hormonal control in developing heat tolerance in turfgrass species remain unclear. Major hormones such as CK and ethylene have also been shown to regulate heat tolerance in grasses (Veselov *et al*., 1998; Zhang *et al*., 2008; Xu & Huang, 2009). Cytokinins (CK) are primarily synthesized in the root system and regulate plant growth and development, including cell division stimulation (Skoog & Armstrong, 1970), suppression of leaf senescence (Gan & Amasino, 1995; Naqvi, 1999), promotion of chlorophyll and photosynthetic protein synthesis (Caers *et al*., 1985; Synková *et al*., 1997), and strengthening antioxidant defense systems (Musgrave, 1994). The drop in CK content most likely results from decreased biosynthesis, increased catabolism, or impaired transport of CK from roots to shoots.

Liu *et al*. (2002) reported that injecting CK into the root zone of creeping bentgrass under heat stress could suppress leaf senescence or improve TQ by maintaining higher levels of active antioxidant enzymes such as SOD and CAT, thereby reducing lipid peroxidation in cells. Warm-season turf, zoysiagrass (*Zoysia japonica*), showed higher heat tolerance than cool-season turf, tall fescue (*Festuca arundinacea*), due to its superior oxidative scavenging capacity, as shown by maintained elevated SOD and POD activities (Du *et al*., 2009). This observation is consistent with the classification of *Zoysia japonica* as one of the most heat-tolerant species (Table 1). This trait is closely linked to its efficient antioxidant defense system and its ability to maintain membrane stability under thermal stress.

Low-temperature Stress

Morpho-physiological and biochemical responses

In plant science, cold stress is categorized into chilling and freezing stress based on temperature thresholds and physiological impacts (Pessarakli, 2008). Chilling stress occurs at non-freezing temperatures (0–15 °C) and primarily disrupts membrane fluidity, enzyme kinetics, and photosynthetic processes without ice formation, posing significant challenges for tropical and subtropical species. In

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contrast, freezing stress arises at subzero temperatures (< 0 °C), where extracellular or intracellular ice crystallization causes mechanical injury, cellular dehydration, and often lethal damage to plant tissues. The key morphological responses to cold/freezing stress include growth cessation, leaf chlorosis (chilling), reduced tillering, dormancy (winter), and crown protection (morphological). Primary physiological responses involve reduced photosynthesis, decreased chlorophyll content, reduced RWC, increased EL (membrane damage), and reduced photochemical efficiency. Biochemically, cold stress triggers proline accumulation, accumulation of soluble sugars (sucrose, fructans), increased antioxidant enzyme activity, the expression of dehydrins and antifreeze proteins, and starch-to-sugar conversion. The primary tolerance mechanisms include cold acclimation (membrane modifications, sugar accumulation), freezing tolerance (antifreeze proteins, osmotic adjustment), and dormancy. The most tolerant species/genotypes are *Zoysia japonica* (some cultivars), *Cynodon dactylon* (cold-tolerant accessions), and *Buchloe dactyloides* (Table 1). Warm-season grasses grow best at 26-35 °C. They are susceptible to cold stress, and their growth decreases at temperatures below 10-12.8 °C and enters dormancy at 0 °C (Christians *et al*., 2016). Low-temperature stress significantly limits the distribution, development, and productivity of warm-season turfgrass species. Low-temperature tolerance differs among species and cultivars, leading to considerable variation in the winter survival rates of warm-season turfgrasses. Extensive research has examined variation in cold tolerance among warm-season turfgrass species (Kauffman, 2010; Esmaili & Salehi, 2012; Akbari & Salehi, 2018; Gopinath *et al*., 2021; Walton, 2022).

Chilling Stress

Chilling stress is characterized by inhibited photosynthesis, loss of membrane function, and oxidative stress resulting from metabolic imbalances (Lyons, 1973; Suzuki & Mittler, 2006; Ruelland *et al*., 2009). These correspond to reduced photosynthesis, decreased chlorophyll content, and increased EL (membrane damage) physiological responses (Table 1). Information on the dormancy of warm-season turfgrasses in fall and winter remains limited. Zhu *et al*. (2008) demonstrated that drought, low temperature, and SDL conditions in winter reflected withered and yellow leaves on *Z. japonica* 'Lanyin No. III. In addition, all SDL treatments showed dormancy, while extended light duration under similar water and temperature conditions maintained normal vegetative growth. This leaf chlorosis (chilling) and dormancy are key morphological responses to cold stress (Table 1). Zhu *et al*. (2008), after research on *Z. japonica* 'Lanyin No. III' stated that prolonging day length in winter yielded growth acceleration, lengthening the vegetative period and decreasing the degree of dormancy.

Freezing Stress

At temperatures below the freezing point of water, plants are vulnerable to ice crystal formation both inside cells (intracellular freezing) and in the spaces between cells (extracellular freezing) (Uemura *et al*., 2006). These ice formations can cause a range of harmful effects, including cellular dehydration, structural damage, protein denaturation, and other metabolic disruptions (Xin & Browse, 2000). Both warm-season and cool-season turfgrasses can suffer fatal consequences from these freezing events (Fry & Huang, 2004).

A key process that enhances freezing tolerance is cold acclimation, which is triggered by exposure to low but nonfreezing temperatures combined with shorter day lengths (Levitt, 1980). Cold acclimation (membrane modifications, sugar accumulation) is a primary tolerance mechanism (Table 1). During this acclimation period, plants undergo molecular, cellular, and physiological adjustments. Biochemical modifications include changes in membrane lipid composition and the accumulation of protective compounds, including specific proteins, soluble sugars, and free amino acids. Cold acclimation also involves reprogramming gene expression, enabling plants to better cope with freezing conditions.

Xiang *et al*. (2023) evaluated how mowing height affects the freeze tolerance of putting green–type bermudagrass. The results showed that increasing mowing height significantly improved freeze tolerance across most genotypes tested. Some showed superior recovery and regrowth after freezing

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stress, indicating greater resilience. These findings suggest that simple management practices, such as raising mowing height in the fall, can improve bermudagrass winter survival in transitional climates, supporting healthier and more sustainable turfgrass maintenance (Xiang *et al*., 2023).

Morpho-physiological characteristics associated with freezing stress

Frost-induced stress in plants primarily results from ice formation within tissues, leading to mechanical injury and/or dehydration damage (Zhang *et al*., 2006). Ice formation begins in extracellular spaces because pure water freezes first. As ice forms, it lowers the vapor pressure, drawing water out of cells toward the extracellular ice crystals. This process causes intracellular dehydration and concentrates solutes within the cell (Bertrand *et al*., 2013). The increased solute concentration helps lower the freezing point, preventing intracellular ice formation and protecting cellular structures. However, as freezing intensifies, the plasma membrane remains tightly attached to the cell wall. If the extracellular space is too small to accommodate expanding ice crystals, it may cause physical damage such as rupture, separation, or compression of cells (Zhang *et al*., 2006). This results in membrane damage, which becomes apparent during thawing, as the membranes become leaky. This leakiness can be quantified using the electrolyte leakage (EL) method, a reliable indicator of freezing injury that correlates well with whole-plant survival and is widely used to assess low-temperature tolerance.

Grass plants adapted to cold climates can maintain photosynthesis and sugar production even at sub-zero temperatures. In autumn, warm-season grasses cease growth and store most of their energy in the crown as starch. This starch-to-sugar conversion is a key biochemical response to cold stress (Table 1). The grass crown, which is vital for plant survival, is well protected morphologically and biochemically, with antifreeze proteins and other molecules that reduce osmotic potential and the risk of dehydration (Merewitz, 2021). During winter, these grasses maintain a basic metabolic rate through aerobic respiration, consuming oxygen and carbohydrates to generate ATP, CO_2, and water (Gendjar, 2025). This adaptation helps them survive extreme conditions. Reduced photosynthesis at low temperatures is often linked to an energy imbalance between the light and carbon reduction reactions, leading to photoinhibition. A key factor is inhibition of sucrose synthesis, which limits the availability of inorganic phosphate needed for ATP regeneration and ultimately hinders carbon reduction reactions (Stitt & Hurry, 2002).

Frost desiccation refers to the gradual dehydration of plants at sub-zero temperatures. At -1˚C, accessible soil water freezes, preventing root uptake. Under these conditions, transpiration losses increase substantially, particularly with wind and radiation, which can cause irreversible dehydration in plant cells (Bhattacharya, 2022).

Temperature and photoperiod significantly influence turf quality (TQ) and various morphological and physiological traits in warm-season turfgrasses such as bermudagrass and zoysiagrass. Traits like shoot length, leaf area, tiller density, mean rooting depth, shoot and root fresh weight, photosynthesis rate, chlorophyll content, relative water content (RWC), carbohydrate accumulation, membrane stability, and proline content are all affected (Esmaili & Salehi, 2012; Zhu *et al*., 2008). These traits encompass morphological responses (growth cessation, reduced tillering), physiological responses (reduced photosynthesis, decreased chlorophyll content, reduced RWC), and biochemical responses (proline accumulation, soluble sugar accumulation) (Table 1).

The decline in temperature from 24 °C resulted in a marked decrease in chlorophyll content, visual TQ, and color in 49 bermudagrass accessions (Akbari & Salehi, 2018). Additionally, root depth and root fresh and dry weights recorded between mid-September and mid-November decreased to 55%, 26%, and 58%, respectively (Esmaili & Salehi, 2012). Conversely, extended photoperiods during the same period increased chlorophyll content (194%), RWC (656%), and photosynthetic rate (23.7%), primarily because of increased leaf number and area. These findings align with Rosenthal & Camm (1997), who noted that longer daylight delayed declines in chlorophyll and photosynthetic capacity. Maintaining chlorophyll content and photosynthetic rate indicates cold-tolerance mechanisms (Table 1).

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Jia *et al*. (2014) evaluated the association between low-temperature tolerance, green color retention in fall and spring, and dormancy period length in seven *Zoysia japonica* cultivars. The study showed that cultivars with lower cold resistance retained their green color longer in the fall but exhibited reduced green-up in the spring. Additionally, those that entered dormancy later experienced delayed spring green-up, resulting in a longer dormant period. Another study on *Cynodon dactylon* [L.] Pers. found that low temperatures and shorter days reduced turf quality, chlorophyll content, and RWC. In contrast, proline content and EL increased, demonstrating a physiological shift under cold stress (Esmaili & Salehi, 2012).

Balanced nutrition plays a key role in cold tolerance. Nitrogen, in particular, is crucial but must be managed carefully. Excessive N applications in the fall can increase turfgrass susceptibility to winter injury (Carroll, 1943). Perennial ryegrass achieved maximum cold hardiness with low to moderate N (49–147 kg ha^{-1} yr^{-1}) and medium to high potassium (K) levels (245–441 kg ha^{-1} yr^{-1}) (Webster & Ebdon, 2005). Understanding winter stress responses in turfgrasses not only aids in turf management but also offers valuable insights applicable to crops. Prolonged exposure to winter stress can severely damage meristematic regions such as crowns, stolons, and rhizomes, impairing spring recovery. Exploring the physiological and biochemical mechanisms behind cold acclimation and evaluating varietal differences is essential for developing new, cold-tolerant cultivars.

Physiological responses

Hormonal regulation

Hormonal signaling is an important component of turfgrass responses to chilling and freezing stress. Low temperatures generally alter stress-related hormones, particularly ABA, JA, and SA. In contrast, changes in auxin, GAs, and CKs are associated with reduced growth and developmental activity during cold acclimation (Li *et al.*, 2018). In perennial ryegrass, freezing stress increased ABA concentrations in leaves, crowns, and roots, together with changes in JA and SA. However, these responses were less pronounced after cold acclimation, suggesting that acclimation involves not only inducing stress-related hormones but also adjusting their levels (Prerostova *et al.*, 2021). Cytokinins may also contribute to perennial ryegrass's ability to withstand freezing conditions. In freezing-tolerant genotypes, changes in the relative abundance of active trans-zeatin and less active cis-zeatin suggest that regulation of CK metabolism may help maintain crown and root function during cold stress (Prerostova *et al*., 2021). Other hormones appear to interact with these responses. For example, exogenous melatonin increased cold tolerance in perennial ryegrass, which was associated with enhanced brassinosteroid biosynthesis and signaling and activation of H_2O_2-related antioxidant responses (Fu *et al*., 2022). Similarly, changes in ABA, GA, JA, and auxin have been associated with improved physiological performance and reduced oxidative damage under low-temperature conditions (Wei *et al*., 2023). These findings indicate that hormonal responses to cold stress are interconnected rather than controlled by a single hormone. Crosstalk among ABA, JA, SA, CKs, BRs, and growth-related hormones may therefore help coordinate cold acclimation, antioxidant defense, and maintenance of cellular integrity in turfgrasses (Reza *et al*., 2023).

Carbohydrate accumulation associated with freezing stress

Nonstructural carbohydrates may prevent lethal protoplast dehydration during intercellular ice formation. Soluble sugar accumulation (sucrose, fructans) and starch-to-sugar conversion are key biochemical responses to cold stress (Table 1). As food reserves, nonstructural carbohydrates fuel respiration during dormancy and support growth resumption in spring. Starch and sucrose increased during fall acclimation in bermudagrass (*C. dactylon* [L.] Pers.); however, freezing tolerance did not appear to be related to carbohydrate levels during the acclimation period (Dunn & Nelson, 1974). TNCs increased during fall hardening in ‘Meyer’ zoysiagrass (*Z. japonica* Steud.) (Rogers *et al*., 1977). This suggests that high TNC levels may have contributed to ‘Meyer's superior freezing tolerance. Maier *et al*. (1994) investigated the freezing tolerance of three St. Augustine grass cultivars. They concluded that

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'Raleigh' had higher freezing tolerance than 'Floratam'. However, 'Floratam' showed an equal freezing tolerance to FX-332. 'Raleigh' showed more than 60% survival in December and January, while 'Floratam' and 'FX-332' had less than 20% survival. 'Raleigh' was the only cultivar that acclimated, and it recorded about a 75% increase in survival between October and December 1990. No significant correlation was observed between starch and sucrose levels or TNC levels, and no survival was observed at –4 or –6 °C for any cultivar (Rogers *et al*., 1977).

The results for 'Floratam' are in accordance with Fry *et al*. (1991), who observed changes in starch and sucrose levels of 'Floratam' stolons, which did not affect its freezing tolerance. In contrast, the sucrose concentration in centipedegrass stolons increased by 47% during acclimation under controlled conditions. This augmented sucrose was positively correlated with stolon survival (Fry *et al*., 1991; 1993).

Sucrose and fructans are carbohydrates that can regulate the oxidative stress response and delay freezing by directly inhibiting apoplastic ice crystal formation (Livingston *et al*., 2009; Parvanova *et al*., 2004). In addition, recent studies have demonstrated that fructans can enhance cell membrane integrity in response to dehydration-induced stressors through direct interactions with cell membranes (Valluru & Van den Ende, 2008; Hincha *et al*., 2002).

Ball *et al*. (2002) and Cai *et al*. (2004) are among numerous studies showing that buffalograss and centipedgrass, which have better freezing tolerance, accumulate more TNC after cold acclimation. According to Ball *et al*. (2002), buffalograss's ability to withstand freezing temperatures depends primarily on its soluble carbohydrates. As cryoprotectants and osmotic adjusters, soluble carbohydrates may increase freezing tolerance by lowering the freezing point. The effects of different temperature regimes (15, 7.5, 0, and -7.5 °C) and photoperiods (16, 12, and 8 h light) on the morphophysiological parameters of C. dactylon were first investigated by Esmaili & Salehi (2012). Shorter light duration and temperature increased sugar content in shoots and roots. An adverse trend was observed in starch content; as such, shoots and roots showed increased starch levels with shorter photoperiods, regardless of temperature. Also, soluble sugars of *C. dactylon* tend to increase at -7.5 ºC (Esmaili & Salehi, 2012). These findings demonstrate the starch-to-sugar conversion biochemical response (Table 1). Similarly, cold treatments generally affected metabolites such as amino acids, organic acids, sugars, and sugar alcohols in bermudagrass leaves (Shi *et al*., 2014).

Photosynthesis

The better photosynthetic performance of zoysiagrass during the fall could partially explain the better freezing tolerance of zoysiagrass cultivars compared to bermudagrass under the cold acclimation period in field conditions (Rogers *et al*., 1977). According to Zhang *et al*. (2011), who studied five bermudagrass varieties, photochemical efficiency decreased significantly (by 0.59 percentage points) after 28 days of cold acclimation at 8/4 °C. This could be because bermudagrass leaf tissues age more quickly in low temperatures than cool-season grasses.

Amino acids and amide metabolism

Proline is a well-studied amino acid involved in plant responses to various abiotic stresses, including freezing stress. As a hydrophilic molecule, proline helps stabilize cellular membranes during dehydration by forming hydration shells around proteins, nucleic acids, and membranes (Hoekstra *et al*., 2001). Additionally, proline is believed to regulate activation of the pentose phosphate pathway, which contributes to the biosynthesis of phenolic compounds, including antioxidants (Shetty & Wahlqvist, 2004). During cold acclimation, warm-season turfgrasses sustain elevated proline levels (Cai *et al*., 2004; Zhang *et al*., 2006; Patton *et al*., 2007; Zhang *et al*., 2011; Manuchehri & Salehi, 2014). Compared with freezing-sensitive cultivars, stolons of freezing-tolerant bermudagrass cultivars showed greater proline deposition (Munshaw *et al*., 2006; Zhang *et al*., 2006; Zhang *et al*., 2011).

Esmaili & Salehi (2012) also found that the proline content of leaves in both growth chamber and field experiments increased noticeably in response to reduced temperature and light duration in common

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bermudagrass. Zhang *et al*. (2006) reported that proline content increased with decreasing temperature, whereas Patton et al. (2007) reported the opposite for *Zoysia* spp. In an experiment on native Iranian cold-tolerant accessions of common bermudagrass, the most cold-tolerant accessions at -15 °C were recognized as Taft, Naein, and Malayer. This further supports identifying cold-tolerant *Cynodon dactylon* accessions as the most tolerant genotypes (Table 1). Regarding the great variation in freezing tolerance among common bermudagrass, the most tolerant genotype showed higher levels of proline, protein, antioxidant enzymes, visual quality, and chlorophyll content. Cold-sensitive accessions showed more severe cell membrane damage (EL) under cold stress conditions (Akbari & Salehi, 2018). These findings correlate with increased EL, physiological responses, and antioxidant enzyme activity (Table 1).

Antioxidant enzyme activity

As temperatures fall below optimal levels, key metabolic pathways can be disrupted, often resulting in energy imbalances. This stress condition also promotes the accumulation of reactive oxygen species (ROS), which can cause oxidative damage to lipids, proteins, and nucleic acids (Mittler *et al*., 2004). In response, plants activate both enzymatic and non-enzymatic antioxidant systems, which play a vital role in counteracting ROS-induced damage. Increased antioxidant enzyme activity is a key biochemical response to cold stress (Table 1). Enhanced antioxidant activity has been associated with greater cold tolerance and improved survival in several plant species under low-temperature stress (Janda *et al*., 2003). Akbari & Salehi (2018) found that antioxidant activity, particularly CAT and SOD, increased as the temperature decreased from 24 °C to 0 °C in common bermudagrass. Scavenging enzymes also directly affect turfgrass cold-season tolerance and improve plant defense mechanisms, but their exact role requires further investigation.

Malondialdehyde (MDA) and H_2O_2 are produced by lipid peroxidation of plants under chilling stress (Leshem, 1987; Wise & Naylor, 1987). The aforementioned indices are critical during low-temperature stress and damage in plants (Xu *et al*., 2006) so that higher tolerance to cold stress was somehow correlated with higher levels of MDA and H_2O_2 in common bermudagrass and tall fescue (Manuchehri & Salehi, 2014). Xuan *et al*. (2013) reported that the cold-tolerant 'Meyer' Zoysiagrass has greater ROS-scavenging ability, more abundant energy supply, and increased photosynthesis and protein synthesis than the cold-sensitive 'Diamond' cultivar.

Shade Stress

Physiological, and biochemical responses

Low-light stress is a common limiting factor for maintaining high-quality grass in urban areas, where most trees, shrubs, and even buildings restrict light penetration (Lazowski *et al.*, 2020). Shade causes individual differences and morphological changes. In shaded conditions, turfgrass shows various morphological changes, such as reduced root numbers and tillering, shorter rhizomes, taller, thinner stems, longer internodes, lighter color and thinner leaves, flatter leaf angles, and slower growth. Wider leaves are an anatomical response to compensate for low net photosynthesis under shade stress (Baldwin *et al.*, 2007)

Shade stress is a limiting factor in turfgrass landscapes. Establishing turfgrass in shaded conditions presents many obstacles, so a low-light regime would ultimately affect turfgrass growth and responses to management techniques. Managing turfgrass in shade is challenging for golf course managers and gardeners. The use of turfgrass for indoor sports facilities has accelerated, and this has led to the development of strategies for turfgrass management when faced with reduced irradiance (Malik *et al*., 2014). Low light can significantly reduce turfgrass quality and cause serious delays in plant growth and development (Yang *et al*., 2014).

Warm-season grasses are generally shown to be less shade-tolerant than cool-season grasses. Bermudagrass is relatively heat- and drought-tolerant but has poor shade tolerance. Zoysiagrass (*Zoysia* spp.) is a heat-tolerant turfgrass that outperformed bermudagrass in the shade. St. Augustinegrass

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(*Stenotaphrum secundatum*) is relatively shade-tolerant among warm-season turfgrasses (McBee & Holt, 1966; Lin *et al*., 2001; Trappe *et al*., 2008; Wherley *et al*., 2011; Malik *et al*., 2014).

Turf quality and morphological characteristics

Low-light stress is a prevalent challenge for maintaining high-quality turfgrass in urban environments, where light availability is often obstructed by trees, shrubs, or buildings (Long *et al*., 2022). Shaded conditions create significant variation among individuals and drive morphological adaptations. In shade, turfgrasses exhibit a range of structural changes, including reduced root and tiller numbers, shorter rhizomes, longer, thinner stems, increased internode length, paler, narrower leaves, more horizontal leaf orientation, and slower overall growth (Koh *et al*., 2003; Baldwin *et al*., 2007).

All turfgrass species showed diminished TQ under high shade, as shown by increased weak, succulent vertical growth and a less dense turf sward (Tegg & Lane, 2004). Wherley *et al*. (2011) evaluated the comparative performance of zoysiagrass (*Zoysia* spp.) cultivars under natural shade (89%). Their findings showed that turfgrass quality declined significantly shortly after introduction to a heavily shaded environment. Nevertheless, certain cultivars performed satisfactorily, including 'Royal', 'Zorro', and 'Shadow Turf'. This study indicates that *Z. matrella* may adapt better to heavily shaded environments with conserved inputs than *Z. japonica*. In a separate investigation conducted by Sladek *et al*. (2009), *Zoysia* spp. 'Shadow Turf' and 'Diamond' showed satisfactory increases in lateral spread and moderate TQ 12 weeks post-planting under 50% shade. Nevertheless, zoysiagrass genotypes under 90% shade performed poorly, resulting in limited turfgrass cover and reduced aesthetic quality. The superior turfgrass quality of 'Shadow Turf' and 'Diamond' received ratings of 4.7 and 3.7, respectively, in 2006, and 5.3 in 2007, twelve weeks post-planting, when cultivated under 90% shade.

Leaf elongation and grass coverage decreased under shade compared to full sunlight in perennial ryegrass (Van Huylenbroeck & Van Bockstaele, 2001). In another study, (Malik *et al*., 2014) reported that under sunny conditions, the color of the turfgrass varieties ranged from light to dark green in hue in all months, with the maximum (8.2) quality scores for the bermudagrass 'Fine Dacca' and minimum scores (6.40) for the local ecotype 'Khabbal' in November, and cv. 'Fine Dacca' had the minimum quality scores (3.6) in January. They indicated that shade influences stolon diameter. Their results revealed that Bermudagrass cultivar 'Fine Dacca' performed better under sunny conditions, whereas Zoysiagrass cultivar 'Korean' performed better under shady conditions.

Physiological changes

Chlorophyll content and photosynthesis

Under high-light conditions, chlorophyll a (Chl a) and chlorophyll b (Chl b) levels generally remain stable in turfgrass. However, low-light exposure significantly reduces both pigments. For instance, in 'TifSport' hybrid bermudagrass and 'Sea Isle 1' seashore paspalum, Chl a and Chl b contents decreased by about 34–36% compared to their respective levels under high-light conditions (Jiang *et al*., 2005).

Jiang *et al*. (2005) indicated that photochemical efficiency (F_v/F_m) remained constant under low light in 'Sea Isle 1' and 'TifSport'. In terms of pigment ratios, the chlorophyll a/b ratio was not significantly affected by low light in 'Sea Isle 1', indicating a stable pigment balance under shade. In contrast, 'TifSport' exhibited an increase in the chlorophyll a/b ratio under low light, surpassing the values observed under high light, suggesting a shift in pigment composition as a possible acclimation response to shading stress (Jiang *et al*., 2005). Guo *et al*. (2022) investigated shade tolerance in two turf-type bermudagrass cultivars from China, Yangjiang (prostrate form) and Guanzhong (upright form), under 0%, 30.4%, 61.2%, and 90.6% shade. Yangjiang showed superior shade tolerance, maintaining higher turf quality, growth rate, chlorophyll a/b ratio, and enzyme activity (SOD, POD, CAT) compared to Guanzhong under high shade (90.6%). Although both showed reduced photochemical efficiency under shade, Yangjiang was less affected.

Jespersen & Xiao (2022) used chlorophyll fluorescence rapid light curves (RLCs) to compare the photosynthetic responses of hybrid bermudagrass 'Tifway' and Japanese lawngrass 'El Toro' under

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high and low light. While F_v/F_m remained stable, El Toro showed consistently higher values. Tifway had higher photosynthesis and respiration under high light, but El Toro was more efficient at capturing light under low irradiance. These results suggest species-specific photoacclimation strategies, and while RLCs don't replace CO_2-based measurements, they offer useful insight into photosynthetic adjustments under varying light conditions.

Photochemical efficiency

Photochemical efficiency, expressed as the F_v/F_m ratio, represents the maximum quantum efficiency of photosystem II (PSII) photochemistry and is widely used as an indicator of plant photosynthetic performance (Trinh & Masuda, 2022). Researchers have investigated photochemical efficiency responses to shade stress in several warm-season turfgrasses, including seashore paspalum and bermudagrass (Jiang *et al*., 2005). According to Jiang *et al*. (2005), F_v/F_m values remained stable under low light conditions in both 'Sea Isle 1' seashore paspalum and 'TifSport' hybrid bermudagrass. This stability suggests that both shade-tolerant and shade-sensitive turfgrass species can maintain similar PSII quantum yields across light intensities.

Wang *et al*. (2024) explored how bermudagrass adjusts its photosynthetic processes in response to different levels of shade, aiming to understand shade tolerance rather than shade avoidance. Under mild shade, chlorophyll b and the expression of light-harvesting complex (LHC) genes increased, while severe shade increased chlorophyll a, carotenoids, and components involved in photosynthetic electron transport. Shade conditions influenced leaves and roots differently, with variations in soluble sugar content. Additionally, shading reduced the expression of nitrogen-assimilation-encoding genes and decreased antioxidant enzyme activities (SOD, POD, CAT) in leaves, whereas these activities were elevated in roots (Wang *et al*., 2024). Overall, the study revealed that increasing shade levels significantly alters photosynthetic energy conversion and metabolic processes, offering new insights into how warm-season C_4 grasses acclimate to shaded environments.

Biochemical responses

Carbohydrate content

Turfgrass exposed to low light produces fewer carbohydrates because photosynthesis declines and it lacks the energy needed for leaf regrowth when frequently mowed. As a result, both non-structural carbohydrate reserves and photosynthetic efficiency decline significantly under shade (Jespersen *et al*., 2025). The balance between photosynthesis and respiration (Pn: Rd) plays a key role in shade tolerance. A low Pn: Rd ratio under stress can deplete carbohydrate reserves and hinder recovery and growth (Jespersen *et al*., 2022). Similarly, Qian & Engelke (1997) reported a 58% reduction in total non-structural carbohydrates in 'Diamond' zoysiagrass under 86% shade, resulting in poor turf density.

Zhang *et al*. (2016) assessed how zoysiagrass cultivars adapt to shade by examining growth traits and biomass allocation. In greenhouse trials, greater plasticity in leaf extension was linked to higher biomass and better turf quality under shade. Zoysiagrass cultivars responded differently in turf quality, growth, and biomass under different light levels. Most maintained acceptable quality up to 61% shade, but Cavalier, Zeon, Zorro, and BA-189 performed poorly. Under 90% shade, JaMur, Empire, El Toro, Palisades, and BA-305 performed best with minimal quality loss.

Combined Stresses

Morpho-physiological and biochemical responses

In arid areas, limited freshwater availability has led to increased reliance on groundwater for irrigation. However, this has caused soil salinity, structural degradation, and reduced crop yields, as excess salts hinder root water uptake and lead to water stress (Huang *et al*., 2014).

Salinity and Drought Stress

Because most arid and semi-arid regions have limited water quantity and quality, municipal wastewater can serve as a valuable source for irrigating turfgrass. To evaluate the potential of treated municipal wastewater for irrigating bermudagrass, the study focused on how different salinity levels affect turf

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performance. Researchers compared three irrigation treatments based on the water's electrical conductivity (EC): potable water (ECw = 0.3 dS m^{-1}), moderately saline water (ECw = 1.6 dS m^{-1}), and higher-salinity wastewater (ECw = 2.4 dS m^{-1}). Results showed that turfgrass yield increased with higher irrigation rates, but the growth response was slightly reduced under higher salinity conditions. The study highlights that wastewater, which contains essential nutrients such as K, can serve as a viable alternative to potable water for turf irrigation. However, elevated salinity levels in the wastewater may limit its effectiveness (Beltrão *et al*., 2014). Additionally, the interaction of salinity and drought stresses significantly influenced these 3 characteristics, with an 84% reduction in chlorophyll content observed in plants irrigated at 8-day intervals with the most saline water. A similar report also reported reduced chlorophyll content in *Paspalum vaginatum* Sw. when plants were irrigated with saline water (50 dS m^{-1}) (Lee *et al*., 2008).

Heat and Drought Stress

Plants mitigate heat stress by dissipating heat through transpiration, a process that requires stomatal opening. However, under combined heat and drought stress, stomatal closure to conserve water results in reduced transpiration and consequently higher leaf temperatures (Rizhsky *et al*., 2002). Moreover, a two-year study evaluated whether foliar application of a seaweed extract–based biostimulant (Utilize®) could enhance heat- and drought-stress tolerance in ultradwarf bermudagrass. The results demonstrated that foliar treatments significantly improved turf quality, leaf color, chlorophyll and carotenoid concentrations, and net photosynthetic rate under stress conditions. In addition, nitrate reductase activity increased markedly, indicating enhanced nitrogen metabolism. Root morphological traits, including root biomass, length, surface area, volume, and root viability, also improved significantly compared with the untreated control (Zhang *et al*., 2022). Overall, the findings suggest that application of a seaweed extract–based biostimulant mitigates heat- and drought-induced damage by enhancing photosynthetic performance, nitrogen metabolism, and root growth and function in ultradwarf bermudagrass.

Salinity and pH Stress

Ye *et al*. (2021) demonstrated that alkali stress, a combination of salinity and high pH, severely affects *C. dactylon*, partly due to an imbalance in carbon metabolism and starvation; consequently, plants tend to accumulate carbohydrates rather than consume them. Metabolomic analysis showed that 37 metabolites were regulated, of which 15 metabolites belong to the amino acid and carbon metabolic pathways (Ye *et al*., 2021).

Salinity and Cold Stress

Taher *et al*. (2023) investigated the response of two warm-season turfgrasses, seashore paspalum (*Paspalum vaginatum* Sw.) and Tifway bermudagrass (*Cynodon transvaalensis* Burtt Davy × *C. dactylon*), to combined cold and soil salinity stress, a scenario common in winter in arid and semi-arid regions. Over two field seasons, the researchers applied foliar sprays of organic (humic acid) and inorganic (ferrous sulfate and two silicon sources) amendments to assess their ability to mitigate stress damage. The results showed that seashore paspalum exhibited greater tolerance to combined stresses than Tifway bermudagrass, maintaining higher vegetative growth, chlorophyll content, nutrient uptake, and turf quality. Among the amendments, ferrous sulfate and humic acid were most effective, significantly improving plant height, leaf dry weight, root length, and visual turf color and density. While silicon treatments also showed positive effects over the control, their impact was less pronounced, potentially due to the high application doses used (Taher *et al*., 2023). This research provides practical evidence that foliar applications of ferrous sulfate and humic acid can effectively sustain warm-season turfgrass growth and quality during cold periods on salt-affected soils, addressing a critical need for turf managers in challenging environments.

Shade and Drought Stress

Chhetri *et al*. (2022) investigated the combined effects of shade and drought stress on the physiological responses of bermudagrass and hybrid bermudagrass cultivars in greenhouse conditions. Three

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cultivars, Latitude 36, Celebration, and Patriot, were grown in growth tubes and exposed to two irrigation levels (well-watered and drought) under two light conditions (adequate and low). Results showed that under drought stress, low light caused a gradual decline in ET, while adequate light led to a sharper decline. The cultivar 'Patriot' used the most water under adequate light. Still, under low light, it showed the lowest water use when well-watered, indicating that shade tolerance may influence drought response in shaded conditions (Chhetri *et al*., 2022). The study also evaluated the effects of combined drought (50% water deficit) and shade (50%) on 13 bermudagrass genotypes collected along longitudinal and latitudinal gradients. Significant genotypic variation was observed, with high-latitude genotypes showing greater tolerance, while longitudinal differences were less distinct. The results provide insight into selecting stress-tolerant bermudagrass accessions under combined environmental stresses (Noor *et al*., 2026).

Conclusions

Over the past three decades, researchers have examined the morphological, physiological, and biochemical responses of various turfgrass species to major abiotic stresses, including drought, salinity, heat, cold, and shade (Table 1). These studies reveal that 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.

Given the increasing impacts of global climate change and environmental instability, there is a growing need to develop turfgrass cultivars with enhanced abiotic stress tolerance. However, because turfgrass anatomy and genetics are complex, introducing stress-tolerance traits from distantly related species is not feasible. Instead, a thorough understanding of grass-specific stress responses, especially in naturally tolerant species, is essential for identifying candidate genes, proteins, metabolites, and molecular markers to support breeding programs. Such information is fundamental for molecular breeding and marker-assisted selection aimed at improving the stress resilience of turfgrass germplasm.

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 mechanisms of cross-tolerance. In this review, by compiling and synthesizing fragmented data spanning decades, we aimed to provide a clearer foundation for species-specific warm-season turfgrass management and to support breeding strategies aligned with the challenges of modern turfgrass cultivation. The complexity of turfgrass stress responses reflects the integration of multiple physiological, biochemical, and morphological mechanisms operating across different temporal and spatial scales. While drought stress relies on osmotic adjustment as its primary defense, salinity stress activates antioxidant systems, heat stress triggers shifts in resource allocation between roots and shoots, cold stress prioritizes chlorophyll retention, and shade stress reveals a fundamental divergence between tolerance and avoidance strategies (Fig. 2).

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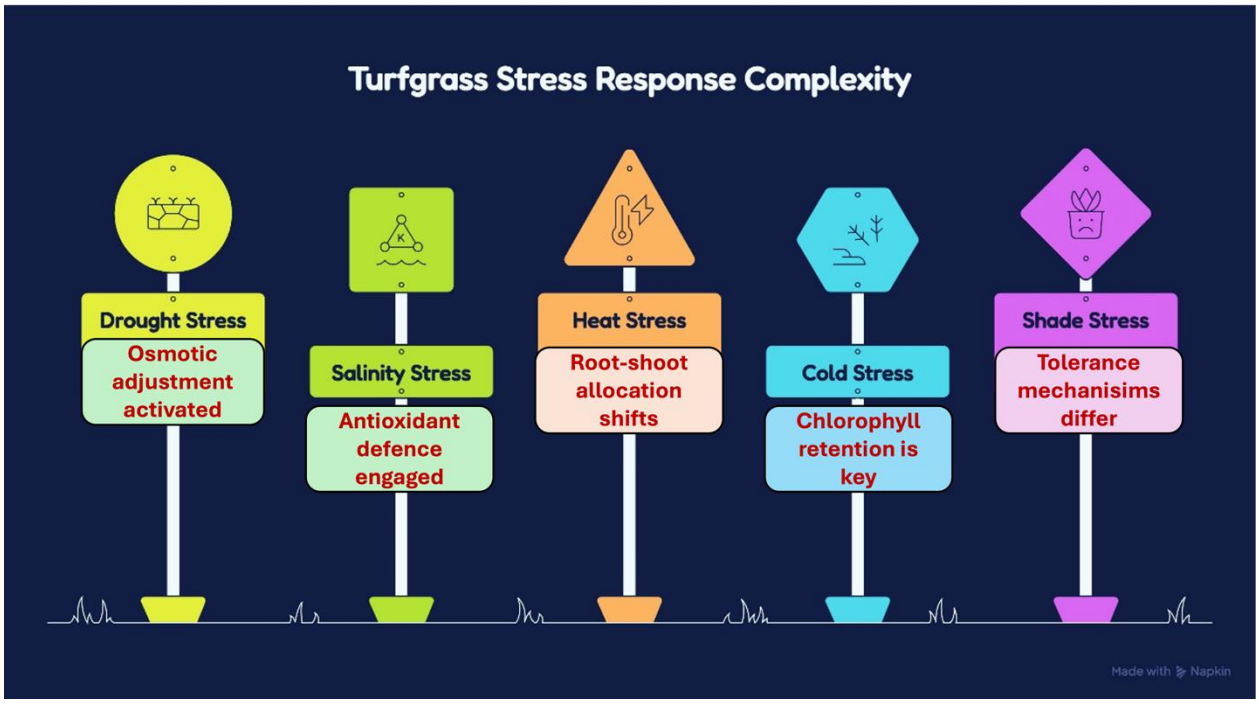

Figure 2. Differential activation of primary tolerance mechanisms in turfgrasses across five major abiotic stresses.

Understanding these distinct physiological signatures is essential for developing targeted management strategies and effective breeding programs. Maintaining turf quality under increasingly stressful environmental conditions requires a comprehensive understanding of stress responses and integrated approaches that recognize both shared mechanisms and stress-specific adaptations that define turfgrass performance.

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