Review

Mechanisms of Environmental Stress Tolerance in Turfgrass

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Abstract: Turfgrasses constitute a vital part of the landscape ecological systems for sports fields, golf courses, home lawns and parks. However, turfgrass species are affected by numerous abiotic stresses include salinity, heat, cold, drought, waterlogging and heavy metals and biotic stresses such as diseases and pests. Harsh environmental conditions may result in growth inhibition, damage in cell structure and metabolic dysfunction. Hence, to survive the capricious environment, turfgrass species have evolved various adaptive strategies. For example, they can expel phytotoxic matters; increase activities of stress response related enzymes and regulate expression of the genes. Simultaneously, some phytohormones and signal molecules can be exploited to improve the stress tolerance in turfgrass. Generally, the mechanisms of the adaptive strategies are integrated but not necessarily the same. Recently, metabolomic, proteomic and transcriptomic analyses have revealed plenty of stress response related metabolites, proteins and genes in turfgrass. Therefore, the regulation mechanism of turfgrass's response to abiotic and biotic stresses was further understood. However, the specific or broad-spectrum related genes that may improve stress tolerance remain to be further identified. Understanding stress response in turfgrass species will contribute to improve stress tolerance of turfgrass.

Keywords: turfgrass; abiotic stress; biotic stress; stress response; plant physiology; phytohormone

1. Introduction

With rapid economic development and advancing urbanization, the ecology of habitats, especially urban areas, has become a central concern for the government and scientists [1]. The application of turfgrass in urban gardens and green spaces is an environmentally friendly way to alleviate the problem due to their cost-effectiveness and higher stress tolerance than that of other plants [2]. Turfgrass consists of warm-season species adapted to tropical and subtropical climates, such as bermudagrass (*Cynodon dactylon* Pers.), Buffalograss (*Buchloe dactyloides* Engelm), Bahiagrass (*Paspalum notatum* Flugge), and zoysiagrass (*Zoysia japonica* Steud), unlike cold-season species, which are adapted to temperate and subarctic climates such as perennial ryegrass (*Lolium perenne* L.), tall fescue (*Festuca arundinacea* Schreb.), fine fescue (*Festuca rubra*), creeping bentgrass (*Agrostis palustris* Huds.), colonial bentgrass (*Agrostis*

capillaris L.), velvet bentgrass (*Agrostis canina* L.) and Kentucky bluegrass (*Poa pratensis* L.). At present, turfgrass is widely used in home lawns, sports fields, golf courses, parks and commercial landscapes, all of which form important constituent of landscape ecological systems in urban and suburban areas.

Unlike animals, plants are sessile; hence, they are usually threatened by adverse environmental conditions throughout their life cycle. In particular, the growth and development process of turfgrass is affected by different kinds of biotic and abiotic stresses such as salinity, drought, water, cold, heat, pests and diseases [3–7]. The germination rate of seeds, growth and development of seedlings and photosynthetic process of leaves in turfgrass are inhibited under these stress conditions [8–10]. Moreover, plasma membrane stability and content of reactive oxygen species (ROS) are affected by sudden changes in habitat. [11,12]. Over millions of years of evolution, plants have developed integrated strategies to adapt to these sudden harsh conditions, e.g., the activities of antioxidant enzymes are increased under stressful conditions [13]. The different ways of using luminous energy between C₃ and C₄ turfgrass species is also involved in alleviation of stress-induced damage [14]. Improving the stress tolerance of turfgrass is critical for the turfgrass industry as well as for environmental sustainability in urban and suburban areas. Thus, it is urgent to investigate the physiological and molecular mechanisms of stress responses in turfgrass species.

Great progress has recently been made in turfgrass stress tolerance, for instance, several compounds have been found to be involved in stress resistance improvement in bermudagrass [15]. This article provides an extensive overview of the current understanding of changes in physiology, metabolism, relative gene expression, and growth/development of turfgrass under different kinds of biotic and abiotic stresses. In addition, suggestions to improve the stress tolerance of turfgrass are also presented. This review can contribute to better understanding the mechanisms of turfgrass species' response to environmental stresses and the progress of studies focusing on stress response in turfgrass in recent years.

2. Response of Environmental Stresses in Turfgrass

2.1. Chemical Stress

2.1.1. Salt Stress

Salinity is a major abiotic stress limiting the distribution of plants around the globe [16]. Growth, development and metabolic processes are inhibited or disrupted in plants under salt stress condition. Generally, the detrimental effects of salinity are due to water loss of cells induced by high osmotic pressure as well as ion toxicity due to a disruption in the K⁺/Na⁺ homeostasis [17]. Responses to salt stress in turfgrass have been extensively investigated. Like other plants, growth and development of turfgrass are limited or inhibited by salinity stress. For example, the leaf elongation rate of tall fescue, shoot growth of seashore paspalum (*Paspalum vaginatum*), shoot and root growth of bermudagrass, and shoot growth of Kentucky bluegrass were all significantly inhibited by salt stress [18–20]. It is well known that the plant growth process refers to cell production and elongation. In tall fescue, the production and elongation of cells was dramatically inhibited by salt stress [20]. This result can also be used to explain growth inhibition in other turfgrass species with medium salt tolerance level. Turf quality (TQ) is an integrated evaluation index that depends on some individual components which refer to aesthetic and functional aspects of turfgrass. So TQ can be used to assess the apparent traits of turfgrass, and in Kentucky bluegrass, the TQ decreased significantly after exposure to salinity [21]. The alterations of morphological characteristics of turfgrass under stressful conditions are derived from the changes of physiological traits such as cell membrane stability and ROS content. Therefore, in order to investigate the salt stress response mechanisms in turfgrass, studies focusing on physiological and molecular mechanisms were conducted. It was reported that malonyldialdehyde (MDA) content and electrolyte leakage (EL) increased by NaCl in perennial ryegrass and Kentucky bluegrass [21–23], that indicated the cell membrane was damaged. Simultaneously, hydrogen peroxide (H₂O₂) and singlet oxygen (O₂^{•−}) concentration increased dramatically in perennial ryegrass and Zoysiagrass after salt stress treatment [23–25]. Negative effects of salt stress were also found within the chlorophyll (Chl),

including Chl *a* and Chl *b* in centipedegrass (*Eremochloa ophiuroides* (Munro) Hack.) [26]. This implies that the photosynthetic process was probably affected by salt stress via inducing Chl decomposition in turfgrass leaves. Furthermore, the Chl biosynthesis process is likely inhibited by long term salt exposure. Chlorophyll is an essential factor of the photosystem. The thylakoid membrane is sensitive to stress conditions, and hence the photosystem of the turfgrass can be affected by salt stress. In tall fescue there was not only distinct degradation of grana and the thylakoid, but also a decline in the quantum yield in photosystem II (PSII) was also detected [27]. A further investigation of PSII with the JIP-test method in perennial ryegrass and seashore paspalum (*Paspalum vaginatum* Swartz cv. 'SeaSpray') revealed that quantum yields, efficiencies and energy fluxes were compromised after salt stress treatment [28,29].

Sodium ion toxicity is a typical effect produced by salt stress, especially NaCl stress. A vast amount of Na⁺ accumulated in plants could induce ionic imbalance in the cells. There are two major strategies for plants to cope with salt stress-induced damage. They include: (i) salt excretion with salt glands via specialized epidermal cells; and (ii) salt avoidance by the root system. In seashore paspalum, which is known as one of the most salt tolerant turfgrasses, decreased amplitude of K⁺ concentration was higher in roots than in shoots. Meanwhile, increased amplitude of Na⁺ concentration was remarkably higher in roots than in the shoots [19]. This result suggested that the salt tolerance strategy of seashore paspalum was via maintaining high K⁺ concentration in the shoots and repressing Na⁺ transference from roots to shoots when exposed to salt stress. In bermudagrass, in addition to higher K⁺ concentration in shoots, Na⁺ exclusion from the surface of leaves was also observed under salt stress [30]. The results implied that unlike seashore paspalum, bermudagrass preferred the strategy of Na⁺ exclusion to withstand salt stress. However, in salt sensitive turfgrass species, such as Kentucky bluegrass, Na⁺ concentration accumulated rapidly and other ion concentrations including K⁺, Ca²⁺ and Mg²⁺ were decreased in response to salt stress [31]. This result revealed that salt stress can induce severe disruption of the ion metabolism in salt sensitive turfgrass species.

To deal with harsh environmental conditions, plants have evolved an integrated defense system. The antioxidant system is well investigated for plants under stressful conditions. The activities of superoxide dismutase (SOD), catalase (CAT), peroxidase (APX) and glutathione reductase (GR) were increased in Kentucky bluegrass and tall fescue under salt stress condition [32]. Similar results were observed in desert wheatgrass (*Agropyron desertorum* L.) and tall wheatgrass (*Agropyron elongatum* L.) [13,33]. The function of oxidant enzymes is to scavenge the ROS generated in plant cells. Hence, high oxidant enzyme activity implies enhanced salt stress tolerance. In addition, phytohormones regulate many kinds of bioprocesses in plants, one being the salt stress response. It was reported that abscisic acid content (ABA) increased whereas indole-3-acetic acid (IAA), trans-zeatin riboside (ZR), and isopentenyl adenosine (iPA) were decreased in Kentucky bluegrass [34]. However, changes in hormonal content in cultivars of creeping bentgrass (*Agrostis stolonifera*) were different from that in Kentucky bluegrass. After salt stress treatment, ABA, ZR, IAA, jasmonic acid (JA), salicylic acid (SA), and ethylene were accumulated significantly in creeping bentgrass [35]. In addition to phytohormones, other metabolites were altered by salt stress. Polyamines such as putrescine (Put) and spermine (Spm) concentrations increased in creeping bentgrass under salt stress [36]. Moreover, proline content also showed an increasing trend in bermudagrass and Kentucky bluegrass after salinity treatment [18]. Polyamines are protective substances in plant cells, and proline can regulate the osmotic pressure of the cell, hence water loss is prevented. Recently, a number of nutrient elements, signaling molecules and metabolites were reported to improve salt tolerance of turfgrass. It is reported that sulfur is not only an important plant macronutrient; but it can also alleviate the damage induced by salt stress in Kentucky bluegrass [37]. Additionally, application of exogenous polyamines such as spermidine could improve salt stress tolerance in Kentucky bluegrass and zoysiagrass [25,31]. Some hormones such as epibrassinolide, salicylic acid and glycinebetaine could enhance the salt tolerance of weeping alkaligrass (*Puccinellia distans*) tall fescue, perennial ryegrass and Kentucky bluegrass [38–42]. Ethylene is a negative regulating hormone in the plant stress response pathway, and its suppression can protect

perennial ryegrass against salt stress [43]. Moreover, signal molecules such as Ca^{2+} and nitric oxide are reportedly involved in improving salt stress tolerance of turfgrasses including tall fescue, bermudagrass, and sheep fescue (*Festuca ovina* L) during the early growth stage [44,45]. Recently, the fungus *Aspergillus aculeatus* is reported to play a protective role on perennial ryegrass and bermudagrass under salinity condition [29,46]. Turfgrass species can be C_3 and C_4 according to their photosynthetic pathways. Generally, C_4 grasses have a higher efficiency of CO_2 utilization [47]. Yu et al. (2015) reported that a relatively high atmospheric CO_2 concentration contributed in alleviating salt-stress-induced physiological damages in bermudagrass (cv. 'Tifway'), a C_4 grass species [14]. This research also suggested a new method to improve salt tolerance of turfgrass.

The salt stress tolerance of different turfgrass species or cultivars can vary [48]. Investigating the salt stress response at the molecular level is a possible way to further understand salt tolerance mechanism of bermudagrass. Transcriptome profilings of Kentucky bluegrass, zoysiagrass, and salt couch grass (*Sporobolus virginicus*) have been analyzed comprehensively, and a number of candidate unigenes related to salt stress responses were identified [49–51]; putatively, a total of 36,587, 1455 and 8340 differentially expressed genes were detected for these species, respectively. Functional annotation indicated that the detected genes were related to transcription factors, processes and pathways such as oxidation-reduction process, ion transport and ROS scavenging. In bermudagrass, a total of 43 differentially expressed miRNAs and putative target genes related to salt stress responses were predicted [52]. Simultaneously, proteomic analyses revealed 1893 putative differentially expressed proteins in *Carex rigescens* that were related to salt stress response as well as a range of other biological processes [53]. A small heat shock protein AsHSP17 was identified in creeping bentgrass that was involved in salt stress response [54]. A *ZmVP1* identified in zoysiagrass could restore the salt tolerance of transgenic *Arabidopsis* [55], while *ZjGRP* could induce salt sensitivity in transgenic plant [56]. These remarkable investigations have provided further insights into molecular mechanisms of salt stress response of turfgrass.

Salt stress is an important environmental factor that affects the growth and development of turfgrass. Salt stress response is also a research hotspot in crop science. In turfgrass, many salt stress response related genes were identified. The functions and regulation pathways of these genes in specific turfgrass species is needed to be study further in the future. In addition, the difference of salt stress response between C_3 and C_4 turfgrass species is an interesting research direction, it should be investigated further in the future.

2.1.2. Heavy Metal Stress

With industrial development, heavy metals including copper (Cu), cadmium (Cd), arsenic (As) and lead (Pb) are released from the minerals into the soil, and their high accumulation can induce environmental stress in plants. Thus, heavy metal stress is of particular concern in urban and suburban areas [57]. Literature on the response of turfgrass to heavy metal stress has also progressed in recent years. It has been proved that heavy metals can induce unprecedented damage and affect metabolic processes in turfgrass. According to studies, a dramatic inhibition of root growth was detected in tall fescue and perennial ryegrass after Cu treatment [58]. The cellular membrane system of turfgrass was damaged because of elevated MDA content and electrolyte leakage [58,59]. When exposed to Pb stress, the activities of antioxidant enzymes were increased and their corresponding genes were up-regulated in tall fescue [60]. Generally, ROS bursts will occur in plants under severe conditions. For example, H_2O_2 and O_2^- were significantly accumulated in bermudagrass under Cd stress [59]. Hence, the protection mechanisms such as the antioxidant system were triggered, resulting in the increase of antioxidant enzyme activity. The activities of APX, dehydroascorbate reductase (DHAR) and GR were increased in Kentucky bluegrass (*Poa pratensis*) seedlings after Cu stress treatment [61]. However, certain concentrations of heavy metals could improve the growth of fescue and perennial ryegrass [62]. Heavy metal stresses not only induce physiological damage, but also inhibit germination and growth of turfgrass. For example, Cu stress can sharply reduce the germination of perennial ryegrass and red fescue, while other heavy metals including zinc and cobalt can inhibit the seedling growth of these

two turfgrass species [63]. However, the mechanism of heavy metal stress response in turfgrass is not well understood. Recently, a number of differentially expressed genes associated with Pb stress response were detected in tall fescue, and further analysis revealed that the genes were related to the metabolism of energy, terpenoids, polyketides and carbohydrate pathways [64]. In particular, four key transcription factors such as WRKY, bZIP, ERF and MYB identified in creeping bentgrass (*Agrostis stolonifera*) were found to play crucial roles in Cd stress response [65].

To improve the heavy metal stress tolerance of turfgrass, several investigations were conducted in recent years. It was reported that signal messengers such as NO, hydrogen sulfide (H₂S) and glycinebetaine (GB) play crucial roles in alleviating cadmium and Cu-induced damages in bermudagrass and perennial ryegrass [59,66,67]. Investigation of perennial ryegrass showed that NO could increase Cu accumulation in roots rather than in leaves [68]. Moreover, the rare element cerium (Ce) was reported to improve the copper tolerance of *Poa pratensis* by regulating ascorbate and glutathione metabolism pathways [61]. Furthermore, composted biosolids are beneficial in improving tolerance to many stresses in plants. It was also reported that tolerance to Zn and Cd stresses was remarkably enhanced in turfgrass species after limestone and biosolids compost treatment [69]. Additionally, perennial ryegrass not only displayed a positive result in reducing leaching of heavy metals in the soil, but also enhancing the uptake of heavy metals in municipal waste compost when assisted with ethylenediaminetetraacetic acid (EDTA) [70,71]. This result revealed an available method of heavy metal phytoextraction of turfgrass.

Heavy metal stress response is well studied in other crops such as rice (*Oryza sativa*) [72], and the response mechanisms of heavy metal stress in plants are investigated deeply [73]. But in turfgrass, the signal transduction under heavy metal stress is not clear. Besides, how do the compounds regulate the heavy stress response in the cells of turfgrass to increase the stress tolerance should be studied further in the future.

2.2. Physical Stress

2.2.1. Drought Stress

Drought stress is one of the primary environmental stresses affecting growth and development of plants including turfgrass. Generally, the drought tolerance of turfgrass is diverse both at intra- and interspecies level. An investigation on bermudagrass showed a relatively low stomatal conductance in the superior drought tolerance genotype, and that drought tolerance had no relationship with geographic origins [74]. The indexes of TQ, relative water content (RWC), and electrolyte leakage (EL) were variable in wheatgrass, fescue and bermudagrass, implying an interspecies difference in drought stress tolerance level [75–77]. Similarly, antioxidant enzyme activity, chlorophyll and proline content were variable within tall fescue species [78]. Moreover, evapotranspiration rate, transpiration sensitivity, soluble carbohydrate contents, H₂O₂ content, fatty acid composition and antioxidant enzyme activity under drought stress were variable in different turfgrass species [79–82]. It was reported that the drought tolerance of Kentucky bluegrass was significantly higher than that of perennial ryegrass [83]. Zoysiagrass showed a more extensive root system, higher leaf hydration levels and TQ than that of Kentucky bluegrass when exposed to drought stress [84]. The leaf water potential and stomatal conductance in Kentucky bluegrass under drought stress conditions were remarkably different from that of tall fescue [85]. These distinctions reveal that different turfgrass species employ different strategies to adapt to drought stress. Furthermore, the drought tolerant cultivar of tall fescue showed higher protein, soluble carbohydrate content and lower H₂O₂ content than that of sensitive counterpart [86]. Growth and development processes are inhibited when turfgrass is exposed to drought stress. It was reported that the growth and development of axillary buds and roots of tall fescue were inhibited by drought stress [10,87,88]. The lateral spread of the turfgrass was delayed with the duration of summer dry-down [89]. The germination rate of turfgrass was diminished under drought treatment [90]. Additionally, the physiological traits of turfgrass change under drought stress condition. Dry forage yield, chlorophyll content and RWC of tall fescue were found to decrease; on the

contrary, the carotenoid and proline content increased under drought stress [86]. The photosynthesis, stomatal conductance, Rubisco activity, and nitrogen content of Kentucky bluegrass were severely disrupted by drought conditions [91,92]. It was reported that the activities of APX, peroxidase (POD) and glutathione peroxidase (GPX) in Kentucky bluegrass increased and then decreased with drought stress, but in desert wheatgrass (*Agropyron desertorum*) a continuous increase in activity of these enzymes was detected [93]. Generally, antioxidant enzymes play a protective role in plant stress response, and after long-term drought stress treatment, antioxidant activity including that of APX, CAT and SOD significantly decreased in turfgrass, implying a decrease in the capacity to scavenge ROS [94]. Additionally, an increase of cuticular wax was observed after drought stress treatment in creeping bentgrass [95]. Cuticular wax is a protective barrier preventing water loss to the atmosphere via transpiration. Thus, an increase of the cuticle suggests another available strategy for turfgrasses to defend themselves against drought stress.

Exploring the molecular mechanisms of drought stress response in turfgrass can contribute to improving their drought tolerance in application research. Recently, many candidate genes related to drought tolerance regulation were identified in turfgrass. Almost all of the candidate genes, such as transcriptional factor (TF) genes and biosynthetic enzyme genes, were positively regulating. When overexpressing an *Arabidopsis DREB1A* gene in Kentucky bluegrass, the transgenic plants showed higher drought tolerance than control [96]. Overexpression of the cytokinin synthesizing gene *isopentenyl transferase* in creeping bentgrass resulted in the regulation of expression of several TF genes including *MYB*, *bHLH* and *WRKY*, and drought tolerance was enhanced [97]. A total of 39 proteins related to pathways of photosynthesis, tricarboxylic acid, glycolysis and N-metabolism were identified by Shi et al. (2014) in bermudagrass under drought stress treatment [98]. Similarly, transcription analysis of creeping bentgrass and annual ryegrass showed that plenty of genes were involved in drought response, and the differentially expressed genes were related to energy metabolism, antioxidants, stress defense, photosynthesis and signaling processes [99,100]. Furthermore, a dehydrin gene in bermudagrass *CdDHN4* was obtained, which was regulated by an ABA-dependent signaling pathway to enhance the drought tolerance of bermudagrass [101]. In addition, a number of quantitative trait loci (QTL) related to drought stress were identified in creeping bentgrass [102]. These genes and QTL contributed to further investigations to understand drought stress response in turfgrass.

It has been confirmed that the concentration of molecules such as phytohormones and signaling molecules play crucial roles in increasing drought tolerance of plants. Drought-induced leaf senescence in creeping bentgrass was alleviated significantly by exogenous melatonin. [103]. Nitric oxide is an essential signaling molecule in both plants and animals. It has been reported that NO is involved in improving drought tolerance of turfgrass by increasing the activities of antioxidant enzymes [104–106]. Hormonal regulation pathways in turfgrass are usually rather complex. For example, abscisic acid could improve the drought tolerance of bermudagrass via the NO signaling pathway [104]. Application of plant growth regulators (PGRs) including trinexapac ethyl, paclobutrazol and abscisic acid alleviated damages induced by drought stress and increased antioxidant enzyme activity in Iranian perennial ryegrass and bermudagrass [107,108]. Meanwhile, trinexapac ethyl could not only increase the contents of other hormones such as ABA, IAA, JA and SA in Kentucky bluegrass, but also improved the TQ and photochemical efficiency of seashore paspalum under drought stress [109,110]. Application of exogenous polyamines could significantly improve the membrane stability, TQ, RWC, and photosynthetic efficiency of creeping bentgrass after drought stress treatment [111–113]. Besides hormones and signaling molecules, some nutritional elements play major roles in protecting turfgrass from drought stress-induced damages. In Kentucky bluegrass, perennial ryegrass and zoysiagrass, the application of silicate alleviated the physiological changes under drought stress [92,114–116]. In addition, elevated CO₂ level is involved in increased drought stress tolerance of tall fescue by the regulation of photosynthesis and hydration in leaves [117]. It was reported that drought tolerance was also enhanced by biosolids in tall fescue and Kentucky bluegrass. According to the research, the beneficial effects of biosolids are mainly due to growth regulation factors rather than the mineral

nutrients [118,119]. The application of super absorbent polymers (SAPs) is another way to improve the drought tolerance of turfgrass. The function of SAPs is to prevent water loss of the soil. After treatment with potassium polyacrylate (K-PAM) in bermudagrass, the damage induced by drought stress was remarkably mitigated [120].

Drought stress is a major environmental stress for turfgrass. However, the mechanisms of drought stress response at molecular level is not very clear, although there are some drought related genes are identified. The function and the regulation pathways of the genes are not very clear and should be studied further in the future. Besides, some phytohormones are reported to contribute to increasing drought stress tolerance. However, how to use them in commercial production is a problem that should be solved in the future.

2.2.2. Flooding Stress

Flooding stress, which includes waterlogging and submergence, is induced by frequent and heavy rainfall or over-irrigation. A severe abiotic stress, flooding can dramatically affect botanical bioprocesses. A comparative investigation on perennial ryegrass revealed that submergence induced more severe damages on the turfgrass than waterlogging [121]. The distinction can be attributed to the differing severity of the two stresses. Waterlogging usually involves the root (only) submerged in water, while submergence is the entire plant being under water. Interestingly, submergence effects are more severe than that of waterlogging. Flooding stress can cause damage to the cell membrane system, induce the production of ROS, and trigger an increase of antioxidant enzyme activity. It was reported that after treatment with waterlogging, the contents of MDA, O_2^- and H_2O_2 were increased, the activities of antioxidant enzymes including SOD, CAT and APX were enhanced and the related genes were up-regulated in Kentucky bluegrass and perennial ryegrass [121,122]. Furthermore, root oxidase activity, growth of seashore paspalum, and centipedegrass were inhibited after waterlogging treatment [123]. Similarly, root dry weight was decreased while MDA content was increased by waterlogging in perennial ryegrass [124]. In addition, water logged soil was reported to contribute to enhance the frost tolerance of red clover (*Trifolium pratense*) and timothy (*Phleum pratense*) at colder temperature [125]. However, waterlogging induced more severe damage in Kentucky bluegrass under heat stress [126].

In recent years, flooding stress response in turfgrass species is not investigated deeply, although several physiological changes are reported in some species. Considering that the mechanisms of flooding stress response in turfgrass is still unknown, further investigation of flooding stress response of turfgrass at physiological and molecular levels should be performed in the future.

2.2.3. Heat Stress

Heat stress is a critical abiotic stress that limits the distribution of plants. It also plays an important role in affecting growth and development of turfgrass, especially the cool-season species. The heat stress tolerance of turfgrass between species varies, but cool-season species are generally more vulnerable to heat damage than warm-season ones [127,128]. It was reported that zoysiagrass maintained higher oxidative scavenging capacity than tall fescue after heat stress treatment [110]. Among the cool-season turfgrass, the annual species are more sensitive to heat stress than perennial species [129]. When exposed to heat stress conditions, physiological changes occurred. For instance, MDA, H_2O_2 and O_2^- accumulated and antioxidant enzyme activities increased. Also, RWC was decreased after heat stress treatment in perennial ryegrass, tall fescue and strong creeping red fescue [130,131]. These changes suggested membrane damage and excessive ROS generation under heat stress conditions. Cellular membrane stability is always disrupted by stress conditions. In hard fescue (*Festuca trachyphylla*), the total amino acid content was increased, while total soluble protein content was decreased. The membrane constituents, including proteins, fatty acids and sterols changed significantly under heat stress conditions [132,133]. Similar results were observed in Kentucky bluegrass, where antioxidant enzyme activities and hormonal contents changed with duration of heat stress [134]. Consequentially, morphological alterations such as growth inhibition, TQ decline and leaf senescence were derived

from the physiological changes. Remarkable leaf senescence and growth inhibition were observed in perennial ryegrass after heat stress treatment [132,135]. Leaf senescence is associated with chlorophyll loss from the leaves. Generally, Chl loss is induced by the suppression of Chl synthesis or acceleration of chlorophyll degradation. When exposed to heat stress, chlorophyll degradation genes in bentgrass were upregulated, while no alteration of chlorophyll synthesizing genes was observed, suggesting that heat stress induced chlorophyll loss in bentgrass was due to acceleration of chlorophyll degradation [128]. In addition, root elongation of tall fescue was significantly inhibited by heat stress, which was revealed by a decrease in root cell number [136].

The heat stress response of plants is regulated by a comprehensive pathway with many signaling molecules and transcription factors involved. The heat stress transcription factor A2c (HsFA2c) and heat shock proteins (HSP) play positive roles in the heat stress responses of plants. When exposed to heat stress conditions, the *HSPs* in creeping bentgrass were dramatically up-regulated [137]. In tall fescue, the genes of *HsFA2c* and *HSPs* were up-regulated by signaling molecules including phosphatidic acid, Ca^{2+} , salicylic acid and trans-zeatin riboside. Similarly, the stress tolerance of tall fescue was increased after foliar application of these molecules [138,139]. Recently, some candidate genes and molecular markers related to HSP, antioxidant defense, protein degradation and cell expansion of bentgrass were identified, which contributed to elucidating the heat stress response mechanisms of turfgrass [140,141]. Meanwhile, the simple sequence repeat (SSR) markers which were associated with heat tolerance of tall fescue were identified [142]. Furthermore, it was reported that “stress memory” played a role in heat stress response regulation of turfgrass. After pre-acclimation with heat, *HSP* genes showed higher transcript abundance and photosynthetic efficiency in tall fescue during subsequent stress, implying an improvement in heat tolerance level [143]. MicroRNAs (miRNAs) are essential in transcriptional regulation, so investigation of the alteration of miRNAs under stress conditions is rather important to understand the response mechanisms of plants. Recently, some differentially expressed miRNAs and their target genes which were related to heat stress responses of tall fescue were identified [144,145]. These results provided essential information for further research.

To improve the heat tolerance of turfgrass, several studies have been done in recent years. It was reported that elevated CO_2 and exogenous citric acid could mitigate heat stress-induced damages in tall fescue and Kentucky bluegrass via increasing photosynthetic rate, carbon assimilation efficiency and enzyme activity [146–148]. Application of NO could significantly alleviate heat damage in the photosystem of tall fescue [8]. Recently, the application of melatonin showed a remarkable effect on stress, including heat response of the plant. Growth inhibition, leaf senescence and other physiological damages were alleviated by exogenous melatonin and 24-epibrassinolide in perennial ryegrass and tall fescue under heat stress [135,145]. In addition, root elongation inhibition of tall fescue under heat stress was alleviated by strigolactones via interference of auxin transport [136]. Moreover, the nutritional element of nitrogen (N) positively affected the heat tolerance of creeping bentgrass which was reflected by an increase in TQ, normalized difference vegetation index, photochemical efficiency and root viability [137].

Heat stress plays an important role in growth of turfgrass. There has been remarkable progress in the investigation of heat stress responses in turfgrass species. Some interesting genes related to heat stress response are identified in turfgrass. But the genes regulatory network and how do these genes regulate heat stress response are not very clear, and it should be studied further in the future. Besides, elevated CO_2 and N fertilizer are reported to improve the heat stress tolerance of turfgrass, so the mechanisms of regulation pathway of these substances in turfgrass and how to use these substances in turfgrass management are the problems to be solved in the future.

2.2.4. Cold Stress

Cold stress, the other kind of temperature stress, is distinguished into chilling and freezing depending on the stress temperature [149]. Cold stress implies plant damage induced by temperatures below the optimum, which is also a crucial environmental factor that limits growth and distribution

of plants. Warm-season turfgrass species are more sensitive to cold stress than cool-season species. Cool-season grass, such as bluegrass, bentgrass, and fescue, showed different freezing tolerance in the field [150]. Examples of severe damage, including the destruction of cell membrane stability, a decrease in photosynthetic efficiency, the decline of TQ, and the inhibition of growth and development, were observed under chilling stress in bermudagrass. In addition, accordingly, the protective system was launched, reflected by an increase in antioxidant enzymes activities, including SOD, POD, and APX [12,151]. Moreover, the fatty acid composition was also altered in bermudagrass under chilling stress [152]. With a decreasing temperature, the demand of N in turfgrass declined, which may be due to plant growth inhibition [153]. The photosystem and metabolism processes of the turfgrass were negatively affected by cold stress. Photosynthetic efficiency decreased, and metabolic contents were altered in bermudagrass when exposed to cold stress [154]. Cold tolerance is distinct in different cultivars of zoysiagrass, and cold acclimation in growth chambers can be used to evaluate the cold tolerance of zoysiagrass [155]. The negative effects of cold stress, including growth and development inhibition and reduced cell membrane stability, were also observed in cool-season turfgrass, such as perennial ryegrass [156]. Under cold conditions, growth was inhibited and turf quality decreased in three bentgrass species, two fine fescue species, and annual bluegrass [157].

The research on the molecular mechanisms of the cold stress responses in turfgrass has recently progressed rapidly. Cold-response-related genes such as *late embryogenesis abundant proteins* (LEA), *C-repeat-binding factor/DRE-binding factor* (CBF1), SOD, and POD were up-regulated by cold stress [152]. The transcriptomic analyses of bermudagrass and zoysiagrass under cold stress revealed that many genes related to photosynthesis, carbon fixation, nitrogen metabolism, and proline synthesis pathways were involved in the regulation of cold response [158,159]. Recently, several differentially expressed proteins related to cold response, including lipid stability, antioxidant enzymes, protein synthesis, and degradation, were identified in bermudagrass [160]. Moreover, a number of metabolites, including amino acids, organic acids, and carbohydrates, were observed to be involved in the cold response of bermudagrass [161]. These investigations contribute to further understanding cold stress responses in turfgrass on the molecular level.

Recently, it was confirmed that the application of signaling molecules could improve the cold tolerance of turfgrass. The foliar application of exogenous melatonin and NO significantly enhanced the cold tolerance of bermudagrass via increasing the photosynthetic efficiency, the enhancement of membrane stability, and the regulation of metabolite contents [154,162,163]. Similarly, after the application of the ABA-mimicking ligand AM1 and Ca^{2+} in bermudagrass, the contents of ROS and MDA were reduced, while antioxidant enzyme activity and proline content were increased, which implied an enhancement of cold tolerance level [164]. On the other hand, it was reported that the phytohormone ethylene negatively regulated the cold response of bermudagrass, notwithstanding their positive effect on other plants [160,161,165]. Besides, cold acclimation, also known as cold hardiness, contributes to enhancement of the cold stress tolerance of a plant [166]. During cold acclimation, soluble phenolics accumulated and antioxidant activity increased in creeping bentgrass, Kentucky bluegrass and perennial ryegrass [167].

Cold stress is a major stress for turfgrass, especially for warm-season species. Because of the global change, cold stress will play a more and more important role in plants. As the climate gets warmer, snow melting will occur (in addition to there being fewer instances of snow) in winter, which will cause ice formation in the soil and then induce severe damages in plants. So, the mechanisms of the cold acclimate of turfgrass should be investigated further in the future.

2.2.5. Traffic/Wear Stress

Traffic or wear stress is an important abiotic stress in turf management, especially in sports fields, golf courses, home lawns, and public green space. Traffic stress can directly damage plant tissues through pressure, tearing, and scuffing and indirectly by limiting grass growth through the changing of physical properties of the soil. Alterations of physical properties such as bulk density, total porosity,

penetration resistance, and relative water capacity, and higher available water content was more highly detected in tall fescue and perennial ryegrass than in *Festuca rubra*, Kentucky bluegrass, suggesting a higher traffic stress tolerance in tall fescue and perennial ryegrass [168]. Traffic stress plays a role in affecting the morphological and physiological features of turfgrass species. Tolerance to this stress is associated with a high vascular bundle number, wide leaves, high leaf angle, and high root length density [169,170]. Physiological changes in turfgrass species were detected under traffic stress, such as a decrease in RWC, shoot density, root length, leaf Chl concentration, non-structural carbohydrates content, and POD activity, while the cell membrane permeability was increased in both warm-season and cool-season turfgrass species after traffic stress treatment [171–173]. Both lignin and carbohydrate concentrations proved to be important factors related to the wear resistance of turfgrass [174].

Additionally, it was reported that the appropriate sand topdressing rate could improve the shear strength turfgrass density on athletic fields [175], and that turf species showed higher traffic tolerance when established on relatively high sand mixtures [176]. Furthermore, the application of trinexapac-ethyl was involved in enhancing the traffic stress resistance of wheatgrass and tall fescue via improving TQ, RWC, soluble sugar content, antioxidant enzymes activities and cell membrane stability [108]. To improve the wear tolerance of fine fescues, the recurrent breeding methods based on selection of replicated clonally propagated genotypes were recommended in recent research [177].

Maybe traffic stress is not very important for crops like rice and maize, but it plays an important role in turfgrass. However, the traffic stress response in turfgrass species is not studied very well. The physiological and molecular changes in turfgrass is still unclear when exposed to traffic stress. Moreover, the morphological characteristic is related to traffic stress tolerance of turfgrass [178]. So the structures and development of vegetative tissues that is related to traffic stress tolerance of turfgrass should be investigated further.

2.2.6. Shade Stress

Light is an essential environmental factor that affects growth and development of turfgrass. Turfgrass growth is often limited by the shade provided by structures such as buildings, trees and shrubs. Therefore, shade stress is one of the most common causes of turf deterioration. The morphological and physiological changes of turfgrass were detected under shade stress [179]. For example, there was an increase in leaf length while decrease of leaf width was observed in tall fescue seedlings after shade treatment [180]. The TQ and vegetation indices of zoysiagrass declined dramatically when exposed to shade stress [181], while the chlorophyll content decreased but chlorophyll a/b ratio increased significantly under shade stress [181,182], which suggested the dysfunction of photosystem. The maximal photosynthetic efficiency of photosystem II decreased in perennial ryegrass after shade stress treatment [183].

To improve the shade tolerance of turfgrass, shade tolerance of several turfgrass germplasm were identified. The bermudagrass genotypes of WIN10F and STIL03 [184], [(*Z. japonica* × *Z. pacifica*)] × *Z. japonica* progeny of zoysiagrass [185], genotype of NE3490 of buffalograss [186] showed relatively high shade stress tolerance. Additionally, it was reported that zoysiagrass cultivars of ‘BA-189’, ‘Shadow Turf’ and ‘Empire’ had faster establishment under shade stress [181]. In addition, exogenous NO was reported to improve the shade stress tolerance of tall fescue [180,182]. In recent years, the molecular mechanism of shade tolerance in perennial ryegrass was investigated, and gibberellins biosynthesis genes were identified to play vital roles in shade stress response [187].

Although there is progress in the study of shade stress response in turfgrass, the mechanisms are still large unknown. The changes on physiological and molecular levels in turfgrass are not clear enough when exposed to shade stress. Therefore, shade stress response related genes including their functions and regulating pathways should be identified in the future.

2.3. Biotic Stress

In addition to the aforementioned abiotic stresses, turfgrasses are also affected by biotic stresses, such as insects, nematodes, fungi, and bacteria, throughout their life cycle. Biotic stress induces

discoloration, thus decreasing TQ, and even plant death. Dollar spot (*Sclerotinia homoeocarpa* F.T. Bennett) is a fungal disease that severely affects many kinds of turfgrass species, such as Kentucky bluegrass and creeping bentgrass [188]. Other pathogens, including anthracnose (*Colletotrichum graminicola*) [189], Fusarium Patch (*Microdochium nivale*), and Typhula Blight (*Typhula ishikariensis*) snow molds are also common turfgrass diseases [190]. It not only reduces the aesthetic and playing quality of the turfgrass but also contributes to weed encroachment and even plant death. Some insects also affect turfgrass performance. For instance, the sugarcane beetle was reported to induce severe damage in turfgrass [191]. There is a variation in the resistance level of turfgrass species. A substantial population development of the southern chinch bug (*Blissus insularis* Barber) was observed on St. Augustinegrass (*Stenotaphrum secundatum* Walt. Kuntze), zoysiagrass, and buffalograss; however, a low population development was recorded on bermudagrass, centipedegrass, seashore paspalum, bahiagrass, and tall fescue [3]. Turf weed is another kind of biotic stress factor critical for turf management. Selecting a turfgrass cultivar that can suppress weed development would be beneficial for turfgrass breeding. It was reported that chewing's fescue and strong creeping fescue were strongly weed suppressive [192]. Interestingly, even to the same disease, the pathogens are different. For instance, for Patch disease, bentgrass and zoysiagrass are the hosts of *Rhizoctonia solani* AG-2-III-B and AG-2-IV, respectively [193]. Moreover, *Curvularia trifolii* is a pathogen that can cause turf yellowing disease in *Paspalum vaginatum* [194]. In addition, some pathogens can induce severe damages in turfgrass associated with abiotic stresses. For example, *Microdochium nivale*, one of the most damaging pathogens of cool-season turfgrass, can induce snow molds in winter [195]. Interestingly, the snow mold disease resistance of plants can be increased by cold acclimation [196]. The mechanisms of the disease resistance of turfgrass are still unclear nowadays. Several quantitative trait loci (QTL) were reported to be associated with the gray leaf spot resistance of ryegrass [197]. The bacteriophage T4 lysozyme gene is related to gray leaf spot and brown patch disease resistance in tall fescue [198].

The application of chemical agents is a common method to avoid biotic-stress-induced damage in turfgrass. For instance, dollar spot disease in turfgrass is caused by the fungus *Clarireedia homoeocarpa*, and it could be suppressed by fungicide in creeping bentgrass [199–202]. Captan and Chlorothalonil are efficient fungicides against *Curvularia trifolii*, which causes foliar yellowing of *Paspalum vaginatum* [5,194]. Other methods could also be used to alleviate the damages of disease. It was reported that compost biosolids are advantageous for enhancing the leaf rust resistance in perennial ryegrass [203], and entomopathogenic nematodes are effective at controlling the development of black cutworm and *Spodoptera ciliatum* (Lepidoptera: Noctuidae) in turfgrass [204,205]. Effective pest management methods are also reported. For example, tea seed pellets, the byproduct of tea oil, expels earthworms in turf [206]. *Metarhizium brunneum* (Petch) is beneficial for controlling the development of the Japanese beetle (*Popillia japonica* Newman) in turfgrass [207]. These observations could provide useful methods for earthworm and beetle management in turfgrass.

Biotic stress is complex stress that includes many biotic factors. To clarify the response mechanisms to a specific pathogen or animal would be an interesting research direction to pursue in the future. In particular, the response to some broad-spectrum virus, fungus, and bacteria among turfgrass species should be studied further.

3. Conclusion and Future Perspectives

In the last decades, research on the environmental stress responses of turfgrass species has progressed rapidly at several levels. In the breeding field, some stress tolerance cultivars have already been selected for application in particular stress conditions [32,127,208].

Harsh stress conditions inhibit the growth and development of turfgrass species. A decline in TQ, root length, and fresh and dry weights are common parameters in turfgrass species exposed to stress conditions [10,20,76]. Furthermore, physiological investigations the stress response of turfgrass displayed stress-induced damages of the cell membrane, photosystem, metabolites, and antioxidant system. The contents of MDA and EL were increased, while chlorophyll content and photosynthetic

efficiency were significantly decreased under stressful conditions [21,27]. To regulate the osmotic potential of the cell after stress treatment, some metabolites, such as proline, soluble sugars, and proteins, accumulated [108,133,164]. Meanwhile, antioxidant enzymes' activities would increase in turfgrass because of the increase in ROS content [80]. These are protective strategies of the plant against unfavorable conditions, but there is a threshold to these changes. For example, the activities of antioxidant enzymes would decrease with prolonging of stress treatments [93].

The rapid development of laboratory techniques, such as RNA-seq and iTRAQ (isobaric tags for relative and absolute quantification), has been applied in transcriptomic and proteomic analysis to investigate the stress response of turfgrass species on the molecular level. Many metabolites, proteins, and genes related to stress response have been identified in turfgrass [53,64,144,145,158,160,161]. These remarkable results reveal deep mechanisms of stress response in turfgrass species. However, *omics* analysis is still basic research. Few actual genes had been identified (Table 1), so in order to understand the stress response mechanisms further, specific proteins or genes that can regulate the stress tolerance of turfgrass effectively should be identified in future research. Besides, it is interesting that one environmental stress can affect the response to another stress in turfgrass. For instance, a certain degree of flooding stress can enhance the frost tolerance of red clover (*Trifolium pratense*) and timothy (*Phleum pratense*) [125]. However, flooding stress plays a negative role in Kentucky bluegrass under heat stress [126]. It is reported that the pathogen activity of snow mold disease is related to cold stress in turfgrass [195]. Hence, the effects of different stresses on turfgrass species on the physiological and molecular level should be investigated further in the future.

To improve the stress tolerance of turfgrass, several methods were exploited. Generally, there are two main strategies: the application of molecules such as phytohormones, signal molecules, and other chemical compounds, or the improvement of the matrix with composts [8,41,69]. Relatively efficient and available exogenous molecules have not been reported yet. Hence, finding an efficient compound that is beneficial for improving the stress tolerance of turfgrass is necessary. Transgenic techniques can be also applied to enhance the stress tolerance of turfgrass species. Considering the few genes that have been identified in turfgrass, future research should focus on the identification of effective genes in different turfgrass species.

Table 1. Stress response genes in turfgrass species.

Turfgrass Species	Genes	Stresses	References
Bermudagrass	<i>SOD, CAT, POD-1, POD-2, LEA, CBF1, COR</i>	salt and cold	[151]
	<i>CAT, POD, SOD, DREB1, AP2/ERF, OSMOTIN-like, ABF1</i>	cold	[164]
	<i>POD-2, SOD, LEA, CBF1</i>	cold	[152]
	<i>CdDHN4</i>	drought	[101]
	<i>CdSOS1, CdNHX</i>	salt	[30]
Tall fescue	<i>HSC70, LMW-HSP, HMW-HSP</i>	heat	[143]
	<i>GPX, GR, pAPX, Cyt Cu/ZnSOD, EXPAs</i>	lead	[60]
	<i>HSC70, LMW-HSP, HMW-HSP</i>	salt	[20]
	<i>HSC70, LMW-HSP, HMW-HSP</i>	heat	[148]
	<i>FaRAX2, FaEXB5, FaCDKB2-1, FaPCNA, FaCycD2, FaDRM1, FaARP, FaD27, FaD17, FaMAX2, FaD14</i>	drought	[10]
	<i>HsfA2c, HSP18, HSP70, HSP90, HSP101, PLDδ, PLC2, PDK1, DGK1, ABI1, TGD2, CaM3, CDPK3, MBF1, RBOHD, MPK3, MPK6</i>	heat	[138]
	<i>FaHsfA2b, FaHsfA2c, FaHsfA2d</i>	heat	[139]
	<i>FaHSFA3, FaAWPM, FaCYTC2, FrbohD</i>	heat	[145]
	<i>FaPCNA, FaCycD2, FaCDKB, FaTIR1, FaPIN1, FaPIN2, FaPIN5, FaD3, FaD14</i>	drought	[86]
		heat	[136]

Table 1. Cont.

Turfgrass Species	Genes	Stresses	References
Creeping Bentgrass	<i>AsSAG12, Asl20, Ash36</i>	heat	[128]
	<i>bHLH148, MYB4/4-like, WRKY28/53/71</i>	drought	[97]
	<i>JUB1, DREB2A, Chlase, PPH, Chl-PRX, TDC1, SNAT1, COMT</i>	drought	[103]
Colonial Bentgrass	<i>HSPs, CAT, CP, EXP, GAPDH, GST</i>	heat	[141]
Perennial ryegrass	<i>CytCu/ZnSOD, ChlCu/ZnSOD, FeSOD, MnSOD, POD</i>	cadmium,	[67]
	<i>CAT, uccrc, PBSP, sucs</i>	salt	[24]
	<i>CAT, pAPX, FeSOD, POD</i>	drought	[108]
	<i>LpSAG12.1, Lph36</i>	heat,	[135]
Kentucky bluegrass	<i>Cu/ZnSOD, APX, CAT, POD</i>	salt,	[21]
	<i>ChlCu/ZnSOD, FeSOD, CytAPX</i>	waterlogging	[122]
Zoysiagrass	<i>ZmVP1</i>	salt	[55]
	<i>ZjGRP</i>	salt	[56]

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