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Review

Acclimation of morphology and physiology in turf grass to low light environment: A review

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This short review elucidated the significance of the research on acclimation of the morphology and physiology in turf grass to low light environment, the mechanism of physiological response and the photosynthetic regulation and control of turf grass to suit low light environment. We also discussed current research problems and provided insight into future relevant research.

Key words: Low light, morphological change, physiological acclimation, regulation mechanism, turf grass.

INTRODUCTION

Turf protects soil and water resources and improves the quality of urban and suburban life. Turf quality is crucial in the development and maintenance of golf courses or sports turf. Current urban greening is mainly trees, shrubs and grass combination of the three organisms, but the understory trees or shrubs often bring the inevitable shady lawn, while the high-rise is so crowded by the shade of the main lawn sources. Due to lack of sunlight, the turf cannot get enough energy to resist trampling, heat, pests and other abiotic stresses, prone to yellowing turf grass pests, diseases and infections. So the shade is caused by stress, which is one of the main lawn recessions. Growing turf grass in shade is a major problem for many homeowners because an estimated 20 to 25% of all grassy areas in the U.S. are shaded to varying degrees (Jiang et al., 2004). China has about 50% of turf in the shade environment (Xu et al., 2010a). Therefore, the study of turf grass under shade series of reactions and adaptation mechanisms for the management as well as turf grass breeding material, selection is of great significance.

The concept of low light stress has no strict definition in plant physiology. It is generally acknowledged that whether due to nature or human activity, if the environment light intensity is permanently or significantly below the plant light saturation point, but no less than the lowest limit for its survival, the plant is considered to endure low light stress. Shade is a common and inevitable problem in the landscape construction and management. High density planting or inapproprite three-dimensional planting structure often leads to low light stress for landscape plants. Turf grass as the garden cover plants are irreplaceable in the function of beautifying the environment, purifying air, adjusting the temperature and noise abatement. With the rapid economic development and urbanization process, high-rise building clusters (high-rise and flyovers) are emerging quickly. So shade environment are produced more and more widely (Jiang et al., 2004; Xu et al., 2010a). Now plant growth metabolic mechanism under shade causes great interest of researchers and become a research hotspot. Therefore, this paper here discuss the low light response metabolism of turf grass in physiological and biochemical level as well as the growth and development under low light, elaborating the plants mechanism of resistance for low light adversity. We also discuss current research problems and provided insight into future relevant research.

EFFECTS OF LOW LIGHT ON PLANTS IN MORPHOLOGICAL AND PHYSIOLOGICAL LEVELS

Plants accept limited quantity of light quantum which is lower than what plants need for normal growth under low light. As such, changes take place in its internal

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physiological and biochemical properties as well as external shape characteristics (Mcbee, 1969).

Morphology

Plants morphological change under environment stress is a kind of subjective reaction and stress is the objective reason leading to plant morphological changes. Plants form some adaptive mechanism to adapt to environmental stresses in the long-term evolution process. Low light is a common stress and plants have formed a variety of adaptation mechanism for shade in the evolution process.

Lack of light causes individual differences of the turf and also causes morphological reconstruction. In the low light stress, turf grass have various morphological changes, such as decline in root numbers, shorter rhizome, tilling decline, higher and thinner stem, longer internodes length, lighter color and thinner leaf, flatter leaf angles and slower growth (Beard, 1997; Bell and Danneberger, 1999; Miller and Edenfield, 2002; Koh et al., 2003; Kitajima, 1994). Among all the performances, the higher specific leaf areas, longer stems and longer petiole are in accordance with phototropism. These morphological performances are aiming to capture more photons in the low light.

Leaf anatomical structure

Leaf anatomical structures adapt to the low light mainly by adjusting shapes and arrangement of the epidermal cells and stockade tissue cells. Epidermis morphological structure turn out to be cell convex thoroughly, with reduced layers, increased size, thinner cell walls, thinner Epidermis cutin membrane or no cutin membrane (Roacaas and Scarano, 2001). The leaf anatomical structure changes enhance the cell ability to capture light, which is an advantage of the light penetrating leaf epidermis reaching mesophyll, or the photochemical reaction process in the leaf epidermis that directly improves photosynthetic capacity.

Photosystem

Plants gain limited light quantum in the low light adversity, so leaf temperature is reduced, stomata limitation increased, stomata conductance decreased, intercellular carbon dioxide concentration decreases, and photosynthetic rate decrease (Philip and Knapp, 1998; Huylenbroeck and Bockstaele, 2001). Low light also have great effects on ultrastructure of chloroplast in cell. The number of chloroplasts and the volume are decreased, but the number of granum and grana lamella are increased. For example, grana number of each chloroplast in turf grass *Festuca arundinacea*, which is not resistant to shade, increased sharply when transferred from sunshine condition to shade condition (Wherley et al., 2005). During low light stress, plants photosystem II (PS II) can be directly or indirectly affected. When environmental conditions change, the chlorophyll fluorescence variation can reflect the influence of the environmental factors on plants to a certain extent (Maxwell and Johnson, 2000; Jiang et al., 2003).

Under the condition of low light, on one hand, turf grass gets fewer illuminations and reduces the production of photosynthesis. So less energy and carbohydrates are accumulated. On the other hand, mowing of turf grass frequently make the plants need more energy for leaves regeneration. Energy stored in the root or in the stolons will be transferred to the aboveground. So the energy stored in the turf grass (carbohydrates) will be reduced. Therefore non-structural carbohydrates and photo-synthetic efficiency of the turf grass are greatly reduced in the low light conditions (Qian and Engelke, 1999; Ervin, 2003).

Antioxidant enzymes

Physiological and biochemical characteristics of the turf grass will change accordingly in low light conditions. For example, those who have scavenging function will be changed, such as superoxide dismutase (SOD: EC 1.15.1.1), catalase (CAT: EC 1.11.1.6), peroxidase (POD: EC 1.11.1.7), ascorbate peroxidase (APX: EC 1.11.1.11), glutathione reductase (GR: EC 1.6.4.2) and low molecular weight antioxidants such as ascorbate (ASC), glutathione (GSH), α-tocopherol and flavonoids (Shainberg et al., 1999; Xu et al., 2010a, 2010b). These changes will further affect the photosynthesis of plants, and this influence shows differences under different growing habitats.

Nutrition

Research results of low light effect on nutrition absorption ability and absorption proportion of plants are not consistent. The contents of nitrogen, and potassium increased and the content of phosphorus stayed intact in tomato leaves under low light condition. Low light also led to nitrate reductases activity reduction in the blade, and activity of nitrate reductases in the root decreased in greater manner, which makes plants to absorb more nitrate in order to satisfy the demand of nitrogen (Takahashi and Sherman, 1993; Gouia et al., 2000).

THE RESPONSE MECHANISM OF THE PLANT TO THE LOW LIGHT

Photosynthetic

Compared with heliophyte, photosynthesis characteristics of shade plants are different. Shade plants display lower light compensation points, higher apparent quantum efficiency, lower saturation light intensity, and lower largest photosynthetic rate. Both carboxylation efficiency and CO_2 compensation point in *Ginkgo biloba* Linn, showed lower under shade condition than exposure to full light (Zhang et al., 2000). As the shade treaments went on, plant net photosynthetic rates and light saturation point decreased (Jiang et al., 2004). When plants have lower light compensation point they can still synthesize organic matter in low light condition. Therefore, plants with low light compensation point and low light saturation point have the ability to more efficiently use light for photosynthesis and organic matter accumulation under low photon flux density (PFD) condition.

There have been many reports about the light effect on the thylakoid structure. Thylakoid of shade plants takes up nearly the whole chloroplasts. Chlorophyll content and the number of the thylakoid membranes are directly related. In the conditions of inadequate illumination, increase of the chlorophyll content and thylakoid membranes will strengthen light capture. Under low light condition, ultrastructure of leaf cells change greatly. In plant growing process in the chloroplast, the number of grana and starch grains keep growing (Zhang et al., 1999), but the number of the vascular bundle decrease (Yang et al., 1999). Chloroplasts ultrastructure detected by electronic microscope showed that there are more stacked grana layers and higher stacked thylakoid (relative to the non-stacked thylakoid) in the chloroplasts of the sponge tissue, but there are less stacked grana in the chloroplast of palisade tissue, and volume ratio of the thylakoid and interstitial is lower than the former (Terashima and Inoue, 1985).

Plants have strong ability to adjust themselves to adapt to different environment light conditions in a certain arrangement. In condition of low PFD, plants synthesize large amount of chlorophyll to capture more photons and light-harvesting complex LHCII will be synthesized to adapt to the shade environment (Nyitrai et al., 1994; Abdul et al., 2003). Leaf pigment composition and content vary in different light intensity. Shade plants have a higher chlorophyll content, and the ratio of chlorophyll a and chlorophyll b (Chl a/Chl b) is lower; between 2.0 and 2.4. The ratio of sun plants is 2.8 to 3.6. The contents of chl b and chl (a+b) per unit area of leaves are closely linked to light absorption and net photosynthesis of plants. The species tolerance of low light conditions and species capacity to shade out competitors are high chlorophyll content (Niinemets, 2010).

Carotenoids function in collecting and transferring light energy. Besides, they play a role in protecting chlorophyll from damage by excessive light (Demmig-Adams and Adams, 1996). The content of carotenoids varies with the light intensity. Different shade degree led to changes in the carotenoids composition of *Agrostis palustris* Huds. The content of zeaxanthin and antheraxanthin decrease in the strong light condition while neoxanthin and *β*-carotene increase in the low light (Mcelroy et al., 2006).

Hormone

Light as an important signal of the environment which extensively and profoundly regulates the growth and development of plants through light receptor (Ma et al., 2001). The differences in photons, light intensity and photoperiod can cause huge differences in plant photomorphogenesis. In the response of plants to low light, changes in phytohormones regulate the balance of phytochrome, especially the content changes of ethylene, gibberellin and auxin. As a result, the elongation of stems and petioles is promoted (Lange, 1998; Tan and Qian, 2003; Pierik et al., 2004). Red light (600 to 700 nm, R) can inhibit the production of ethylene; far-red light (700 to 800 nm, FR) has the opposite function. The ratio (R/FR) of red and far-red light has an important influence on plant photomorphogenesis, and plant height adjustment, making it an important evaluation parameter in controling plant morphology (Holmes and Smith, 1975; Wang et al., 2002). Under low light, brassinolide steroid controls the cell elongation and the expression of light- regulating gene. It also promotes the apical dominance and accelerate the leaf senescence (Chory et al., 1997; Lopez-Juez et al., 1995). When treated with lower R/FR value, the content of endogenous gibberellic acid increased, loosing the cell wall and promoting cell elongation. Plants phytochrome doubled in response to shade tolerance in physiological level. Studies have shown that two signal of transduction regulators (PIF3 and ATHB-2) affect the plants morphogenesis. PIF3 interact with phytochrome molecular directly, and ATHB-2 has influence in the pathway of auxin synthesis (Morelli and Ruberti, 2000).

Antioxidant enzymes

In environment stress, plants continually produce reactive oxygen species during growth process. Lipid peroxidation is a response under environment stress. The degree of cytoplasmic peroxidation reflects the level of plants suffering from stress. Low light has significant effect on plant metabolism and membrane protection. In low light, the plant leaves protective enzymes SOD and POD increased their activity and the activity of CAT decreased (Huang et al., 2002; Xu et al., 2010a, 2010b).

Nitrogen

Nitrogen is one of the most important limiting factors in plants growth. The content of nitrogen in the blade is much more than in the other organs. A large number of studies show that the distribution of nitrogen in different photosynthetic components can better reflect the degree of photosynthetic capacity in different light environment (Niinemets and Tenhunen, 1997; Rosati et al., 1999; Le et al., 2001; Walcroft et al., 2002). In the leaves of shade plants, more nitrogen resources in plants contribute to photosynthetic apparatus, especially the chlorophyl weight, so as to absorb photons and maintain photosynthesis efficiently. In leaves of sunshine plants, parts of nitrogen resources in plant are used to protect the photosynthetic organ from heat injury. There is no need for the plants to invest too much nitrogen in the photosynthetic organs in adequate photons condition (Bazzaz, 1997). Under the low light stress, nitrogen utilization is limited in turf grass and carbohydrate synthesis is less than the use of nitrogen. Nitrogen available in plant is in used in protein synthesis rather than carbohydrate synthesis (Schmidt, 1969).

The photosynthetic regulation of plants in low light

About 70 to 80% nitrogen in leaves exists in the chloroplasts (Makino and Osmond, 1991). Nitrogen in leaves affects the assimilation of CO_2 directly by affecting chlorophyll, Ribulose-1, 5-bisphosphate carboxylase oxygenase/Rubisco and the structure of photosynthetic organs (Rufty et al., 1988). It also has indirect effects on photosynthesis product accumulation and the feedback adjustment of photosynthesis in plants through affecting plant growth and development (Boot et al., 1992). The influence of nitrogen on chloroplast protein synthesis is better than on the cytoplasmic protein (Rhiel et al., 1986), and it has effect on the content and function of PṢIand PSII. Studies found that the two photosystems respond differently to nitrogen deficiency. The influences on PSII are far more than that on PSI, because nitrogen shortening decreased the content of protein or degraded the protein in PSII (Berges et al., 1996; Kolber and Falkowski, 1988).

From the point of energy view, the absorption and the assimilation of different forms of nitrogen has great relationship with the physiological processes in plants and the status of nutrition. The assimilation process of nitrogen specially requires a lot of energy to supply: assimilation of 1 mol ammonium nitrogen (NH_4^+ -N) needs 5 ATP, and assimilation of 1 mol nitrate (NO^3 - N) nitrogen, even in the lowest energy-assuming way, needs 15 to 16 ATP at least (Raven, 1985; Louis et al., 1987). Under low light condition, different nitrogen forms (NO_3^- N, NH_4^+-N) have impact on the photosynthesis capability. They influence the consumption of coenzyme II (nicotinamide adenine dinuleotide phosphate, NADPH) for plants, because the reduction and assimilation process for NO_3-N requires energy, which must be obtained from photosynthesis or respiration (Huppe and Turpin, 1994). Under the stress of low light, nitrate compete with CO_2 for reducing power in plants. As nitrate reductase is a light-induced enzyme, the low light intensity reduced the activity of nitrate reductase so that nitrate cannot be used by plants. The photosynthetic energy consumed by NO_3-N is 145% as large as NH_4^+-N (Raven and Farquha, 1990). So in comparison with using NO_3-N , the assimilation rates of carbon dioxide for plants is higher using NH_4^+-N as nutrient sources (Bowler and Press, 1996; Claussen and Lenz, 1999). Plants supplied with NH_4^+-N, had higher chlorophyll and rubisco content, and the activity of rubisco proved higher to a certain degree. Different nitrogen forms also resulted to different stomatal conductance and intercellular CO_2 concentration in plants, for example, NH_4^+-N can improve Gs and Ci in leaves (Raab and Terry, 1994; Watanabe et al., 2000).

THE PROSPECTION OF THE RESEARCH ON LOW LIGHT RESISTANCE FOR TURF GRASS

Light is the major environmental constraint factors to growth and reproduction of understory turf grass species. High-light intensities might have contributed to a degradation of chlorophyll contents, where low-light intensities likely prevents breakdown of chlorophyll tall fescue leaves (Wherley et al., 2005). Thus, anatomical and physiological adaptations limited photosynthetic capacity and the ability to respond to increased irradiance and CO_2 of tall fescue grown continuously in low light intensities (Allard et al., 1991). Recent research indicated that the value of Fv/Fm has been used to understand the photosynthesis affected by light intensities. The lower Fv/Fm in plants was due to photo-inhibition under high-light stress, and turf grass grown under low light might suffer photo-inhibition when they were removed to high-light stress (Jiang et al., 2005).

Photo-inhibition occurs when plants are exposed to a PPFD higher than that required for the rate of CO_2 fixation, which further leads to increased ROS (reactive oxygen specie) generation (Asada, 2006; Xu et al., 2010a, 2010b). Previous studies have reported that transfer from low light to high light caused enhanced H_2O_2 accumulation in plant leaves (Ali et al., 2005; Burritt and Mackenzie, 2003). Our study showed that the levels of H_2O_2 and O_2 increased in tall fescue transferred-leaves. The increased SOD activity may account for the increased accumulation of O_2 in transferred-leaves (Xu et al., 2010a, 2010b). Over production of ROS caused the oxidation of membrane lipids, proteins, and enzymes necessary for the proper functioning of the chloroplasts and cells as a whole (Mittler, 2002). The increase in membrane permeability, MDA and carbonyl content under high-light stress indicated that high light induced oxidative damage on membrane lipid and proteins. Pronounced increase in antioxidant enzymes activities and the relatively low level of ROS in transferred-leaves indicated that tall fescue alleviated oxidative injuries through raising antioxidant enzymes activities to scavenge newly-produced ROS (Xu et al., 2010a, 2010b).

Low light stress is a common abiotic stress for turf grass. While shade resistance is an important trait for turf grass, research on it has profound theoretical and practical significance. But the mechanism of the turf grass resistance to the low light stress has not been very clear so far. Besides, there are no clear standards for the evaluation of shade resistance, and the majority of studies were limited to the interpretation of some phenomena. Future research can start with solving the following questions. Under low light stress, how does phytochrome modulate endogenous hormones in turf grass? How is the electron flow transfered and distributed in PSII and PSI? What are the connections among the transformation of assimilation products, the heterogeneity of space allocation and nutrient assimilation pathway? What is the protective role of the unsaturation thylakoid membrane? What are the role and the physiological function of NADPH dehydrogenase complex in the chloroplast? Whether low light stress induces the production of ROS and the protection mechanisms of turf grass, and how about the mechanism?

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