Research Advances on Tall Fescue Salt Tolerance: From Root Signaling to Molecular and Metabolic Adjustment

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ABSTRACT. Soil salinity is one of the major abiotic stress factors that constrain plant growth and limit crop productivity. About a quarter of the global land area is affected by salinity; therefore, there is increased need to develop salt-tolerant crops. Tall fescue (*Festuca arundinacea*) is one of the most important cool-season turfgrasses, which has medium tolerance to salinity and has a promising potential to be used as a turfgrass under saline conditions. However, up to now, the maximum use of tall fescue under salinity stress is still limited by inadequate scientific literature. Recent studies have attempted to identify various adaptive responses to salinity stress at molecular, cellular, metabolic, and physiological levels in tall fescue. The successful integration of information concerning signal sensing, molecular tools with recent advances in -omics would certainly provide a clue for creating salt-tolerant tall fescue. Because salinity limits water availability to plants via hindering water absorption, and by inducing physiological drought, here we review and propose a probable mechanism of tall fescue response to salinity stress and to similar effects induced by drought based on published literature.

Soil salinity is a critical environmental problem that affects about one-third of the world's irrigated agricultural land and is a major constraint on agricultural productivity (Allakhverdiev et al., 2000; Cheeseman, 1988). Despite being one of the most important cool-season turfgrasses, the use of tall fescue in tropical regions has been constrained by remarkably poor salt tolerance compared with warm-season turfgrasses (Alshammary et al., 2004; Watkins et al., 2011). Interestingly, there are remarkably great intraspecific cultivar variations in tall fescue water stress tolerance (Carrow, 1996). The decisive factor in the intraspecific variations has been attributed to differences in morphological characteristics especially the roots (Beard, 1989; Huang and Fry, 1998; Marcum et al., 1995; Youngner et al., 1981). Generally, the salt-tolerant cultivars usually develop longer and extensive roots compared with salt-sensitive cultivars (Fig. 1). Because roots play integral roles in nutrient uptake in tall fescue, any unfavorable soil conditions such as elevated salinity would adversely affect growth (Dean et al., 1996). Salinity and drought-triggered water deficit have been one of the major causes of root death of tall fescue; hence, to enhance salt adaptation, persistent tall fescue root growth is a prerequisite (Weaver and Zink, 1955). Understanding the mechanisms of tall fescue salt tolerance will uncover new information that can be incorporated into breeding programs to improve salinity tolerance.

Response of Tall Fescue Roots to Salinity

Water absorption efficiency by plant roots is a vital determinant of salinity resistance, and water absorption relies on

the root size and its spatial distribution (Gupta and Huang, 2014). Recently, many studies on roots have focused on the morphological and growth characteristics, whereas extensive rooting has been positively correlated with increased resistance to water deficiency (Hays et al., 1991; Taylor, 1983). Tall fescue roots are closely associated with the surrounding soil and develop highly intricate branching that enables them to explore their environment (Bennett and Doss, 1960; Beyrouthy et al., 1990; Bonos et al., 2004; Hu et al., 2015; Newman and Moser, 1988). Like other plants, the detrimental effects of salinity on tall fescue can be attributed to ion toxicity, and osmotic and nutrient imbalances (Bowman et al., 2006). The NaCl-induced toxicity, ionic imbalances, and water deficiency in plants result from the osmotic stress caused by excess Na⁺ levels in the surrounding soil and a gross disruptions in the cytosolic Ca²⁺ as well as K⁺ homeostasis (Apel and Hirt, 2004; Gorham et al., 1990; Hu et al., 2011; Lynch et al., 1989; Munns, 1988, 1993, 2011; Munns and Tester, 2008; Schachtman et al., 1991). Putatively, each of the limiting factors can be sensed by an elaborate system of stress sensors and then translated into a broad array of physiological and genetic changes that optimize plant performance under saline conditions. Moreover, it is highly probable that the salt-stress response pathways may function simultaneously (Bray, 1997). Thus, the prevention of salt-induced root desiccation and subsequent detriments is one of the mechanisms to ameliorate the adverse effects of salt (Fu et al., 2004).

Salt-Stress Signaling and Transcriptional Regulation

When plants are exposed to environmental stress, their signaling pathways undergo a complex and interlinked network of processes which triggers response. Plants specificity to stress

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Fig. 1. Differences in root sizes of salt-tolerant 'Pure Gold' and sensitive 'Wolf Pack' tall fescue accession collected from U.S. Department of Agriculture. The plants were cultivated in Wuhan Botanical Garden, Chinese Academy of Sciences and evaluated for salinity tolerance.

signals makes it easy to figure out their specific signal sensor (Boudsocq et al., 2010; Dinnyen et al., 2008; Dubiella et al., 2013). Currently, only a few salt-stress sensors have been identified, and there is a scarcity of evidence to confirm the presence of a crosstalk between the sensors in tall fescue. Tall fescue has a medium salt tolerance, and its yield is decreased 50% at an electrical conductivity of $12 \text{ dS}\cdot\text{m}^{-1}$ (Richards, 1954); therefore, a complete rearrangement of cellular homeostasis via multiple pathways is a prerequisite for their acclimation to elevated environmental salinity. Recently, phytohormones, secondary messengers, and protein kinases cascades, which are vital components within the salt-stress-induced signaling network, have been reported to regulate a multitude of biochemical and physiological processes in plants under salinity stress (Hirayama and Shinozaki, 2010). In particular, the regulation of gene expression under salinity stress is entirely dependent on the signals.

Nonhormonal signaling

As sessile organisms, tall fescue perceives environmental cues such as salinity via changing its morphologies. The initial step of salt response in plants is hormonal or nonhormonal signaling (Knight, 2000). In this section, the nonhormonal mechanisms of salt-stress-signaling systems that trigger tall fescue response to salinity are discussed. These signals are first sensed by elaborate receptors and transmitted to the nucleus by a complex network.

Ca^{2+} SIGNALING. Apart from being one of the essential nutrients, Ca^{2+} also acts as a secondary messenger which mediates response to salt stress (Blumwald, 1987; Cabot et al., 2009; Dodd et al., 2010; Harper et al., 2004; Kanchiswamy et al., 2010; Sheen, 1996; Srivastava et al., 2013). Intracellularly, Ca^{2+} serves as a secondary messenger during abiotic stress signaling (Chidananda et al., 2010; Sanders et al., 2002). The Ca^{2+} signaling channels have been associated with salt-stress-induced cytosolic Ca^{2+} elevations (DeWald et al., 2001; Takahashi et al., 2001). Studies have reported that exogenous application of Ca^{2+} alleviated salt stress in tall fescue seedlings (Maeda and Nakazawa, 2008). In separate studies, it was observed that the

exogenous addition of Ca^{2+} to the growth medium ameliorated salt stress in various plants (El-Hamdaoui et al., 2003; Lahaya and Epstein, 1969; Sotiropoulos, 2007). Recently, Hu et al. (2016a) investigated the interplay between Ca^{2+} and hydrogen peroxide (H_2O_2) signaling in salt-stressed perennial ryegrass (*Lolium perenne*), which is a close relative of tall fescue. They observed that Ca^{2+} signaling remarkably enhanced the physiological response to salty conditions. The Ca^{2+} signaling pathway maintained high levels of reactive oxygen species (ROS) homeostasis in the stressed grass by increasing the responses of antioxidant genes, proteins, and enzymes. Studies have reported that exogenous application of Ca^{2+} alleviated salt stress in tall fescue seedlings (Maeda and Nakazawa, 2008). Xu et al. (2016) observed that Ca^{2+} induced antioxidant enzymes activity in tall fescue under oxidative stress. The effects of Ca^{2+} application were connected with the decrease in the Na^+ content in the plant roots and shoots and increased *ATPase* activity in tall fescue roots. In addition, tall fescue shoot selectively took Ca^{2+} under salinity stress (Gao et al., 2012). These results agree with those of Lunt et al. (1961) and Torello and Symington (1984) on tall fescue and of Kinraide (1999) on rice (*Oryza sativa*). It was also reported that the alleviatory effects of Ca^{2+} on salt stress in tall fescue might be caused by a reduction in the Na^+ intake and transfer from roots to the shoots (Cramer et al., 1989). Thus, understanding the Ca^{2+} signaling and the subsequent calcium-dependent events would be essential for improving tall fescue productivity under salinity stress.

POTENTIAL CROSTALK BETWEEN Ca^{2+} AND SALT OVERLY SENSITIVE (SOS) PATHWAYS. Along Ca^{2+} , the SOS signal-transduction pathway may play a key role in the ionic homeostasis and salt tolerance in plants (Batelli et al., 2007; Ji et al., 2013; Yang et al., 2009; Yue et al., 2012). Ma et al. (2014) reported that the overexpression of arabidopsis (*Arabidopsis thaliana*) *SOS1* + *SOS2* + *SOS3* genes enhanced salt tolerance in tall fescue. In their study, they observed that *SOS1* + *SOS2* + *SOS3* overexpressing tall fescue plants exhibited high growth rates and accumulated less Na^+ and more K^+ in the roots after NaCl treatment. The Ca^{2+} influx was higher in the transgenic plants than in the wild-type regimes, and the *SOS* overexpressors exhibited higher antioxidant enzyme activities suggesting increased ROS scavenging capacity. Recent studies have attempted to uncover the link between SOS and Ca^{2+} signaling pathways in plants under salinity stress. Interestingly, it was found that *SOS3* is actually a Ca^{2+} sensor, which transduces the signal downstream after activating and interacting with the *SOS2* protein kinase. The *SOS3*–*SOS2* complex was found to restore cellular ion homeostasis in tall fescue (Mahajan et al., 2008). Verslues (2007) observed that the interaction between *SOS2* and protein kinases enhanced the H_2O_2 signaling and led to water stress tolerance in arabidopsis. Collectively, these results show that there might be a complex crosstalk between the SOS and Ca^{2+} in tall fescue during the salt-stress response. In a closely related species, Hu et al. (2016a) observed that H_2O_2 signaling could activate ROS homeostasis by inducing antioxidant genes via the Ca^{2+} signaling pathway in perennial ryegrass leaves. Having described the role of the *SOS3*–*SOS2* complex, it would be important to find out the contribution of *SOS1* in salt tolerance of tall fescue. The *SOS1* genes encode a plasma membrane Na^+/H^+ exchanger (antiporter), and during salt stress, the upregulation of *SOS1* transcript level was diminished in the *sos3* and *sos2* mutant plants (Shi et al., 2000). This suggests that

SOS3–SOS2 kinase complex may control both the expression and activity of *SOS1*. High *SOS1*-encoded Na⁺/H⁺ antiporter activity in tonoplast vesicles was observed in tall fescue as a result of overexpression of the *AtNHX1* gene, and it enhanced salt tolerance to the transformed tall fescue progenies (Zhao et al., 2007). In addition, tall fescue plants that overexpressed *AtNHX1* gene were more resistant to salinity stress. The results suggest that this accumulation of Na⁺ in the vacuoles of root cells, mediated by vacuolar Na⁺/H⁺ antiporters, might reduce the toxic effects of salinity to tall fescue and thus enhance its salt tolerance.

PROTEIN KINASES. Recently, many expressed sequence tags of the known stress response genes have been identified from stressed tall fescue tissue libraries, and most of the identified tags represented genes that code for antioxidant proteins as well as various transcription factor protein families (Li et al., 2017; Mian et al., 2008). In addition, through de novo assembly and characterization of tall fescue transcriptome under water stress, some important revelations about the gene regulatory mechanism of water stress responses in tall fescue have been unraveled. In particular, after osmotic stress treatment, many sequence contigs have been annotated to signaling and water stress-related gene functions. Interestingly, protein kinases have constituted the highest group among the molecular function ontology (Talukder et al., 2015). This suggests that protein kinases and their complexes might play a crucial role in signal sensing and transduction in tall fescue during physiological drought caused by salinity stress. Several mitogen-activated protein kinases (MAPKs) were activated by cold, salt, and drought in monocot and dicot plants (Ichimura et al., 2000; Jonak et al., 1996; Kiegl et al., 2000), and genetic manipulation of MAPK signaling altered plant tolerance to abiotic stresses (Blanco et al., 2006; Lzwy and Morris, 2007; Shou et al., 2004; Xiong and Yang, 2003). For example, *Festuca arundinacea* zinc finger (*FaZnF*) is an MAPK gene, which encodes a zinc finger (ZnF) protein that was identified during salt-stress analysis in tall fescue. A *FaZnF* gene was upregulated in response to osmotic stress suggesting they may play a key role in enhancing salt-induced drought tolerance. The genes were upregulated in the calli overexpressing *FaZnF* genes when compared with control cell lines. In detail, *FaZnF* is a ZnF protein that is involved in the regulation of pathways initiated by the salt-stress response (Martin et al., 2012), which might influence the transcription of oxidative stress pathway genes in tall fescue. Apart from salt-related genes, recent studies have revealed the positive role for the MAPK-based signaling pathway in salt stress-induced proline accumulation (Kong et al., 2011; Zhang et al., 2011). The capacity to accumulate proline has been correlated with stress tolerance (Barnett and Naylor, 1966; Hasegawa et al., 2000; Kiyosue et al., 1996; Stewart and Lee, 1974; Vendruscolo et al., 2007). Proline acts as a vital osmolyte, an ROS scavenger, and as a molecular chaperone, which stabilizes the structure of proteins, thus protecting cells from stress-induced damage (Hare and Cress, 1997; Szabados and Savoure, 2010; Verbruggen and Hermans, 2008; Voetberg and Sharp, 1991). Proline accumulates in many plant species in response to different environmental stresses including high salinity (Rhodes et al., 1986). Man et al. (2011) investigated the osmotic stress tolerance associated with proline in two tall fescue genotypes. The major differences between the two tall fescue genotypes were related to the higher proline accumulation in the water stress-tolerant accession compared with the sensitive counterpart. Collectively,

high proline content lowered the osmotic potential and helped to maintain cell turgor, which enabled cell enlargement and excellent tall fescue growth during water stress. Alves and Setter (2004) had previously confirmed that proline and some phytohormones jointly allowed CO₂ assimilation by partially opening stomata, and served as a free radical scavenger which suppressed free radical-mediated damage during osmotic stress in tall fescue.

Hormonal signaling

Phytohormones act as crucial molecules that perceive and relay stress signals to downstream molecules to trigger transduction pathways in tall fescue under salt stress. Thus, to understand clearly the roles of different plant hormones in salt-stress tolerance in tall fescue, a clear and practical link should be achieved.

ABSCISIC ACID (ABA). Abscisic acid plays a vital role in the response of plants to salinity, and ABA-deficient plant mutants performed poorly under salinity stress (Xiong and Zhu, 2003; Xiong et al., 2001). In arabidopsis, exogenously applied ABA induced a number of genes that responded to osmotic stress (Kazuo and Yamaguchi-Shinozaki, 2007; Zhu, 2002). In response to salt stress, small molecules such as ABA and Ca²⁺ are used by plants to induce various signaling cascades (Pei, 2000). Salt-stress signaling via Ca²⁺ and ABA mediated the expression of the dehydration-responsive element (DRE). The DRE was identified as an ABA-independent *cis*-acting element, which was vital for the regulation of gene expression in response to high salinity in arabidopsis (Yamaguchi-Shinozaki and Shinozaki, 2005). Subsequently, DRE was identified in many promoters of salt-stress-inducible genes in tall fescue, and DRE overexpressor lines exhibited tolerance to salinity. Previously, DRE was overexpressed in tall fescue and other plants (Dubouzet et al., 2003; Ito et al., 2006; Oh et al., 2005; Pellegrineschi et al., 2004). The transgenic plants showed tolerance not only to drought and cold but also to high salinity. Transgenic tall fescue, which contained *DRE* genes, accumulated a significantly higher level of antioxidant enzymes and proteins under osmotic stress conditions than control plants (Zhao et al., 2007). These data suggest that the DRE regulon exists in tall fescue and can be used to improve tolerance to high salinity via gene transfer. Previous metabolic studies in tall fescue focused on ABA-mediated stomatal closure. Gao and Li (2014) reported that salt-tolerant tall fescue exhibited slower ABA accumulation rate than sensitive cultivars during short-term salt stress. This may suggest that low accumulation rate of ABA in tall fescue leaves could be beneficial for the maintenance of photosynthesis during a salt-induced physiological drought in tall fescue. Apart from being an integral regulator of abiotic stress signaling, ABA also may promote stomatal closure to reduce water loss by transpiration, induce the expression of numerous stress-related genes and initiate stress-induced metabolic adjustments (Cutler et al., 2010; Raghavendra et al., 2010; Umezawa et al., 2010).

CYTOKININS AND INDOLE-3-ACETIC ACID (IAA). Cytokinins delay plant senescence process by maintaining the integrity of the tonoplast membrane (Thimann, 1987). Plants with higher cytokinins exhibit greater osmotic stress tolerance and exogenously applied cytokinins could improve tall fescue tolerance to water stress (Zhang and Schmidt, 2000; Zhang et al., 2005). Indole-3-acetic acid is associated with root initiation and growth (Nordstrom et al., 1991). A recent study has shown that leaf tissue IAA content was positively correlated with

Fig. 2. Proposed mechanism of salinity tolerance in tall fescue. Salt-stress activates changes in the production of abscisic acid (ABA), indole-3-acetic acid (IAA), and cytokinins by tall fescue roots. The signal is transduced leading to the expression of genes that are responsible for biosynthesis superoxide dismutases (SOD) and ascorbate peroxidase (APX) enzymes to scavenge excess reactive oxygen species (ROS) and drought responsive elements (DRE). The nonhormonal response involves activation of the Ca^{2+} pathway to maintain ionic homeostasis and biosynthesis of osmolytes (such as sucrose and fructans), which decreases the osmotic potential of cells thus facilitating water intake. In addition, tall fescue-endophyte symbiosis also provides crucial metabolites (such as alkaloids and organic carbon) which play important role in osmotic adjustment thus enhancing salt tolerance; SOS = salt overly sensitive, FaZnF = *Festuca arundinacea* zinc finger protein, MAPKs = mitogen-activated protein kinases.

drought tolerance, and exogenous application of indole-3-butyric acid increased endogenous IAA, which improved osmotic stress tolerance in tall fescue (Zhang et al., 2009). Osmotic stress reduced turfgrass quality, relative leaf water content, leaf IAA and cytokinin content, and increased proline content. Taken together, these findings show that the metabolism of ABA, cytokinins, and IAA might be associated with salinity tolerance in tall fescue. Selection of cultivars that are sensitive to exogenous application of phytohormones under salt stress may be a practical approach to improving tall fescue salinity tolerance.

Metabolism and Osmotic Adjustment

Osmotic adjustment is one of the most important strategies adopted by many plants to help them overcome salt stress (Bernstein, 1961, 1963). Kirkham et al. (1969) observed that highly salt-tolerant barley (*Hordeum vulgare*) had lower osmotic potential than salt-sensitive green bean (*Phaseolus vulgaris*). West et al. (1990) reported that young tall fescue plants exhibited high resistance to water deficit due to a remarkable decline in water potential and turgor. Metabolite-driven osmotic adjustment is vital for plants response to osmotic stress to ensure their proper growth and development. Elucidation of the metabolism of various compounds and how they are controlled at the transcriptional level in tall fescue would contribute to our understanding of salt tolerance and provide tools to improve crops. Because of their crucial roles in plant growth under environmental stress, the metabolism of several compounds has been studied in tall fescue under salinity stress.

SUCROSE. Sucrose serves as a crucial osmotic solute in plants under salt and drought stress (Fu et al., 2007; Premachandra et al., 1992; Rekika et al., 1998). The effect of water deficits on sucrose levels has been reported in some plants. For example, improved response of a bean (*P. vulgaris*) to osmotic stress was associated with sucrose metabolism (Castrillo, 1992; Vassey et al., 1991). Zhang and McManus (2000) reported an increased

sucrose level in white clover (*Trifolium repens*) growing under osmotic stress. Fu et al. (2010) observed that tall fescue that was exposed to a short-term osmotic stress accumulated higher sucrose content than well-irrigated controls, which enabled water intake. Higher sucrose levels in water-stressed tall fescue might contribute to improved salt-induced osmotic stress by decreasing the osmotic potential of the roots.

FRUCTAN. Fructan is a metabolite that is synthesized directly from sucrose as the sole precursor and consists of polymeric chains of fructose (Pavis et al., 2001). Temperate grasses such as tall fescue accumulate water-soluble fructans. The biosynthesis and accumulation of fructans showed remarkable seasonal variation (Pollock and Jones, 1979), and their mobilization played

an important role in tall fescue regrowth and defoliation (Morvan-Bertrand et al., 2001). However, it is unclear how fructan metabolism is actively involved in tall fescue salinity tolerance. Fructan content was reported to increase with osmotic stress as sucrose concentration increased in tall fescue. This might be attributed to the fact that sucrose is the substrate for fructan synthesis (Schnyder and Nelson, 1987). Later, Spollen and Nelson (1994) analyzed the behavior of fructan to salt stress in tall fescue. The main outcome of that study was that fructan metabolism was involved in osmotic-stress tolerance and shoot growth via lowering cellular osmotic potential which might confer higher salinity tolerance.

REACTIVE OXYGEN SPECIES. Reactive oxygen species are produced in both stressed and unstressed plants cells. Plants have well-developed defense systems against ROS which involves both limiting its formation as well as instituting its removal (Huang, 2001; Munns, 2002). In particular, plants respond to high ROS via increased enzymatic and nonenzymatic antioxidant processes (Alscher and Hess, 1993), but the precise mechanism underlying the process in tall fescue is still not understood. Many studies have revealed high accumulation of antioxidant enzymes in tall fescue under lead (Lou et al., 2017), aluminium (Jin et al., 2011), heat (Du et al., 2009; Hu et al., 2015, 2016b; Jiang et al., 2001). Bi et al. (2016) investigated the behavior of antioxidant compounds in tall fescue during induced water stress. They observed a high production of superoxide dismutases (SOD), peroxidases (APX), and catalases. At the same time, a decline in the level of malonaldehyde in osmotic tolerant tall fescue compared with osmotic-sensitive counterpart was observed. At the gene level, Lee et al. (2007) observed that simultaneous overexpression of both CuZnSOD and APX in transgenic tall fescue plants conferred an increased tolerance to a wide range of abiotic stresses including salinity. This was supported later by the observation that the genes encoding copper-zinc SOD (CuZnSOD) and APX enzymes were overexpressed under salt stress which decreased ROS and subsequently improved salt tolerance of tall fescue (Kravchik and Bernstein, 2013).

Symbiotic Metabolite Sharing

A symbiotic association that is specific to tall fescue is the infection with the *Neotyphodium* and *Epichloë* fungal species, which may provide tall fescue with the beneficial metabolites (Christensen and Voisey, 2009; Clay and Schardl, 2002; Leuchtmann et al., 2000). Recently, Hosseini et al. (2015) reported that tall fescue-endophyte association profoundly increased crucial plant metabolites in the soil especially carbohydrates. The specific mechanisms of endophyte-enhanced salt-stress avoidance or tolerance in tall fescue are still complex and might involve direct and indirect effects of the fungal metabolites on the host plant. Elmi and West (1995) reported that infection of tall fescue with endophyte influenced the osmotic adjustment and water-deficit recovery of tall fescue. Metabolomic responses to osmotic stresses are usually linked to changes in the availability of essential nutrients (Nagabhyru et al., 2013). Recently, it was reported that endophytes might actually produce growth regulators in tall fescue (Debattista et al., 1990). Recent advances in analytical chemistry, such as mass spectrometry-based methods, have allowed botanists to explore metabolomic profiles of tall fescue under environmental stresses such as salinity (Balmer et al., 2013). Metabolomics analyses which compared endophyte-infected with uninfected tall fescue plants showed a significant decrease in the nitrogenous compounds, and some fiber components with a profound increase in simple sugars and organic acids (Bush et al., 1997; Rasmussen et al., 2008). In addition, tall fescue biomass and phenolic and organic carbon contents were influenced by endophyte status of tall fescue cultivar and their interaction (Guo et al., 2015). Achevaleta et al. (1989) observed an increased N level in endophyte-infected plants compared with noninfected plants and higher tolerance to osmotic stress. When tall fescue was grown in saline soils, the endophyte infection also significantly increased the tiller number, shoot height, and the total biomass of the host grass (Yin et al., 2014). The results indicate that there are positive benefits derived from the endophyte-tall fescue association which resulted in growth stimulation, improved survival, and osmotic stress tolerance to the host plant. Apparently, this association could be vital for salinity tolerance enhancement in tall fescue. However, the enhanced salt tolerance in tall fescue via endophyte modification is not reliable and universally expressed, moreover, tall fescue responses to endophytes involve complex adjustments, which are poorly understood. In addition, because alkaloids produced by many endophytes cause severe animal health hazards, the focus should shift to replacing the common toxic fungal strain with novel cultivars that do not produce the mammal-toxic alkaloids but still maintain salt tolerance benefits.

Conclusion

Apparently, research advances in tall fescue salt-stress signaling and the subsequent molecular and metabolic processes will be critical for the analysis of salt tolerance. However, currently, the improvement of tall fescue performance under salinity is still impaired by complexities in the genomic and integral physiological traits. The recent research advances in -omics technologies should be incorporated into the currently available information. In addition, a recent breakthrough in association mapping techniques in tall fescue using molecular markers will enable the production and analysis of

a large number of mutant tall fescue plants which will allow botanists to identify many alleles that are involved in salt tolerance. Collectively, the incorporation of all research breakthroughs and other advancements through collaborative approaches is expected to redesign tall fescue for the future world. Figure 2 shows our proposed mechanism of salt tolerance in tall fescue.

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