Turfgrass Responses to Water Deficit: A Review

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ABSTRACT. Drought is a major limiting factor in turfgrass management. Turfgrass responses to water deficit depend on the amount and the rate of water loss as well as the duration of the stress condition. This review paper was designed to understand responses such as photosynthesis, canopy spectral reflectance, plant cell, root, hormone and protein alteration when turfgrass got drought stress. Furthermore, mechanisms to recover from drought conditions were reviewed in detail. However, there are still many questions regarding plant adaptation to water deficit. It is not clear that the mechanism by which plants detect water deficit and transfer that signal into adaptive responses. Turfgrass research should focus on the best management practices such as how to enhance the ability of self-defense mechanism through understanding plant responses by environmental stress.

Key words: Cellular response, Drought stress, Hormone, Water deficit, Protein alteration

Introduction

Drought is defined as a condition caused by a prolonged period of dry weather to cause plant damages and water supply shortages (Kneebone et al., 1992). Drought is a major limiting factor in turfgrass management (White et al., 1993). Drought suppresses turfgrass growth and causes deterioration of turf quality. As turfgrass species have different water needs, the use of cultivars and species with superior drought resistance is one way that water use can be reduced while maintaining good quality and growth of turfgrass (White et al., 1992). Plant responses to water deficit depend on the amount and the rate of water loss as well as the duration of the stress condition. Water deficit occurs when the rate of transpiration exceeds water uptake. Such water deficit can result in concentration of solutes, changes in cell volume, disruption of water potential gradients, loss of turgor, and denaturation of proteins (Bray, 1997).

When plants get solar radiation in the leaves during day, stomata remain open to uptake CO_2 for photosynthesis. At this time water is vaporized by driving force of the energy supply. Water in the soil is absorbed by root hair. In this water flow pathway, there are two pathways where the one is the path through apoplasts such as cell walls and intercellular space and the other is the path through symplasts such as cellular membrane and living cells. Water flows by diffusion in the path through apoplasts and by osmosis in the path through symplasts. Through these two pathways, water reaches leaf through epidermis, cortex,

endodermis, pericycle, and xylem. In the leaf, water is evaporated through stomata to atmosphere. Water flows through a plant because water potential drops all along the flow pathway when plants get sunlight. The ultimate driving force of water is vapor pressure deficit. Thus, the force inducing water absorption by transpiration initiates in the leaves and transmitted to the roots. As atmospheric water potential is very lower than leaf water potential, water diffuses into atmosphere from the leaves by the principle that water moves from the region of high water potential to the region of low water potential.

Soil and water relation

Permanent wilting point is the soil water content at which plants remain wilted overnight or in a humid chamber unless they are rewatered. At over permanent wilting point, plants can not be recovered even if they are rewatered. Permanent wilting point also depends on the soil water potential not on the volumetric soil moisture. Richards and Wadleigh (1952) found that the soil water potential ranged from -1.5 to -2.0 MPa at permanent wilting for many herbaceous plants, with most values near -1.5 MPa, which is now generally used as the approximate soil water potential at permanent wilting. In permanent wilting point, plant roots can not uptake water from the soil. Plants lose internal water and wilt through forced transpiration because atmosphere water potential is much lower than leaf water potential in spite of the defense mechanisms such as stomatal closure by abscisic acid (ABA) production, osmotic adjustment, and drought resistance related gene expression. The volumetric soil moisture content is expressed as a percentage water content of soil volume. However, the volumetric soil moisture content tells little about the amount of soil available water to plants because

soils having the same volumetric soil moisture can have a different amount of soil available water. For instance, sandy soil can be oversaturated at the water content that is the wilting point for a clay soil. Normally a sandy soil has a permanent wilting point at 2~3% of volumetric soil moisture content or at -1.5 MPa of soil water potential. A clay soil has a permanent wilting point at 20~30% of volumetric soil moisture content or at -1.5 MPa of soil water potential. It means that plants can't uptake or utilize soil water at 2~3% of volumetric soil moisture content in sandy soil or at 20~30% of volumetric soil moisture content in clay soil. Thus, soils have different volumetric soil moisture content at permanent wilting point depending on their properties such as soil texture and structure. Each soil type also has a different field capacity which means when the water content after downward drainage has become negligible and water content has become relatively stable. This situation usually is attained several days after a soil has been thoroughly wetted by rain or irrigation. Normally a sandy soil has a field capacity at 5~13% of volumetric soil moisture content or -0.03 MPa of soil water potential. A clay soil has a field capacity at 40~50% of volumetric soil moisture content or -0.03 MPa of soil water potential.

Physiological responses to water deficit

Photosynthesis

Water deficit limits photosynthesis. Photosynthetic rate is sensitive to water deficit. Severe water stress can cause stomatal closure, which reduces CO_2 uptake and dry matter production (Mayaki et al., 1976). Iturbe-Ormaetxe et al. (1998) investigated the correlation between photosynthesis, stomatal conductance, transpiration and soluble protein in pea (*Pisum sativum* L. cv Lincoln) plant leaves resulting from water deficit treatments. Photosynthesis, stomatal conductance, and transpiration were significantly decreased by deficit irrigation. The moderate water deficit (water potential of -1.3 MPa) to pea leaves led to a 75% inhibition of photosynthesis. Severe water deficit (-1.9 MPa) almost completely inhibited photosynthesis. Huang and Gao (1999) examined net photosynthetic rate, stomatal conductance, transpiration rate, relative water content, and photochemical efficiency during drought progression in tall fescue cultivars. The decline in photosynthesis rate resulted mainly from internal water deficit and stomatal closure under mild drought stress conditions.

Cellular responses

Water status of plants is defined by the cellular water potential and relative water content. Water deficit results in turgor reduction, which is the plant cellular response. The first step in the regulation of the water deficit response is the recognition of the stress. Loss of water from the cell is perceived, triggering a cellular signal transduction pathway. This is an example of converting a physical stress into a biochemical response. There are several aspects of cellular water loss that could be measured by the stress recognition mechanism. These include loss of turgor, change in cell volume or membrane area, and change in solute content. Cellular osmotic adjustment facilitates maintenance of plant water status through stomatal closure under water deficit conditions by increasing solute content, accumulation of ions, and synthesis of organic solutes. These organic solutes may include K^+, sugars, organic acids, and amino acids. Osmotic adjustment is one mechanism for increasing drought tolerance (Humble and Hsiao, 1970). Osmotic adjustment is also called "the accumulation of osmolytes compounds" and is often proposed as a solution to overcoming the negative consequences of water deficits in crop production (Serraj and Sinclair, 2002). Plant water deficit occurs when the rate of transpiration exceeds water uptake from roots. At the cellular level, cellular water deficit can result in a concentration of solutes, changes in cell volume and membrane shape, disruption of water potential gradients, loss of turgor, disruption of membrane integrity, protein alteration, and denaturation of protein (Bray, 1997). Cells shrink as the volume of water decreases inside. The membranes can't resist the shrinkage, and the organelles become distorted when dehydration is severe. Vacuole is shrunken, cell wall is folded, and chloroplasts are contorted in the cell. Water potential in the cell becomes significantly dropped compared to outside of cell. Osmotic adjustment is initiated by this water potential difference between inside and outside cell (Kramer, 1995). Osmotic adjustment is one of the most interesting adaptive mechanisms under drought stress condition. When a cell is dehydrated, its water potential decreases because the cell contents become more concentrated. In this situation, Water potential of outside cell is higher than inside cell. Water moves from an area of high potential energy to an area of low potential energy. Thus, water in the outside cell diffuses into the inside cell and turgor pressure increases. This osmotic adjustment mechanism is also conducted by the synthesis of osmolytes which include amino acids, sugar alcohols (e.g. pinitol), and other sugars. Water deficit reduces cell expansion and biomass production. Cell expansion is more sensitive to drought stress than photosynthesis. Reduced cell expansion limits biomass production because photosynthesis of a plant is proportional to leaf area, particularly early stages of the life cycle. Reduced leaf area increases the proportion of carbohydrates that can be translocated to the root. It is the mechanism that water deficit enhances root elongation in a short period. Stomatal closure also is a plant response of adaptive mechanisms under drought stress not to lose

internal water.

ABA hormone mediates stomatal closure. Potassium (K^+) is the principal osmotic solute that leads to stomatal opening and closure. ABA produced in roots as a response to water deficit is transported to leaves through the xylem. This hormone stimulates the efflux of potassium ions out of guard cell. The efflux of K^+ induces stomatal closure. On the contrary, guard cell solute potential is lowered by the influx of K^+ and water flows into guard cell. In this process, cell volume is increased, which leads to stomatal opening. Osmotic potentials are uniform throughout the cell. Osmotic balance among cells is enhanced by the plasmodesmata, and cells in tissues tend to behave osmotically as though there is one highly interconnected protoplasm. Osmotic balance becomes more difficult when plants are subjected to dehydration for a long period. Cell structures are distorted and the plasmalemma and vacuolar membrane can break or become leaky (Lucas et al., 1993). All changes that occur at the cellular level lead to water deficit-induced gene expression such as protein alteration and production of heat shock protein. Every plant has its own characteristics to tolerate, avoid, or recover drought stress. These abilities are called drought resistance. Through this drought resistance mechanism, plants will develop or evolve their characteristics step by step.

Hormonal responses

Following cellular perception of water loss, a signaling mechanism is activated by signals. The major signal operating during drought stress is ABA. The plant hormone ABA is the best-known signal. It can move throughout the vascular system in the plant acting as a signal for changes in stomatal conductance and gene expression in response to water deficit (Trejo et al., 1995). ABA is synthesized in roots in response to water deficit. It is also synthesized in the chloroplasts of mesophyll cells. ABA synthesized from roots by water deficit is transported to guard cells of leaves via the xylem. In the guard cell, this ABA mediates processes that lead to stomatal closure by inducing K^+ efflux, which is the principal osmotic solute that leads to stomatal closing.

Plants do sense the drying of the soil around the root and communicate this information to the shoot by some means other than a reduction in the flux of water to the shoots. Roots produce ABA by the response of water deficit. Thus, roots of plants are primary sensors of water stress. As the soil dries, there are root metabolisms such as a decrease in cytokinin production and an increase in ABA production. These hormones produce physiological changes such as a decrease in growth, stomatal conductance, and rate of photosynthesis, regardless of the water status of the leaves (Kramer and Boyer, 1995). ABA has an asymmetric carbon atom which means that two optical isomers are possible. The naturally occurring isomer of ABA is referred to as (+) ABA. ABA

prepared by chemical synthesis is ($\pm$) ABA. These two types are the usual form of the growth substance available for physiological studies (Noggle and Fritz, 1976). ABA produced in roots as a response to water deficit is transported to leaves via the xylem. This hormone controls stomatal behavior and leaf growth and leads to stomatal closure and reduces cell expansive growth. ABA is thought to stimulate the efflux of potassium ions out of guard cell (Humble and Raschke, 1971). The efflux of K^+ induces stomatal closure by the mechanism that K^+ influx is blocked and turgor is lost. Stomatal closure reduces photosynthesis rate in result. ABA has also the ability to inhibit auxin-induced growth and interferes synthesis of proteins and other enzymes. High concentrations of cytokinin can dominate the effects of ABA on stomata (Blackman and Davies, 1983). As the soil dries, reduction in cytokinin supply amplify shoot responses to an increasing concentration of ABA. Thus, it seems possible that ABA and cytokinin may combine and interact in their effects on shoot processes (Davies and Zhang, 1991). ABA is the best-known signal at both the whole plant and the cellular levels. It can move throughout the plant in the vascular system, and acts as a signal for changes in stomatal conductance and gene expression in response to soil drying. It regulates a wide range of cellular processes including responses to environmental stresses. ABA levels in plant cells remain low under non-stressful conditions but can increase drastically during stress periods.

Jiang and Huang (2002) investigated physiological changes associated with the synthesis of dehydrin and a cytosolic heat shock protein (HSC 70) in response to drought stress in two tall fescue cultivars 'Southeast' and 'Rebel Jr.' and evaluated the effects of ABA application in the drought tolerance of the cultivars. The results indicated that turf quality and leaf relative water content (RWC) decreased and electrolyte leakage increased during drought stress for both cultivars. Two tall fescue (*Festuca arundinacea* L.) cultivars treated with ABA also maintained higher turf quality and leaf RWC, and lower electrolyte leakage (EL) than untreated plants under drought stress conditions. Lu et al. (2003) investigated the effects of abscisic acid (ABA) on the drought resistance of turfgrass. Carpetgrass, Tifdwarf and Tifway bermudagrass were subjected to drought stress by withholding water, after spraying ABA and the relative water contents (RWC) were measured. ABA increased RWC of the three grasses, indicating increased drought resistance. The results showed increased activities of superoxide dismutase (SOD), catalase (CAT) and peroxidase (POD) after ABA treatment and these were maintained at higher levels in ABA-treated plants during drought stress. Wang et al. (2003) investigated effects of exogenous ABA application on turf performance and physiological activities of kentucky bluegrass (*Poa pratensis* L.) in response to drought stress. Two cultivars of

Kentucky bluegrass, 'Brilliant' (drought susceptible) and 'Midnight' (drought tolerant), were treated with ABA or water by foliar application and then grown under drought stress (no irrigation) or well-watered (irrigation on alternate days) conditions in a growth chamber. The two cultivars responded similarly to ABA application under both watering regimes. Foliar application of ABA had no effects on turf quality or physiological parameters under well-watered conditions. ABA application, however, helped maintain higher turf quality and delayed the quality decline during drought stress, compared to the untreated control. ABA-treated plants exposed to drought stress had higher cell membrane stability, as indicated by less electrolyte leakage of leaves, and higher photochemical efficiency, expressed as Fv/Fm, compared to untreated plants. Leaf water potential was not significantly affected, whereas leaf turgor pressure increased with ABA application after 9 and 12 d of drought. Osmotic adjustment increased with ABA application, and was sustained for a longer period of drought in 'Midnight' than in 'Brilliant'. The results suggested that exogenous ABA application improved turf performance during drought and drought-sensitive and tolerant cultivars of Kentucky bluegrass. This positive effect of ABA could be related to increased osmotic adjustment, cell turgor maintenance, and reduced damage to cell membranes and the photosynthetic system. Gas exchange parameter and stomatal physical properties were measured in *Tradescantia virginiana* plants grown under well-watered conditions and treated daily with either distilled water (control) or 3.0 mM ABA. ABA-treated plants operated with significantly lower photosynthesis. ABA-treated plants had significantly smaller stomata and higher stomatal density in their lower epidermis. This study showed that exogenous ABA-induced plants could improve water-use efficiency that may be invoked under prolonged drought conditions (Franks and Farquhar, 2001). Pelah et al. (1995) identified a novel 66 kDa boiling stable protein (BspA) in cultured shoots of aspen (*Populus tremula* L.) which was highly expressed in response to gradual water stress. This BspA protein, which was highly expressed as early as 1 h after initiation of a drought treatment, was accumulated during progressive water stress, decreased on rehydration, and was expressed in response to exogenous ABA application. In summary, the primary hormone in response to drought is ABA. The application of this exogenous hormone can significantly reduce damages from drought stress through drought adaptive mechanisms such as stomatal closure, osmotic adjustment, and cell turgor maintenance.

Protein alterations

The alteration of protein synthesis or degradation is one of metabolic processes affected by water deficit (Chandler and Robertson, 1994). Riccardi et al. (1998) investigated protein change by progressive water deficit in Maize (Zea mays). Changes induced in leaf proteins were studied by two dimensional electrophoresis and quantitatively analyzed using image analysis. 78 proteins out of a total 413 showed a significant quantitative variation and 38 proteins exhibited a different expression in the two genotypes. The dehydrin family of proteins accumulates in a wide range of plant species under drought stress (Close, 1996). Arora et al. (1998) reported that the accumulation of dehydrin proteins (25-60 kDa) in Zonal geranium (Pelargonium hortorum) leaves was induced by drought stress. These dehydrin proteins protect other proteins and help maintain the physiological integrity of cells (Bray, 1993). Drought stress also alters protein synthesis in turfgrass. Jiang and Huang (2002) examined physiological changes associated with a cytosolic-heat shock protein (HSC 70) by drought stress in two tall fescue (*Festuca arundinacea* L.) cultivars, 'Southeast' and 'Rebel Jr.'. HSC 70 protein was more highly detected in drought-stressed plants than well-watered plants.

Mechanisms to recover from drought conditions

Drought resistance mechanisms are comprised of drought avoidance and drought tolerance. Drought avoidance is "the ability of a plant to avoid tissue-damaging water deficits under conditions of water deficit". Thus, plants that have drought avoidance characteristics may show increased root depth, enhanced root water uptake properties, or reduced evapotranspiration (ET). ET reductions are due to reduced surface area, stomatal regulation to keep internal water, and leaf surface properties such as epidermal hair and wax. Drought tolerance is the ability of a turf to endure low water potentials caused by drought. This mechanism includes osmoregulation and desiccation tolerance achieved via protoplasm resistance (Kneebone et al., 1992).

Cellular adaptation

Cellular adaptive responses to water deficit involve mechanisms to avoid water loss, protect the cellular machinery and repair damage (Bray, 1993). One response to plant water deficit is the synthesis of osmolytes. These are compatible solutes that can accumulate to high levels without disrupting protein function. Osmolytes may include amino acids (e.g. praline), sugar alcohols (e.g. pinitol), other sugars (e.g. fructans) and quaternary ammonium compounds (Bray, 1997). The accumulation of osmolytes improved drought tolerance in tobacco (*Nicotiana tabacum*). This produced a decreased osmotic potential, which maintains a favorable water potential gradient and protects cellular turgor (Tarczynski et al., 1993). Transport proteins, ion channels and carriers also play an important role in water deficit avoidance.

Serraj and Sinclair (2002) identified that the one mechanism of osmolyte accumulation is in the maintenance of root development in the soil profile. This mechanism might be explained by photosynthate partitioning theory that moves in plants and is partitioned among different organs of the plant. Further research should be required about why root/shoot growth rate increases under drought stress.

Root responses

Water deficit enhances root elongation. Roots have the capacity to grow and mine water in the deeper regions of the soil when turfgrass is under a water deficit. This occurs because cell expansion may be more sensitive to water deficit than to photosynthesis. Reduced leaf area increases the proportion of photosynthate that can be translocated to the root. Conley et al. (1997) found that drought stress induced the activity of a protein kinase in the elongation zone of the Maize. primary root. In maize seedlings, primary roots adapt to low water potentials so that substantial rates of elongation can continue when shoot growth is completely inhibited. Water deficit activation of this kinase occurred within 30 min after transplanting seedlings to conditions of low water potential. In this study, protein kinase assays identified water deficit activated protein kinases. This shows that the 45-kD, Ca^{2+}-independent serine/threonine protein kinase acts in the response of maize primary roots to water deficit and is possibly involved in regulating the adaptation of root growth to low water potential. The responses of root characteristics and activity in response to surface soil drying were also examined to determine the major root characteristics that could contribute to difference in drought resistance. Root vitality was quantified by two methods, measuring electrolyte leakage of root membrane, and the other is dehydrogenase activity with the triphenyltetrazolium chloride (TTC) reduction method (Joslim and Henderson, 1984). Root characteristics associated with greater drought resistance when the soil surface was drying down included enhanced water uptake from deeper in the soil profile, root proliferation into deeper soil layers, and persistent root growth or maintenance of root viability in the drying soil surface. Wide variations in root distribution, root viability, and water uptake pattern were found in different species or ecotypes within Seashore paspalum (Paspalum vaginatum) (Huang et al., 1997). Huang and Fry (1998) analyzed genetic variations in morphological, physiological, and anatomical rooting factors that might influence drought resistance in tall fescue cultivars. Tall fescue cultivars 'Kentucky-31', 'Mustang' and 'MIC18' (dwarf, turf type) were examined under well-watered or drought-stress conditions in a greenhouse. Root hairs became less extensive after 28 d of drying. After 14 and 21 d of drying, Kentucky 31 (forage type) roots showed significantly lower electrolyte leakage than those of MIC18. Cultivar variations in anatomical,

morphological, and physiological features of roots accounted for the variability in shoot performance under drought stress.

Canopy spectral reflectance response under drought stress

Light includes variable spectral wavelengths and these wavelengths are reflected, transmitted and absorbed by plants or water. Among these various spectral wavelengths, plants absorb visible ranges (380 ~ 760 nm) by light receptors such as chlorophyll. In infrared ranges, the ranges of 780 and 1300 nm are almost reflected or transmitted and the ranges of 1300 ~ 2500 nm are strongly absorbed by internal water. Plants have light receptors such as chlorophyll a, chlorophyll b, carotenoids, and phytochrome which are essential for photosynthesis. They have different absorption rate at various wavelengths. For instance, chlorophyll a and b absorb 400 ~ 500 nm and 600 ~ 700 nm, respectively. This light absorbed by light receptors excites and transports electron in photosystem I and II. Finally it produces ATP energy and NADPH. These products are used for dark reaction of photosynthesis system. By this principle of light and plant relation, turfgrass physiological condition can be identified and assessed. Theoretically a healthy plant has a low reflectance by strong absorption by light receptors in visible region and by water in the leaf in infrared region (1300 ~ 2500 nm) and a high reflectance in infrared region (780 ~ 1300 nm) by internal leaf scattering. On the contrary, stressed plants has a high reflectance in visible region because light receptors lose activity to absorb light and a low reflectance in infrared region (780 ~ 1300 nm) by reduced internal leaf scattering, reduced leaf area, or reduced density. With this principle, vegetation indices such as normalized difference vegetation index (NDVI) and stress indices can be developed from the combination of measured wavelengths of visible and infrared regions (Carter, 1991).

Conclusion

Although many researchers have investigated plant responses to water deficit, there are still many questions regarding plant adaptation to water deficit. The symptom of water deficit occurs when cell water content is below the cell water content when fully hydrated. However, it is not clear that the mechanism by which plants detect water deficit and transfer that signal into adaptive responses. Water deficit reduces cell expansion and biomass production by reduced photosynthesis. This phenomenon could be closely related with trying to recover and maintain their plant status. For example, with reduced water supply, ABA accumulation

in the root induces stomatal closure in the leaf to reduce water loss through transpiration. Plant water status is maintained by cellular osmotic adjustment (Humble and Hsiao, 1970). It can be explained by the effort to try to increase drought tolerance.

Water deficit enhances root elongation. Shoots grow until water demand is limited by the capacity of roots for uptake and roots grow until carbon demand is beyond the capacity of the shoot to produce photosynthate. One reason for root elongation under drought stress condition is that root system is developed through the deeper regions of the soil when plants are under water deficit because roots have photosynthate to grow (Wu et al., 1996). Another is that reduced leaf area increases the proportion of photosynthate that can be translocated to the root.

The other aspect is soil moisture content. The plants such as turfgrasses can maintain acceptable visual quality even 6% of soil moisture content by deficit irrigation. Turfgrass quality dramatically reduced below 6% of soil moisture (Lee et al, 2006). This visual quality was evaluated by national turfgrass evaluation program (NTEP) guide. It implies that turfgrasses can maintain good quality until water in the soil is supplied with irrespective of the amount of water. Further study is needed to investigate the correlation between shoot/root growth rate and deficit irrigation. The concept of turfgrass management should be differentiated to that of crop management. For instance, the turfgrass managers want turfgrasses to be lower growth rate because lower growth rate can be cut down expenses by less mowing, fertilization, and water use. Thus, maintaining an acceptable quality with reducing growth rate could be the main goal for turfgrass managers. The plant responses by water deficit were closely interrelated with the functions of self-recovering and avoidance by the synthesis of osmolytes (Bray, 1997). With this integrating information about plant responses by water deficit, deficit irrigation induces self-recovering function of the plant such as root elongation, ABA accumulation, and inducing specific genes.

Turfgrass research should focus on best management practices such as how to reduce vegetative development with keeping good turfgrass quality. Water management by deficit irrigation could be one of best management practices. Thus, deficit irrigation is the key to enhance the ability of self-defense through drought hardening.

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요 약: 잔디가 건조 스트레스를 받은 상태에서 잔디의 생리학적 메커니즘과 건조 상태에서 식물이 회복하는 생리학적 메커니즘을 보다 깊이 이해하고자 한다. 증산작용과 Stomatal Conductance의 상호 관계로 인한 광합성량의 변화, 식물 세포 내부의 변화, 삼투압 조절능력의 변화, 호르몬의 변화, 단백질 변성 등의 생리학적 반응들을 이해하고 건조 스트레스 상태에서 회복하는데 세포내부의 적응 과정, 뿌리의 반응과 같은 생리학적인 측면에 대해 이해하고 건조 스트레스 상태에서 엽록소가 흡수하고 반사하는 Spectral Reflectance의 변화를 이해하고자 한다. 하지만 건조스트레스로 인한 식물의 생리학적 메커니즘에는 아직 많은 의문점을 가지고 있으며 향 후 외부환경 스트레스에 의한 식물의 Self-defense 메커니즘을 더욱 깊게 이해하여 보다 수준 높은 관리기법들을 연구하는데 초점을 맞추어야 할 것이다.

주요어: 세포반응, 건조, 스트레스, 호르몬, 단백질 변성, Water deficit