3 Physiological, Biochemical and Molecular Mechanisms Regulating Post-Drought Stress Recovery in Grass Species

Cathryn Chapman and Bingru Huang

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3.1 INTRODUCTION

Drought stress is an important environmental factor that can negatively impact the growth and development of many plant species. In recent decades, there has been an increase in the frequency and duration of drought events, which is of great agricultural concern worldwide (Karl et al., 2008, 2009; Mishra and Singh, 2010; IPCC, 2014). The demand for water continues to grow, and there is a constant struggle for optimum resources. Drought stress causes various damages, including decreases in leaf water relations, membrane stability and metabolic activities (Hsiao, 1973; Levitt, 1980; Nilsen and Orcutt, 1996). Because an adequate supply of water is essential to the normal functioning of plants, its limited availability due to lack of precipitation can have detrimental ecological and economic effects.

One of the major plant species adversely affected by drought stress is the grass family, Poaceae. The Poaceae family, which is one of the largest flowering plant families, is comprised of an estimated 11,000–12,000 different species (Kellogg, 2015; Soreng et al., 2017). Included are various annual cereal species, such as maize (Zea spp.), rice (Oryza spp.), wheat (Triticum spp.) and sorghum (Sorghum spp.) (USDA, 2018) which are cultivated as food staples. Various perennial grass species are widely cultivated or grown in natural areas, such as those used as forage, turfgrass and biofuels (USDA, 2018).

Grass species in arid and semi-arid regions can be adversely affected by a moderate or severe drought stress level brought on by lack of water availability, which makes it critical for understanding the mechanisms that these plants have developed in order to survive during drought events. While there is a great interest within this particular area, there should be an equal interest in learning more about the mechanisms behind regrowth and re-establishment after the drought stress is relieved, or rather when the level of precipitation resumes to that of a more sustainable level, after which any water use restrictions can be removed to allow for normal irrigation once again.

Strategies for plant drought resistance is an area of research that has been widely studied across a variety of grass species, including wheat (Morgan, 1983; Ritchie et al., 1990; Gunasekera and Berkowitz, 1992; Rampino et al., 2006; Han et al., 2015; Abid et al., 2018), switchgrass (Panicum virgatum) (Sun et al., 2012; Meyer et al., 2014; Liu et al., 2015) and Kentucky bluegrass (Poa pratensis) (Perdomo et al., 1996; Wang et al., 2003; Hu et al., 2010; Xu et al., 2011a, 2011b; Xu et al., 2013), to name a few. Indeed, it is important for grass species to be able to survive and tolerate long-term drought, but it is also critical that they can recover from drought stress through regrowth and re-establishment once the stress is removed (Levitt, 1980; Chaves and Oliveira, 2004; Lopes et al., 2011). In other words, grass plants need to be able to maintain normal functions under varying levels of water deficits, and then rapidly recover after the stress is relieved. The ability of grass species to withstand drought and recover is the key to ensuring a more sustainable grass crop for future generations.

This chapter will discuss physiological, biochemical and molecular factors associated with the recuperative ability of grass species from drought stress by addressing the questions on how drought-resistance traits may affect post-drought recovery, and identifying the specific mechanisms involved in post-drought stress recovery that enable plants to regenerate or re-establish and restore normal functions?

The following sections will discuss the details of important drought-resistance mechanisms and their relation to post-drought recovery mechanisms on a physiological, biochemical and molecular level.
3.2 CARBOHYDRATE ACCUMULATION AND REMOBILIZATION

A major area of post-drought recovery regrowth potential involves the use of carbohydrate reserves that are stored within tissues of certain plant organs during drought, which provides a recovering plant with the necessary resources for rapid regrowth. Under prolonged drought conditions where photosynthesis is limited, carbohydrates can accumulate due to a decrease in respiration and overall decrease in carbohydrate demand caused by growth inhibition (Levitt, 1980; Chaves, 1991; Nilsen and Orcutt, 1996; Thomas and James, 1999; Chaves and Oliveira, 2004; Fry and Huang, 2004; Huang et al., 2014). Managed turfgrasses that are used on home lawns or sports fields are a classic example of a type of grass that can store carbohydrate reserves within meristematic tissues during drought stress and then utilize them for rapid regrowth of tissues upon re-watering. In order to gain a better understanding of this type of post-drought stress recovery mechanism, however, it is relevant to understand the growth habits of turfgrass species. Unlike other plant species, whose growing points, or meristems, are at the tips of the plant, turfgrass species have meristematic tissue located near the soil level at the base of the plant, within an organ called the crown (Beard, 1973; Turgeon, 2012; Emmons and Rossi, 2016). This feature of turfgrass, as well as other perennial grasses, is what allows them to be cut down or mowed so long as the meristematic region remains intact and uninjured (Turgeon, 2012; Emmons and Rossi, 2016). Cells located in the meristematic region can divide and enlarge, thus providing overall plant growth.

In addition to the primary lateral shoots, or tillers, that grow from crowns, some turfgrass species generate new growth from stolons or rhizomes, which can form shoots and roots from their nodes to produce new above-ground daughter plants using axillary buds (Beard, 1973; Turgeon, 2012). The spreading growth habit of stolons or rhizomes can also strengthen the ability to recuperate from drought stress, allowing the turfgrass to spread laterally to fill in bare spots that may have been damaged during drought.

Since growth can be inhibited while a plant is experiencing drought, it would seem that such damages may subsequently inhibit the growth of new or established daughter plants once re-watering occurs. However, perennial grasses, such as turfgrass, have developed other mechanisms to rapidly recover using their important growing points that contain meristematic tissues. In this case, maintaining the viability of the meristematic tissues within stolons, rhizomes and crowns during drought stress is very important for continued plant survival (Chai et al., 2010; Sarath et al., 2014). The post-drought recovery mechanism that perennial grass species utilize is that they store carbohydrates during stress in various plant structures and are then able to remobilize the carbohydrates and send them to axillary buds in order to make new roots and shoots when the stress is relieved (Beard, 1973; Huang and Fu, 2000; Huang and Gao, 2000; DaCosta and Huang, 2006a, 2006b; Chai et al., 2010; Yang et al., 2013). Thus, research has focused on finding ways to ensure these organs are protected so that they can allow the turfgrass to recuperate from the effects of drought. Additionally, by protecting the axillary buds of stolons and rhizomes during periods of drought, they can contribute to active growth and development of new daughter plants once water becomes available again.

It is worth noting that there are differences in drought recuperative ability of various turfgrass species. For instance, compared to bunch-type grasses that lack stolons or rhizomes, such as perennial ryegrass (Lolium perenne), stoloniferous and rhizomatous turfgrass species, such as creeping bentgrass (Agrostis stolonifera) and Kentucky bluegrass, respectively, may have a greater potential to survive during longer periods of drought and also have the ability to make new daughter plants (with roots and shoots) more rapidly after the stress is relieved, and they are re-watered (Beard, 1973).

In a previous study, which measured total nonstructural carbohydrate (TNC) content in the rhizomes of Kentucky bluegrass (KBG) and in the crowns of perennial ryegrass (PRG), it was found that the recuperative potential of PRG might be less than that of KBG, as exhibited by the TNC content decrease in the crowns of PRG during drought, when compared to the non-stressed control (Chai et al., 2010). According to this report (Chai et al., 2010), storage of carbohydrates in the rhizomes of KBG increased in comparison to the non-stressed control during drought stress, and then decreased upon re-watering, most likely because they were remobilizing to form new tissues, which was shown by an increase in the production of both new roots and new tillers by the end of the recovery period in comparison to PRG. It seems that due to the reduced carbohydrate storage in the crowns of PRG during drought stress, these plants, in comparison to KBG, had fewer reserves to remobilize upon re-watering and, therefore, could not form new roots or shoots as quickly or efficiently.

This trend of accumulating sugars during drought stress, including water-soluble carbohydrates, and subsequent improved growth potential upon re-watering has also been observed in various other grass species, including drought-tolerant populations of Dactylis glomerata (Volaire, 1994, 1995), rice (Oryza sativa) (Mostajeran and Rahimi-Eichi, 2009), barley (Hordeum vulgare) (Sicher et al., 2012) and wheat (Triticum aestivum) (Gupta et al., 2011). Studies have attributed the increase in water-soluble carbohydrates, such as sucrose, during drought stress, to the decreases in acid invertase which controls sucrose breakdown, and increased activities of two sucrose synthesizing enzymes, either sucrose synthase or sucrose-phosphate synthase (Kaur et al., 2007; Fu et al., 2010; Yang et al., 2013). Although certain water-soluble carbohydrates are most often associated with drought tolerance, fructans are the major contributor to regrowth of tissues during re-watering after drought (Volaire, 1994, 1995; Yang et al., 2013).

Of course, the concept of regrowth from stored reserves can also be applied to other grass species in addition to the aforementioned C₃ grass species. For example, many C₄ perennial grasses, such as switchgrass and miscanthus (Miscanthus x giganteus), must also utilize their storage organs to overcome
adverse environmental conditions, including drought, by maintaining viable meristems (Sarath et al., 2014). This recovery mechanism, although not unique to drought stress, is made possible by the induction of a commonly known drought escape mechanism called dormancy, which prevents growth of the meristems during the adverse conditions, and ultimately stores reserves and resumes growth using those reserves once the stress is relieved (Sarath et al., 2014).

### 3.3 OSMOLYTE ACCUMULATION AND PROTECTIVE BENEFITS

Plants also accumulate other compounds in addition to the accumulation of some forms of carbohydrates during drought stress which may contribute to the post-drought recovery of plants. Under drought stress, plants accumulate various solutes in order to maintain cell turgor pressure and volume known as osmotic adjustment, which protect plant tissues from dehydration damages (Turner and Jones, 1980; Hale and Orcutt, 1987; Nilsen and Orcutt, 1996; Hopkins and Hüner, 2004). Common osmoregulants include inorganic ions, such as potassium, calcium, or sodium, organic compounds, such as sugars (sucrose, glucose and fructose), organic acids (malic or citric acid), sugar alcohols (mannitol or sorbitol) and amino acids (proline or glycine betaine). These compounds may accumulate within the vacuole and the cytoplasm, lowering the osmotic potential of plant tissues. When a plant accumulates a higher concentration of solutes, the more negative the osmotic potential becomes, which essentially results in higher osmotic adjustment ability and greater water retention potential when plants are exposed to drought stress.

Osmotic adjustment does not only maintain cell turgor, but also has the functions of protecting membranes, proteins, cellular organelles and enzymes from dehydration damages (Hoekstra et al., 2001; Oliver et al., 2010). Osmotic adjustment capacity can play a major role in a plant’s ability for recovery once re-watering occurs. For instance, during shorter periods of drought, osmotic adjustment allows stomata to remain open through its maintenance of turgor pressure, allowing carbon gain and cell growth to occur despite the low water potential brought on by mild drought stress (Nilsen and Orcutt, 1996).

Through their ability to tolerate drought stressed conditions and maintain carbon balance via turgor pressure, plants can have overall greater recovery potential upon re-watering by their ability to continue necessary metabolic functions despite the lack of water availability.

Osmotic adjustment has been shown to help improve post-drought recovery in various plant species, and many studies have correlated greater osmotic adjustment ability with greater post-drought recovery potential, as shown in studies with analysis of metabolite content in plants during drought and re-watering. Many metabolites, including glycine, isoleucine, asparagine, threonine, spermine, proline, adenosine, fructose and valine, found in leaves and roots of maize (*Zea mays*) that were responsive to drought stress were also responsive to re-watering (Sun et al., 2013). Additionally, the accumulation of amino acids, which are nitrogen enriched compounds, has shown to be a key factor in promoting recovery upon re-watering. In studies on maize where many amino acids accumulated during drought stress, it was found that upon re-watering there was a decrease in isoleucine, leucine, valine and proline levels, suggesting that accumulated nitrogen from these amino acids might be used as a substrate for protein replacement during recovery (Sun et al., 2016). The overall accumulation and subsequent decrease in the levels of various osmolytes during drought stress and recovery has also had positive outcomes for improvements in synthesizing new biomass upon re-watering (Warren et al., 2012), and can be a major component in plant recovery through its assistance in resuming metabolic functions, such as photosynthesis and stomatal conductance (Souza et al., 2004; Foster et al., 2015). It is thought that drought-injured photochemical systems involve important repair processes to resume photosynthesis upon re-watering (Miyashita et al., 2005) and various abiotic stress-tolerance-related metabolites, such as the polyamine spermine, may be utilized for this purpose. For example, spermine can elicit repair processes that help prevent further damage to membranes or photosynthetic functions (Yamaguchi et al., 2007; Farooq et al., 2009; Zhou and Yu, 2010), and increases in photosynthesis are often seen during re-watering (Sun et al., 2013).

The benefits of osmotic adjustment and the accumulation of solutes for post-drought recovery have generally been positive in numerous studies; however, some have had conflicting results stating that this process occurs at the expense of yield. In the case of agricultural crops, where a large and profitable yield is the main goal, osmotic adjustment in this light could then be seen as a negative mechanism. There has been some controversy (Munns, 1988; Serraj and Sinclair, 2002) as to whether or not osmolyte accumulation benefits the recovery of growth or gas exchange directly, as seen by a poor correspondence between osmotic adjustment and yield at the end of the post-drought recovery period. This may lead some to think that this type of drought tolerance mechanism may only be useful in terms of post-drought recovery for turfgrass or other perennial forage grass species where a high yield is not necessarily as desirable. However, it is evident that there are many protective benefits that osmolytes can have, which may lead to rapid resumption of metabolic functions upon re-watering, such as increased photosynthetic activity (Chaves et al., 2009) or signaling of important compounds, which would most likely lead to overall improvements in crop biomass yield and should be considered a positive outcome for overall plant survival.

### 3.4 OXIDATIVE STRESS AND ANTIOXIDANT PROTECTION

One of the unfortunate effects of drought stress is oxidative stress, or the increased production of harmful reactive oxygen species (ROS) within plants, which include radicals such as superoxide or hydroxyl, and non-radicals such as hydrogen peroxide and singlet oxygen. Under mild stress conditions, ROS are formed, but can quickly be quenched by antioxidants,
including either enzymatic antioxidants, such as superoxide dismutase (SOD), peroxidase (POD), catalase (CAT), or ascorbate peroxidase (APX), or non-enzymatic antioxidants, such as ascorbate, glucose, or tocopherols (Smirnoff, 1993; Chaves and Oliveira, 2004; Ahmad et al., 2008; Koyro et al., 2012). However, during prolonged and severe drought stress, the production of ROS is typically greater as a result of the overall limitation in photosynthesis, which causes decreased intercellular CO₂ and subsequent limited carbon reduction by the Calvin Cycle (Hsu and Kao, 2003; Chaves and Oliveira, 2004; Ahmad et al., 2008). More specifically, the decreased photosynthetic activities result in an increased transfer of electrons to oxygen (Smirnoff, 1993; Navari-Izzo and Rascio, 1999). Then, in a chain reaction, more ROS will be formed in multiple sites in addition to the chloroplast, including mitochondria or peroxisomes. Injury to these organelles can include the following: damages to lipids (through oxidation of unsaturated fatty acids, in a process called lipid peroxidation, as well as membrane leakage of solutes); proteins (through loss of function or modifications); or DNA (through mutations and other lethal genetic effects) (Møller, 2001; Foyer and Noctor, 2003; Apel and Hirt, 2004; Foyer and Noctor, 2005; Ahmad et al., 2008). The enzymatic and non-enzymatic antioxidants can work either alone or in combination to scavenge and detoxify ROS (Smirnoff, 1993; Apel and Hirt, 2004; Foyer and Noctor, 2005; Ahmad et al., 2008; Koyro et al., 2012).

Some amino acids also play positive roles in antioxidant functions when accumulated during drought stress (Smirnoff and Cumbes, 1989; Ashraf and Foolad, 2007; Molinari et al., 2007). Because of these benefits, certain amino acids can be applied exogenously to plants to aid in drought stress tolerance and, ultimately, in post-drought recovery. One example is proline, which is a well-known amino acid that accumulates in a variety of plant species during drought. Increases in endogenous proline content have been associated with increases in leaf hydration levels, better growth and yield and antioxidant defense (Szabados and Savouré, 2010; Anjum et al., 2012; An et al., 2013; Bandurska et al., 2017; Zegaoui et al., 2017). Proline levels accumulate during drought stress and subsequently decrease upon recovery (Krasensky and Jonak, 2012), a trend that is often seen with osmoregulants when the stress is relieved. For example, in cotton (Gossypium hirsutum) during drought stress, the accumulation of drought-induced proline has also been associated with increases in Δ1-Pyrroline-5-carboxylate synthetase (P5CS) and Δ1-Pyrroline-5-carboxylate reductase (P5CR), two major enzymes in the biosynthetic pathway for proline synthesis (Parida et al., 2008). Other studies have also seen increases in P5CS and proline synthesis in cowpea (Vigna unguiculata) (Zegaoui et al., 2017) and grass species, such as barley (Bandurska et al., 2017). It has also been noted that there are decreases in proline dehydrogenase (PDH), a proline degrading enzyme, during drought stress (Parida et al., 2008; Zegaoui et al., 2017). Upon recovery, the levels of P5CS and PDH decreased and increased, respectively, thus shedding more light on the regulation of these enzymes for controlling proline levels during drought stress and post-drought recovery.

GABA (γ – Aminobutyric acid) is another amino acid that has been found to accumulate in plant species under drought stress, which has also been associated with better growth and yield, as well as increases in chlorophyll content and decreases in oxidative damage (Shelp et al., 1999; De Diego et al., 2013; Bown and Shelp, 2016; Yong et al., 2017). GABA is a non-protein amino acid that plays a role in carbon/nitrogen balance, and can also regulate proline metabolism and assist proline in ROS scavenging (Bouché and Fromm, 2004; Signorelli et al., 2015). When exogenously applied, both proline and GABA have been known to have positive effects for alleviating damages due to drought in wheat (Farooq et al., 2017), creeping bentgrass (Li et al., 2017) and perennial ryegrass (Krishnan et al., 2013), and increases in endogenous concentrations of each, respectively, are often seen. Studies have found that in addition to the improvements in plant-water relations and lesser oxidative damage that the exogenous application of GABA can provide, it was also accompanied by up-regulation of genes encoding antioxidant enzymes, such as CAT, SOD and APX, as well as up-regulation of stress-protective genes, such as the following: genes that are involved in stress defense response signaling (mitogen-activated protein kinase [MAPK]); ROS neutralization (Metallothionein [MTI]); and defense proteins (heat shock protein [HSP70]) (Li et al., 2018). Although the complete mechanisms behind proline- and GABA-assisted drought tolerance and post-drought recovery are not fully understood, exogenous application of these particular osmolytes deserves further attention in order to learn more about their potential to prevent irreversible damages to membranes or proteins that would have otherwise been caused by ROS from oxidative stress.

### 3.5 Hormone Metabolism and Plant Growth Regulation

Drought stress can have a major impact on hormonal metabolism, and changes in hormone levels are often observed. For instance, during the initial effects of drought, when the plant begins to wilt, there can be decreases in growth promoters, such as cytokinins (CK), gibberellins (GA) and auxin, and increases in growth inhibitors, such as abscisic acid (ABA) and ethylene (Nilsen and Orcutt, 1996; Gupta, 2005). The effects of drought can be altered through exogenous application of hormones or plant growth regulators (PGRs), which can have benefits for promoting both drought stress tolerance and recovery upon re-watering. Therefore, the following section will discuss some key players in the hormone regulation of drought tolerance and post-drought recovery.

ABA is one of the most commonly known drought stress-induced hormones. It has been widely studied that under stressful environmental conditions, such as during initial drought responses, ABA production will increase and will reduce stomatal aperture in order to limit transpirational water loss so that the plant tissue can regain turgor (Hiron and Wright, 1973; Hsiao, 1973; Aspinall, 1980; Hale and Orcutt, 1987; Gupta, 2005; Tuteja, 2007). ABA production
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During drought stress is a vital drought avoidance mechanism, as expressed by its contribution to maintaining a favorable water status via either controlling water uptake through an extensive root system, or via reduced water loss from leaves (Levitt, 1980; Nilsen and Orcutt, 1996). In fact, studies on Kentucky bluegrass have shown that although ABA levels are much higher in drought-susceptible cultivars in comparison to drought-tolerant cultivars, it is thought that the drought tolerance is actually related to stomatal sensitivity of accumulated endogenous ABA content during mild drought stress, which was exhibited by less severe declines in stomatal conductance, photosynthetic rate and leaf water potential for the more drought-tolerant cultivars (Wang and Huang, 2003).

Ultimately, this allows drought-tolerant plants to conserve more water and survive longer under drought stressed conditions. Additionally, due to the stomatal sensitivity, it can mean that even a low accumulation of ABA in drought-tolerant cultivars may lead to better maintenance of photosynthesis under short term drought and allow for more dry matter accumulation that can help survive longer drought periods and promote more rapid recovery (Wang and Huang, 2003).

Although the level of drought-induced ABA and its specific role may differ by species, the severity of the drought and/or plant developmental stage, it is generally understood that the increased ABA is related to chemical signaling, which can occur between the roots and the shoots in response to drought stress. This has been studied by others in depth (Levitt, 1980; Reid and Wample, 1985; Nilsen and Orcutt, 1996; Davies et al., 2002; Gupta, 2005). However, the question remains as to how regulation of ABA can increase the recuperative ability of plants after drought stress. In order to answer this question, it is important to think of how this drought avoidance mechanism can be utilized as more of a drought tolerance mechanism, which would promote survival and post-drought recovery. One way of doing so is to use ABA as a PGR to initiate earlier stomatal closure. This can be especially helpful for drought-susceptible cultivars of plants, which may have stomata that are not as sensitive to ABA levels compared to drought-tolerant cultivars. On an agricultural scale, this can be helpful for drought-susceptible grass crop species to promote earlier stomatal closure and, thus, more tolerance which can aid in post-drought recovery. In fact, when ABA is applied exogenously, both drought-tolerant and drought-susceptible cultivars respond more quickly to the application, closing stomata more rapidly and ultimately enhancing plant-water relations by inducing osmotic adjustment and causing less cell membrane damage, which has been seen in Kentucky bluegrass (Wang et al., 2003) and wheat (Kirkham, 1983).

Additionally, low concentrations of exogenously applied ABA have been shown to induce antioxidative defense responses in maize seedlings (Jiang and Zhang, 2001) and Bermuda grass (Cynodon dactylon) (Lu et al., 2009).

During prolonged drought stress the stomata may remain closed, further limiting necessary metabolic functions. Since plants may have different rates at which stomata re-open upon re-watering, one way to promote the rapid resumption of photosynthesis and subsequent plant recovery could be with the use of another PGR, such as CK. For instance, post-drought recovery foliar treatment of synthetic cytokinin, 6-benzylaminopurine (6-BA), was able to recover Kentucky bluegrass plants from drought stress by enhancing stomatal re-opening and initiating photosynthesis (Hu et al., 2012a, 2012b). It has also been reported that the exogenous application of 6-BA promoted tiller growth and regeneration after re-watering, and induced endogenous accumulation of CK, which caused a decrease in the content of ABA (Hu et al., 2012a). In addition to the rapid post-drought recovery benefits that accompany the endogenous ratios or balance of CK to ABA upon re-watering (DaCosta and Huang, 2007), it is important to note that exogenous application of CK could have many benefits at the whole plant level during adverse environmental conditions, as observed in wheat (Monakhova and Chernyad’Ev, 2004; Kumari et al., 2018) and maize (Blackman and Davies, 1983; Wang et al., 2016). Overall, the rapid re-opening of stomata due to CK is critical for the resumption of gas exchange and photosynthetic activities that facilitate post-drought recovery, which makes this mechanism very applicable to the agricultural system for overall improved yield upon re-watering.

In addition to PGRs being utilized for the resumption of photosynthetic activities to promote growth upon re-watering, their use for promoting rapid regrowth in general is also significant. For instance, endogenous GA is known for promoting cell elongation and vertical shoot growth (Hopkins and Hüner, 2004; Gupta and Chakrabarty, 2013; Huang et al., 2014; Small and Degenhardt, 2018). In addition to the studies already discussed that have shown improved drought tolerance and post-drought recovery growth potential as a result of exogenous applications of CK, it has been found that exogenous applications of GA in combination with CK at the vegetative stage can also promote increases in plant biomass and grain yield in maize due to better maintenance of photosynthesis (Akter et al., 2014). This can be a very promising aspect for more sustainable post-drought recovery growth potential.

Application of PGRs is beneficial for modifying physiological responses to drought stress, which can eventually lead to adaptations that are sustainable for drought tolerance and subsequent recovery upon re-watering. Further, the growth effects of using PGR application can be enhanced through the use of a nitrogen source application upon re-watering. Application of nitrogen is a post-stress recovery practice that is often used by turfgrass managers to facilitate more rapid growth and re-greening of turfgrass (Beard, 1973). Nitrogen application in combination with CK has also shown to improve drought tolerance through enhanced antioxidant metabolism in creeping bentgrass (Chang et al., 2016). Therefore, perhaps using GA and CK for cell elongation and cell division for lateral root and shoot growth, in combination with a growth-promoting nitrogen source, could be the key for further enhancing drought tolerance and post-drought recovery. Such knowledge could be of great significance for developing effective post-drought management programs, taking advantage of the fact that these growth-promoting hormones and nutrients can enhance rapid
regrowth or re-establishment of grass crop species during re-watering periods in areas with limited irrigation or rainfall.

### 3.6 CONCLUSIONS AND FUTURE RESEARCH PERSPECTIVES

Drought stress is a major factor limiting the growth and productivity of both annual grass crop species and perennial grasses, while rapid recovery from drought damages is critically important for the drought survival of perennial species. Rapid regeneration of new shoots and roots enable re-establishment of new plant stands and resumes growth and functions once water becomes available due to rainfall or irrigation. Drought-resistance traits and post-drought recovery mechanisms discussed in this chapter should provide a better understanding of how grass plants can survive, overcome and resume productivity in an ever-changing, unpredictable environment. Enhancing survival during drought stress through drought-resistance mechanisms is essential not only for maintaining functional metabolic processes, but also to ensure the plant will be able to recover upon re-watering. It is worth noting, however, that although there have been many studies done on the effects of drought and water deficit on different grass species and their coping strategies, the mechanisms behind their recovery from drought stress still deserves further investigation.

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