Bermudagrass (Cynodon spp.) is an important turfgrass grown commonly in home lawns, sports fields and parks. Due to its strong vegetative growth and its abilities to tolerate trampling, heat and drought stresses (Harlan et al. 1970), bermudagrass is also grown as a forage crop to provide tender and nutritional food to animals (Huang et al. 2011). Bermudagrass is a perennial turfgrass indigenous to the Mediterranean area and has now been found in more than 100 countries, ranging from the tropical to subtropical regions of the world (Harlan and Wet 1969). Numerous bermudagrass genotypes and hybrids are now used for commercial cultivations (Tari et al. 2013) and over one thousand Cynodon accessions are now available at the U. S. National Plant Germplasm System.

In field, plants need to counteract various environmental stresses, including nutritional deficiency, drought, salinity, cold, and/or heat conditions (Huang et al. 2014). These abiotic stresses may further be intensified in future, due mainly to the global warming-induced temperature increases and water shortages. As a turfgrass, bermudagrass also needs to tolerate wear injuries caused by crushing, tearing, and shearing (Trenholm et al. 1999). Consequently, maintaining proper growth of turfgrass under unfavorable environmental conditions is a great challenge to farmers and requires new knowledge and breeding technologies to create new and improved bermudagrass germplasms with good stress tolerances. Current studies on molecular mechanisms controlling plant adaptations to various growth conditions have provided invaluable information to plant breeders during their productions of abiotic stress tolerant germplasms (Bonos and Huang 2006, Huang et al. 2014). In this paper, we will focus on recent progress on the identification and validation of abiotic stress-responsive genes, and the biochemical and molecular mechanisms controlling bermudagrass tolerance to various stresses.

Current knowledge of bermudagrass responses to abiotic stresses

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Bermudagrass (Cynodon spp.) is a common turfgrass found in parks, landscapes, sports fields, and golf courses. It is also grown as a forage crop for animal production in many countries. Consequently, bermudagrass has significant ecological, environmental, and economic importance. Like many other food crops, bermudagrass production also faces challenges from various abiotic and biotic stresses. In this review we will focus on abiotic stresses and their impacts on turfgrass quality and yield. Among the abiotic stresses, drought, salinity and cold stress are known to be the most damaging stresses that can directly affect the production of turfgrass worldwide. In this review, we also discuss the impacts of nutrient supply, cadmium, waterlogging, shade and wear stresses on bermudagrass growth and development. Detailed discussions on abiotic stress effects on bermudagrass morphology, physiology, and gene expressions should benefit our current understanding on molecular mechanisms controlling bermudagrass tolerance against various abiotic stresses. We believe that the rapid development of transcriptomics and proteomics, as well as bermudagrass stable transformation technologies will promote the production of new bermudagrass cultivars with desirable tolerance against abiotic stresses.

Key Words: bermudagrass, abiotic stress, stress tolerance, genetic resources, transcriptomics and proteomics, gene editing.

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Effect of nutrient availability

In the southern part of the USA, bermudagrass is often grown as a forage grass for cattle production (Day and Parker 1985). Many reports have shown that the yield and quality of bermudagrass are influenced by nitrogen (N) application, which is also known to improve the efficiency of inorganic nutrient absorption (Day and Parker 1985, Haby 2007, Wilkinson and Langdale 1974). For example, bermudagrass production with no nitrogen (N) fertilizer application gave only one-ton forage production while application of 400 pound N per acre gave 8-ton forage production (Burton and DeVane 1952). In addition, efficient N application was reported to increase protein content in bermudagrass forage (Burton et al. 1956, Gilbert and Davis 1971, Westerman et al. 1983). It was reported that sufficient N fertilization increased the concentrations of N and potassium (K) in the aerial forage and root of bermudagrass cv. Tifton 85. It had, however, no significant effect on phosphorus (P) concentration. Except for K, N fertilization-induced changes of nutrient compositions and proportions were reported to be limited (Liu et al. 2017). Abundant N fertilization was shown to increase shoot and leaf growth, whereas lower amounts of N fertilization resulted in reduced shoot growth and forage quality (Heshmati and Pessarakli 2011, Schmidt and Blaser 1969). The length of bermudagrass root was found to be shorter when less amount of N was applied (Heshmati and Pessarakli 2011). Different N sources have also been reported to have effects on bermudagrass yield and N uptake. The relative efficiency of different N sources was shown as in the order of (NH4)2SO4 (AS) > urea-ammonium-nitrate (UAN) > urea > anhydrous ammonia (AA) > ammonia after passing through a Cold-Flo adapter (ACF) (Westerman et al. 1983). Silveira et al. (2007) reported that ammonium nitrate (AN) and AS increased bermudagrass forage yield and N uptake when compared with urea and UAN in Gallime soil. However, N sources made no clear effect on dry matter (DM) production when the plants were grown in libert soil.

Increasing amount of N, P and K application increased total nutrient uptake, total protein content, and P and K contents in Coastal bermudagrass forage (Adams et al. 1966). Higher rate of K application was considered to improve turfgrass appearance and growth. However, when the amount of K fertilizer exceeded the N/K ratio of 0.5 to 1, no significant K effect on bermudagrass growth or root weight was observed (Snyder and Cisar 2000). It was reported that the ratio of (4-5):(4-5):1 (N:K:P) could benefit bermudagrass regrowth while the ratio of 4:1:6 (N:K:P) could enhance bermudagrass tolerance to cold stress (Snyder and Cisar 2000). Sulphur (S) fertilizer application was reported to increase the N/S ratio, but had no impact on bermudagrass forage yield, N uptake or efficiency of N utilization (Westerman et al. 1983). More recently, Chen et al. (2017) showed that application of exogenous melatonin to bermudagrass up-regulated the expressions of K+ transport-related genes, leading to higher accumulations of K+ in both bermudagrass shoots and roots. Their results indicated that melatonin has an important role in regulating bermudagrass responses to low K+ stress.

Cadmium stress

Cadmium (Cd) is a highly toxic and water soluble heavy metal, and can be easily up-taken by plants in fields (Arasimowicz-Jelonek et al. 2012a, 2012b). Because Cd is stable in water, high concentration of Cd in soil can cause serious public concerns about human food safety (Agami and Mohamed 2013, Shi et al. 2014b, Uraguchi and Fujiwara 2013). Cadmium contamination in soil was also reported to inhibit plant shoot and root growth, leading to a reduction of crop production (Bhardwaj et al. 2009, Tan et al. 2017). Phytoremediation is a method used to remove heavy metals from soil through cultivation of specific plants (Cunningham and Berti 1993, Salt et al. 1998).

It was reported that bermudagrass biomass, leaf chlorophyll content, photosynthetic pigment production and gas exchange parameters could all be affected by Cd stress (Mukhtar et al. 2013, Xie et al. 2014). Compared with the Cd susceptible bermudagrass ecotypes, the Cd tolerance bermudagrass ecotypes often showed higher net assimilation rate, higher water usage efficiency, thickened leaves, reduced leaf surface stoma density, and lower water transpiration rate (Mukhtar et al. 2013, Xie et al. 2014). Under heavy metal stresses, a large number of glandular-like structures were found to form on root surfaces. Formation of these glandular-like structures on root surface was considered as an adaptive response to Cd stress (Kuo et al. 2005). A total of 39 metabolites in bermudagrass were found to be responsive to Cd stress. These metabolites included some amino acids, organic acids, sugars, and fatty acids (Xie et al. 2014). Shi et al. (2014b) reported that application of exogenous nitric oxide (NO) donor or hydrogen sulfide (H2S) donor could induce bermudagrass tolerance to Cd stress. The authors speculated that the oxide-activated hydrogen sulfide is essential for inducing Cd tolerance in bermudagrass. In a different study, Li et al. (2006) found that over-expression of Phytochelatin synthase (CdPCh) gene in tobacco also increased the accumulation level of Cd.

Drought stress

Bermudagrass is considered to be a drought tolerant species with genotypic variations (Husmoen et al. 2012). Several bermudagrass genotypes were found to have deep root systems, thick leaf cuticles and smaller stomatal openings (Carrow 1995, 1996, Qian et al. 1997, Zhou et al. 2009). Deep and large root system is a well-known character for plant drought tolerance (Beard 1989). The capacity of water absorption by root depends largely on root size and spatial distribution (Carrow 1996, Huang 2000, Huang et al. 2014). Besides, Zhou et al. (2014b) found that the Mediterranean...
bermudagrass evolved a large rhizome system adapting to drought stress. Unlike cold-season grasses, warm-season grasses can continue to grow their roots in the summer (Beard 1973). In regular soils or in acidic soils, the depth of grass roots ranged as bermudagrass cv. Tifway > common bermudagrass or tall fescue cv. Rebel > tall fescue cv. Kentucky-31 > St. Augustinegrass [Stenotaphrum secundatum (Walt.) Kuntzel] cv. Raleigh > common centipedegrass [Eremochloa ophiuroides (Munro) Hack.] > Meyer’ zoysiagrass (Zoysia japonica Steud.) (Carrow 1996). Baldwin et al. (2006) reported that the root weight of six well-irrigated bermudagrass cultivars was significantly greater than that of the same cultivars with less irrigation. Leaf wilting is a major visual phenotype caused by drought stress and several other biotic and/or abiotic stresses. Compared with other turfgrasses (e.g., centipedegrass, tall fescue and Meyer’ zoysiagrass), bermudagrass has a much lower leaf wilting rate, indicating its better drought tolerance than other grasses. Besides, bermudagrass cv. Tifway was reported to have a lower leaf wilting rate than other commonly grown bermudagrass (Carrow 1996). To reduce leaf desiccation, plants have evolved a defense mechanism to control stomatal closure. By controlling stomatal closure, plants are able to reduce their evapotranspiration rate (ET) (Huang et al. 2014). Compared with other turfgrasses, Carrow (1995) indicated that bermudagrass had a lower ET rate than other turfgrasses. In the same report, he also indicated that the ET rate of well-irrigated bermudagrass is lower than that of less well-irrigated bermudagrass. Consequently, drought tolerance has a direct effect on bermudagrass forage quality (Baldwin et al. 2006).

Drought stress causes significant physiological changes, including photosynthesis and antioxidant metabolism, in plant. It is generally accepted that greater volume of root systems and slower shoot growth allow bermudagrass to maintain enough water content and normal cellular function during drought seasons. Several metabolites have been reported to be important for maintaining a proper cell osmotic pressure and reducing water evaporation (Hu et al. 2015a). For example, under drought stresses, Arizona Common and Coastal bermudagrass were shown to have higher levels of free proline, asparagine and valine but lower level of free alanine (Barnett and Naylor 1966). Compared with the drought susceptible variety Yukon, cultivar Tifgreen had much higher levels of proline and soluble sugars (Shi et al. 2012). Du et al. (2012) studied a hybrid bermudagrass using a gas chromatograph coupled with a mass spectrometer and determined that the levels of three organic acids, ten amino acids and seven sugars were significantly up-regulated. In many recent studies, relative water content and electrolyte leakage have been used as indications of plant drought tolerance and the degree of cell membrane damage. Accumulation of unsaturated fatty acids in membrane lipids was considered to reduce cell membrane damage during drought stresses (Zhong et al. 2011). Besides osmotic regulation, dehydrin proteins were also reported to protect membrane damage. Several studies have shown that, under drought stresses, accumulations of 16-, 23-, 31- and 40-kDa dehydrins in drought tolerant bermudagrass cultivars were different from that in the drought sensitive bermudagrass cultivars (Hu et al. 2010, Su et al. 2013). Hybrid bermudagrass cv. Tifway and regular bermudagrass cv. C299 both showed a decline in photosynthetic rate, caused by stomatal closure during an early drought stress stage (Hu et al. 2009, Huang et al. 2014). However, compared with cultivar C299, cultivar Tifway was able to maintain a higher photosynthetic rate even though the stomatal conductance was decreased to near zero (Hu et al. 2009). Higher Rubisco enzyme activities and more stable carbon assimilation proteins in cultivar Tifway were found to be responsible for greater carboxylation capability (Hu et al. 2009, Huang et al. 2014). Huang et al. (2014) reported that accumulation of reactive oxygen species (ROS) in plant was significantly induced by drought stress and, at the same time, plant has its own strategies scavenge ROS. One of the most effective ROS scavenging strategies is to regulate the expression and/or activities of antioxidant enzymes, including superoxide dismutase (SOD), catalase (CAT) and ascorbate peroxidase (APX). Lu et al. (2008, 2009a) demonstrated that the increased activities of SOD, CAT, and APX in leaves of mutant bermudagrass plants could clearly improve their drought tolerance. Compared with bermudagrass cv. TifEagle, three somaclonal variants of triploid bermudagrass showed higher CAT activity during drought stress, and two variants showed higher APX activity during short-term drought stress and higher SOD activity after long-term drought stress. The same research group reported in the same year that the activities of ABA-induced SOD and CAT could be inhibited by application of ROS scavenger H2O2 or NO (Lu et al. 2009b).

Analysis of cDNA libraries constructed using bermudagrass cv. Tifway and C299 through suppression subtractive hybridization, Zhou et al. (2014a) identified a total of 277 drought responsive genes. The up-regulated genes identified in that study included those related to drought avoidance traits (i.e., CER1 and sterol desaturase), drought tolerance traits (i.e., dehydrins, HVA-22-like protein, superoxide dismutase, dehydro-ascorbate reductase [DHAR], and 2-Cys peroxiredoxins), and stress signaling (i.e., EREBP-4 like protein and WRKY transcription factors). In a different study, 120 genes, including a putative delta-pyrroline-5-carboxylate synthetase (ES92694) and a putative MYB17 protein (ES925217), were found to be up-regulated (Kim et al. 2009). The putative delta-pyrroline-5-carboxylate synthetase is an essential enzyme for proline synthesis and MYB17 is known as a stress responsive transcription factor (Kim et al. 2009). Analysis of the upstream part of CdDHN4 gene in tobacco leaves showed that the promoter of CdDHN4 could be regulated by ABA application, or by drought or cold treatment. Further study on this gene showed that CdDHN4 played an important role in the ABA-dependent signaling pathway induced by drought stress.
Chen et al. (2015b) showed that over-expression of Cdt-NF-YC1 gene in rice not only increased plant tolerance against drought or salt stress but also increased the sensitivity to ABA treatment. Protein synthesis and degradation are also important during drought stresses. Zhao et al. (2011) observed that multiple bermudagrass genes were involved in the maintenance of protein metabolism during drought stresses. Among these genes, genes encoding Chl a-b binding protein, ATP synthase or phosphoribokinase were important during photosynthesis, genes encoding SOD, APX or DHAR were involved in antioxidant defense, and a gene encoding ADP-glucose pyrophosphorylase took part in starch synthesis (Huang et al. 2014). It was suggested that drought stress responsive genes could be classified into five different categories: metabolism category (e.g., glycine dehydrogenase, aminomethyltransferase, phosphoribokinase, short-chain dehydrogenase/reductase, methionine synthase, ADP-glucose pyrophosphorylase, aspartate aminotransferase and beta-1,3-glucanase); energy category (e.g., putative aconitate hydratase, succinate dehydrogenase (ubiquinone) flavoprotein subunit and glyceraldehyde-3-phosphate dehydrogenase); defense category (e.g., dihydroliyol dehydrogenase, SOD, APX and monodehydroascorbate); protein synthesis category (e.g., 30S ribosomal protein S1, elongation factor Tu and ribosomal protein L12); and cell growth/division category (e.g., actin-depolymerizing factor 2) (Zhao et al. 2011). This classification was supported by more recent proteomics studies via MALDI-TOF-MS (Shi et al. 2014a, Ye et al. 2015, 2016).

### Waterlogging stress

Flooding also has great effect on plant vegetative and reproductive growth, and dry mass production (Promkhambut et al. 2011, Tari et al. 2013). Flooding stress often related to a low bermudagrass root growth rate, less accumulation of soluble sugar and starch, and induction of SOD and APX activities (Li et al. 2015). To investigate the changes of bermudagrass anti-oxidant enzyme activities and carbohydrate content during flooding, Tan et al. (2010) collected and analyzed bermudagrass samples after various submergence treatments. Their results showed that increased duration and/or depth of submergence further enhanced the activities of CAT, SOD, APX, peroxidase (POD), and glutathione reductase (GR) in bermudagrass roots while the accumulation of total soluble carbohydrate and starch in shoots and roots were decreased. A recent proteomics and metabolomics study showed that the metabolism and dormancy of bermudagrass under flooding was significantly decreased (Ye et al. 2015). The authors speculated that these retarded activities might help bermudagrass to survive during submergence stress (Ye et al. 2015).

### Wear stress

Bermudagrass is a common turfgrass in golf course and sports fields in the southern region of the USA, and in countries with warm climate (Trenholm et al. 1999). High frequencies of human and equipment trafficking often cause significant wear stress on turf quality (Griffin et al. 2006). It was reported that wear stress could cause severe damages to bermudagrass canopy appearance followed by leaf senescence (Trenholm et al. 1999). Lulli et al. (2012) reported a positive correlation between lignin content and plant wear tolerance. They have also indicated that starch content in rhizome and stolon, and glucose content in rhizome correlated negatively to turfgrass wear tolerance (Lulli et al. 2012). It is noteworthy that wear tolerance varies significantly among different bermudagrass cultivars. For example, bermudagrass cv. Riviera showed the best recovery of green canopy after one, two, or three time simulated wear
treatments per week (Bayer 2006) or by using the Cady traffic simulator (Henderson et al. 2005). Trappe et al. (2008) also showed that bermudagrass cv. Riviera had a superior tolerance to wear stress compared with other bermudagrass cultivars, except hybrid bermudagrass Tifway. In a separate study, Williams et al. (2010) also found that bermudagrass cv. Riviera had a similar wear tolerance as cv. Princess 77, but better than all other four cultivars tested in that study. Trappe et al. (2011) reported that bermudagrass cvs. Rivera and Tifway had better wear tolerance than cvs. Princess 77, TifSport, and three zoysiagrass cvs. El Toro, Palisades, and Zorro. It was reported that over-seeding could reduce bulk density but increase canopy coverage, thatch accumulation, and saturated hydraulic conductivity that can protect bermudagrass from wear stresses (Thoms et al. 2011). Applications of exogenous plant growth regulators (i.e., ethephon, trinexapac ethyl (TE), paclobutrazol, flurprimidol, flurprimidol plus TE, and ethephon plus TE) were also found to improve bermudagrass wear tolerance (Brosnan et al. 2010). Besides, the depth of crumb rubber other than the size of crumb rubber particle were shown to improve the wear tolerance (Dickson et al. 2017).

Salt stress

Plant can tolerate salt stresses by secreting Na⁺ out of the cells, slower up-taking of Na⁺, and translocating Na⁺ into vacuole inside cells through specific mechanisms (Tari et al. 2013). And osmotic-changing and ionspecific are two distinct phases for salt response (Munns and Tester 2008). Though bermudagrass is considered as an efficient grass to revegetate sodic land, there is a series of morphology, physiology, molecular changes under salt stress (Singh et al. 2013). Pessarakli and Touchane (2006) showed that bermudagrass shoot and root length were increased in a solution containing 5,000 or 10,000 mg/L NaCl, and decreased when the NaCl concentration was further increased. Salt stress was shown to reduce turf quality, stolon number per plug, and shoot weight and height, but to increase root number and length, fresh root weight, and root/shoot length ratio of salt-tolerant bermudagrass genotypes (Dudeck et al. 1983, Hu et al. 2012). Shahba (2010a) reported that a positive correlation between root mass and salinity tolerance in bermudagrass cvs. Tifway, TifDwarf and Tifgreen. Hu et al. (2012) did a similar work using bermudagrass cvs. Tifway, TifDwarf, Dacca and ‘Khabbal, and found that at five salinity stress levels, the root number and dry weight of these four cultivars were all significantly decreased. Bizhani and Salehi (2014) confirmed later that salt stress could indeed decrease root fresh and dry weights. It is possible that the different results described above were caused by different salt stress tolerance in different bermudagrass cultivars and/or the salinity treatments used in above studies. Hameed et al. (2010, 2013) examined the root, stem and leaf morphological changes using a natural salt stress adaptive population. Their results showed that the morphological changes induced by salt stress were influenced by plant tolerance to salt stress and its ability to retain water.

Salt stress often causes significant reduction of leaf relative water content (RWC), transpiration rate, leaf net photosynthetic rate (Pn), total chlorophyll content, starch level, stomatal conductance, and cellular membrane stability (Bizhani and Salehi 2014, Yu et al. 2015). It also reduces K⁺ concentration but increases Na⁺ and Cl⁻ concentrations in turfgrass stolon and shoots (Chen et al. 2014a, Dudeck et al. 1983, Nadeem et al. 2012). Hu et al. (2012) treated two different bermudagrass genotypes with 200 and 400 mM salt and found that the concentrations of malondialdehyde and hydrogen peroxide in mature leaves of the salt-sensitive genotype C198 were higher than that in the salt-tolerant genotype C43, while the activities of SOD, CAT, APX, DHAR were much higher in the salt-tolerant genotype compared with the salt-sensitive genotype. Elevated concentration of CO₂ as well as accumulation of soluble sugars, proline, and glycine betaine (GB) were found to reduce the negative effects caused by salinity stress (Yu et al. 2015). Hu et al. (2015a) also indicated that the reduced shoot length and increased root length might be caused by an increased accumulation of soluble sugars and metabolites, important to nitrogen metabolism, and this physiological change could improve root absorption capability and enhance bermudagrass salt tolerance. Liu et al. (2016a) found that sodium nitroprusside (SNP, a donor of NO), could alleviate salt toxicity to bermudagrass by maintaining the stability of cell membrane, ion homeostasis, photosynthesis.

With increasing levels of salt stress, the expressions of antioxidant-related genes were up-regulated in young leaves but down-regulated in mature leaves (Hu et al. 2012). Through comparative proteomics, 77 differentially expressed proteins were identified upon drought and salt stresses. Most of these identified proteins are known to be involved in glycolysis, oxidative pentose phosphate, photosynthesis and redox metabolic pathways. Thirteen of the identified proteins were found to be regulated specifically by salt stress (Ye et al. 2016). With the same approach, Shi et al. (2013) identified 12 up-regulated, 20 down-regulated, and four specifically expressed proteins after the polyamines treatment. Most of these proteins are known to participate in electron transport and energy pathways. Recently, Hu et al. (2018) analyzed four small RNA libraries from mock-, cold-, salt- or cold plus salt-treated bermudagrass plants, and identified 449 miRNAs. Compared to the mock-treated plants, 49 and 39 miRNAs were found to be up- and down-regulated after the salt treatment, respectively.

Salt stress causes significant changes in plant morphological, physiological, and molecular functions. However, these changes can vary greatly among different bermudagrass cultivars or phenotypes. Dudeck et al. (1983) compared the salt tolerance in eight bermudagrass cultivars, and determined that cvs. TifDwarf and Tifgreen showed the best tolerance to salt stress, while cvs. Common and Ormond were the most sensitive cultivars. Peacock et al. (2003) reported
that bermudagrass cv. Quickstand produced more total shoot biomass than cvs. Tifton-10, Tifway, Navy Blue, GN-1 and TifSport under a salt stress condition. Chen et al. (2014b) evaluated salt stress tolerance in various bermudagrass germplasms collected in China. Based on the percentage of leaf firing and relative shoot weight, the authors classified the germplasms into four groups. Dudeck et al. (1983) analyzed four bermudagrass cultivars and found that cv. Tifway had the best salinity tolerance and cv. Khabbal was the most susceptible cultivar against salt stress. Lu et al. (2007) developed an in vitro selection method for screening salinity tolerant calli on solid medium containing high concentrations of salt. Through this screening method, the authors were able to regenerate several plants with higher salt tolerance than the parental cv. TifEagle. Besides, exogenous polyamine and mowing were reported to increase salt tolerance of bermudagrass (Shahba 2010b, Shi et al. 2013).

**Cold stress**

Low temperature is one of the main factors that limit the geographical distribution of bermudagrass. Cold stress was shown to decrease turf quality, growth, dry weight, tiller density, leaf size, chlorophyll content, transpiration rate and RWC. Cold stress could also increase electrolyte leakage, and malonaldehyde and hydrogen peroxide contents in RWC. Cold stress could also increase electrolyte leakage, density, leaf size, chlorophyll content, transpiration rate and geographical distribution of bermudagrass. Cold stress was the most susceptible cultivar against salt stress. Low temperature is one of the main factors that limit the geographical distribution of bermudagrass. Based on the percentage of leaf firing and relative shoot weight, the authors classified the germplasms into four groups. dudeck et al. (1983) analyzed four bermudagrass cultivars and found that cv. Tifway had the best salinity tolerance and cv. Khabbal was the most susceptible cultivar against salt stress. Lu et al. (2007) developed an in vitro selection method for screening salinity tolerant calli on solid medium containing high concentrations of salt. Through this screening method, the authors were able to regenerate several plants with higher salt tolerance than the parental cv. TifEagle. Besides, exogenous polyamine and mowing were reported to increase salt tolerance of bermudagrass (Shahba 2010b, Shi et al. 2013).

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Variations of cold resistance were also found among different bermudagrass cultivars. For example, Anderson et al. (1988) indicated that bermudagrass cv. Mldiron was able to tolerate −11°C condition while cv. Tifgreen was able to tolerate −7°C condition in winter. In 2011, Anderson and Wu reported that bermudagrass cvs. Hardie, Goodwell, Midland 99 and Ozark showed better freezing tolerance than the reference cv. Midland. In that study, cvs. Coastcross, Tifton 85 and Tifton 68 were ranked the most susceptible bermudagrass cultivars. The lethal temperature for causing 50% of the plants to die (LT50) for bermudagrass cv. Midiron and Tifgreen without a pre-cold-acclimation were at −6.5 and −3.6°C, respectively. After pre-cold-acclimation, the LT50 of the two cultivars were increased to −11.3 and −8.5°C, respectively (Gatschet et al. 1994). This finding indicates that cold-acclimation can be an effective method for cold tolerance improvement. It was also reported that the cold-acclimation treatment could increase the production of proline, a 25 kDa dehydrin, and abscisic acid (ABA), but decrease the level of t-zeatin riboside (a kind of cytokine) that was reported to increase the cold tolerance of bermudagrass (Zhang et al. 2011a, 2011b). ABA was found to enhance the cold tolerance of bermudagrass by maintaining the cell membrane integrity, improving the function of photosystem II as well as increasing the carbon isotopic fractionation (Huang et al. 2017). Cold-acclimation was also reported to increase sugar and proline accumulations, and enhancing SOD activity to improve the survival rate under cold stress conditions (Zhang et al. 2011a). Cold-acclimation was shown to induce gene expressions (De los Reyes 2001, Zhu et al. 2015), leading to better tolerance of bermudagrass to cold stress. In addition, exogenous melatonin application was found to improve bermudagrass cold tolerance by increasing antioxidant enzyme activities, altering cold responsive metabolite productions (e.g., carbohydrates, organic acids and amino acids), and affecting the function of photosystem II (Hu et al. 2016b). Comparative proteomics allowed the identification of 51 differentially expressed proteins after a cold and calcium chloride (CaCl2) treatment. Most of these identified proteins are known to be involved in photosynthesis, redox, glycolysis, tricarboxylic acid cycle, oxidative pentose phosphate pathway, and amino acid metabolisms. Regulations of amino acid, organic acid, sugar, and sugar alcohol productions indicated that application of exogenous CaCl2 could improve bermudagrass chilling or freezing tolerance (Shi et al. 2014c). Munshaw et al. (2004) reported that applications of moderate amount of salt or use effluent water could increase bermudagrass cold hardiness (Zhang et al. 2008). Hu et al. (2016b) reported that application of
Conclusions and future perspectives

Significant progress has been made on our understandings of morphology, physiology and molecular mechanisms associated with bermudagrass tolerance to salinity, drought and cold stresses, however, the research mainly focuses on physiological and biochemical aspects. Numerous studies have shown that under various stress conditions, the cell membrane permeability, photosynthesis rate, antioxidant enzyme activity, soluble sugar and protein content of bermudagrass have changed accordingly (Table 1). But these changes are just a physiological adjustment of the bermudagrass in order to adapt to changes in the environment. The upstream mechanism for these changes is not much studied. As a non-model plant, when bermudagrass faces different abiotic stresses, it needs to be verified that whether its signal transduction pathway is similar to that of model organisms. At the same time, the changes in the molecular level of bermudagrass before and after the adversity are still unclear, and the research results obtained are limited.

Based on the morphology and physiological data, significant genetic variations have been found in bermudagrass genotypes with various tolerance to drought, salinity, and cold stresses. These genotypes have offered researchers with valuable resources for future studies on bermudagrass gene function, abiotic and biotic stress responses, and improvement of bermudagrass production and quality. For example, Zhou et al. (2013) tested the drought tolerance of

| Type of stresses | Phenotypic effects | Adaptive characteristics | Genes confirmed to be involved |
|------------------|-------------------|--------------------------|-----------------------------|
| cadmium stress   | reduce biomass, leaf chlorophyll content, photosynthetic pigment production and gas exchange parameters (Mukhtar et al. 2013, Xie et al. 2014) | thickened leaves, reduced leaf surface stoma density, glandular-like structures form on root surfaces (Kuo et al. 2005, Mukhtar et al. 2013, Xie et al. 2014) | CjPCS1 (Li et al. 2006) |
| drought stress   | accumulation of osmotic (such as proline, asparagine, valine and soluble sugars), dehydrin proteins (such as 16-, 23-, 31- and 40-kDa dehydrins) and ROS, decline in photosynthetic rate (Barnett and Naylor 1966, Hu et al. 2009, 2010, Huang et al. 2014, Shi et al. 2012, Su et al. 2013) | deep root systems, a large rhizome system, thick leaf cuticles and smaller stomatal openings (Carrow 1996, Huang and Gao 2000, Huang et al. 2014, Zhou et al. 2014b) | Cdt-NF-YC1 (Chen et al. 2015b, Lv et al. 2017) |
| waterlogging stress | low bermudagrass root growth rate, less accumulation of soluble sugar and starch, and induction of SOD and APX activities (Li et al. 2015) | | |
| shade stress     | a clear reduction of turf quality, canopy photosynthetic rate, chlorophyll a and b contents, total soluble protein content, water-soluble carbohydrate content, and CAT and APX activities (Beard 1973, Sladek et al. 2009, Trappe et al. 2011) | high lignin content (Lulli et al. 2012) | |
| wear stress      | cause severe damages to bermudagrass canopy appearance followed by leaf senescence (Trenholm et al. 1999) | increased exodermis, sclerenchyma, endodermis, cortex and pith parenchyma in roots; increased stem area, increased epidermis, sclerenchyma thicknesses, cortex thickness, increased number and area of vascular tissue in stem; increased development of vesicular hairs and less affected parenchymatous tissue in leaf (Hameed et al. 2010, 2013) | |
| salt stress      | reduction of leaf relative water content, transpiration rate, leaf net photosynthetic rate total chlorophyll content, starch level, stomatal conductance, and cellular membrane stability (Bizhani and Salehi 2014, Yu et al. 2015) | | |
| cold stress      | decrease turf quality, growth, dry weight, tiller density, leaf size, chlorophyll content, transpiration rate and RWC; increase electrolyte leakage, and malonaldehyde and hydrogen peroxide contents in plant (Esmaili and Salehi 2012, Fan et al. 2014, Liu et al. 2016b) | | |
460 genotypes collected from different climatic zones of Australia, the result showing that genotypes experienced Mediterranean climates showed better drought tolerance. However, it may need more time for screening resistant varieties. From the information present in the article, we know mowing and applications of exogenous plant growth regulators can improve the wear tolerance, and application of exogenous ABA mimic 1 (AM1) improved bermudagrass seedling cold tolerance but it will increase labor costs. As a mature technology, transgene would be a better choice for the future bermudagrass breeding.

Recent developments of technologies, including transcriptomics, proteomics, and metabolomics let us have a deeper understanding of its regulatory mechanisms. In order to adapt to osmotic stress caused by salt and drought, bermudagrass will form a layer of wax on the leaf surface. The up-regulation of CER1 and sterol desaturase may contribute to the formation of waxy (Zhou et al. 2014a). Osmotic stress has great damage to the cell membrane, dehydrins and late-embryogenesis abundant (LEA) proteins may play the role of protective protein (Zhou et al. 2014a). The induced expression of genes involved in ROSs scavenging (CAT, SOD, POD) and the increased activities of antioxidant enzymes (CAT, SOD, POD) can remove excess ROS produced by osmotic stress (Shi et al. 2014a, Ye et al. 2016). Up-regulation genes function as solute synthase (such as sucrose synthase2, galactinol synthase1, stachyose synthase, delta 1-pyrroline-5-carboxylate synthetase 1) and accumulation of osmotic regulator (such as amino acid, sugars, etc.) will maintain cell turgor (Huang et al. 2014, Zhao et al. 2011, Zhou et al. 2014a). There are also some photosynthesis, carbon fixation and energy supply proteins (such as RuBisCO-related proteins, ferredoxin-thioredoxin reductase, ferredoxin-NADP reductase) activated by osmotic stress (Zhou et al. 2014a). For cold stress, there exists a similar resistance mechanism in the activation of the proteins involved in maintenance of cell homeostasis, osmotic adjustment, ROS scavenging, photosynthesis and energy supply (Chen et al. 2015a, Liu et al. 2016b, Zhu et al. 2015). The first step of the resistance to adversity is the perception of adversity. As a second messenger, Ca\(^{2+}\) plays an important role in signal transmission. Different stress can cause different calcium signals, generating the so-called Ca\(^{2+}\) signature, which can be sensed by Ca\(^{2+}\) sensors (CDPK, CaM (CML) and CBL) and then transduced through interacting with downstream proteins, including transporters, channels, transcription factors, enzymes, phosphatases and so on (Chen et al. 2015a).

The new technologies also provided us powerful tools for identifications of genes, proteins and metabolites associated with various stress tolerances (Table 2). We have selected many candidate genes involved in different stresses

| Type of stress | Technology | Main research result                                                                 | References                  |
|---------------|------------|-------------------------------------------------------------------------------------|-----------------------------|
| cadmium stress | metabolomics | thirty-nine metabolites included some amino acids, organic acids, sugars, and fatty acids are found to be responsive to Cd stress | Xie et al. 2014              |
| drought stress | transcriptomics | two hundred and seventy-seven drought responsive genes are identified, the up-regulated genes contain genes related to drought avoidance and tolerance traits and stress signaling | Zhou et al. 2014a            |
| stress         | transcriptomics | one hundred and twenty up-regulated genes are involved in proline biosynthesis, signal transduction pathways, protein repair systems, and removal of toxins, while 60 down-regulated genes are mostly related to basic plant metabolism | Kim et al. 2009              |
| waterlogging cold stress | proteomics | stress-responsive proteins are mainly involved in metabolism, energy, cell growth/division, protein synthesis and stress defense and there exists a different level of protein accumulation between hybrid and common bermudagrass | Zhao et al. 2011              |
| stress         | proteomics | thirty-nine proteins with significantly changed abundance between drought sensitive and tolerant variety were identified, most of which are involved in photosynthesis glycolysis, N-metabolism, tricarboxylicacid and redox pathways | Shi et al. 2014a              |
| waterlogging cold stress | metabolomics | about 75 proteins, mainly involved in photosynthesis, biodegradation of xenobiotics, oxidative pentose phosphate, glycolysis and redox pathway are identified | Ye et al. 2015, 2016          |
| cold stress    | proteomics and metabolomics | forty-five showed abundance changes after submergence treatment with 10 increased and 35 decreased; 34 of 40 metabolites contents exhibited down-regulation or no significant changes photosynthesis, nitrogen metabolism and carbon fixation pathways play key roles in bermudagrass response to cold stress | Ye et al. 2015, Chen et al. 2015a |
| salt stress    | transcriptomics | a total of 5867 genes are differentially expressed in cold acclimate versus non-acclimated bermudagrass, large numbers of AP2, NAC and WRKY family members are associated with cold stress | Zhu et al. 2015               |
| salt stress    | proteomics | seventy-seven differentially expressed proteins are identified upon drought and salt stresses and most of which are known to be involved in glycolysis, oxidative pentose phosphate, photosynthesis and redox metabolic pathways it identifies candidate genes encoding TFs (MYB, bHLH, WRKY) involved in the regulation of lignin synthesis, reactive oxygen species (ROS) homeostasis controlled by peroxidases, and the regulation of phytohormone signaling that promote cell wall loosening and therefore root growth under salinity | Ye et al. 2016, Hu et al. 2015b |
through the method, however, the function of the genes need to be verified. The information presented in this review and the studies currently been conducted in laboratories worldwide should be very helpful when efficient stable transformation methods for bermudagrass become available. Our laboratory is now focusing on the improvement of bermudagrass transformation technologies, including protoplast transformation method (Huang et al. 2018). We can also express bermudagrass candidate genes in model plants like rice, tobacco and Arabidopsis, to identify their functions. Then we can improve the resistance of bermudagrass to related adversity by transgenic means. At the same time, we can transfer resistance genes in bermudagrass to crops to improve their resistance to related stress. As global climate change continues, it is essential for researchers to generate more and new stress tolerant plants, including bermudagrass, to ensure world food safety.

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