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Research article

Abscisic acid improves drought tolerance of triploid bermudagrass and involves H_2O_2- and NO-induced antioxidant enzyme activities

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A B S T R A C T

Drought is a major limiting factor for turfgrass growth. Protection of triploid bermudagrass against drought stress by abscisic acid (ABA) and its association with hydrogen peroxide (H_2O_2) and nitric oxide (NO) were investigated. ABA treatment increased relative water content, decreased ion leakage and the percentage of dead plants significantly under drought stress. Superoxide dismutase (SOD) and catalase (CAT) activities increased in both ABA-treated and control plants, but more in ABA-treated plants, under drought stress. Malondialdehyde, an indicator of plant lipid peroxidation, was lower in ABA-treated plants than in control plants, indicating that ABA alleviated drought-induced oxidative injury. ABA treatment increased H_2O_2 and NO contents. ABA-induced SOD and CAT activities could be blocked by scavengers of H_2O_2 and NO, and inhibitors of H_2O_2 and NO generation. The results indicated that H_2O_2 and NO were essential for ABA-induced SOD and CAT activities. Both H_2O_2 and NO could induce SOD and CAT activities individually. SOD and CAT induced by H_2O_2 could be blocked by scavenger of NO and inhibitors of NO generation, while SOD and CAT induced by NO could not be blocked by scavenger of H_2O_2 and inhibitor of H_2O_2. The results revealed that ABA-induced SOD and CAT activities were mediated sequentially by H_2O_2 and NO, and NO acted downstream of H_2O_2.

1. Introduction

Bermudagrass (*Cynodon dactylon*) is a warm-season grass widely used for turfgrass on home lawns, sports fields and golf courses in warm climatic regions. Triploid bermudagrass (*C. dactylon* × *Cynodon transvaalensis*, $2n = 3x = 27$) is sterile and propagated vegetatively. 'TifEagle' is a recently released cultivar of triploid bermudagrass, which produces tighter and denser turf with excellent tolerance to low mowing [14], and is mainly used for greens on golf courses. In turfgrass management, drought is a major factor limiting grass growth. Irrigation is a primary cultural practice in turfgrass management and needs large amounts of water. While genetic modification may help improve drought tolerance, applications of plant growth regulators to protect plants from drought damage could be another choice.

The plant hormone abscisic acid (ABA) regulates plant adaptive responses to various environmental stresses and diverse physiological and developmental processes. Among them, ABA induces stomatal closure and reduces water loss via transpiration, which leads to an increased resistance to water stress-related environmental conditions [6,31]. ABA induces gene expression in response to various environmental stresses, such as drought, salt or chilling [4]. Signal molecules, such as hydrogen peroxide (H_2O_2) and nitric oxide (NO), are involved in the ABA-induced stomatal closure and the enhanced activities of antioxidant enzymes [3,7,18,32–34]. ABA-induced H_2O_2 production mediates NO generation, which, in turn, activates mitogen-activated protein kinase (MAPK) and results in up-regulation of gene expression of these antioxidant enzymes [33]. ABA is also related to drought-tolerance responses in turfgrass species. ABA accumulates in response to drought stress, and less accumulation of ABA is found in drought-tolerant species [5] or cultivars of turfgrasses [29], when compared to drought-susceptible species or cultivars under drought stress. Application of exogenous ABA increases drought tolerance of Kentucky bluegrass by increased osmotic adjustment, cell turgor maintenance, and reduced damage to cell membranes and the photosynthetic system [30]. In our previous study, application of ABA has been shown to increase drought tolerance of bermudagrass through promotion of antioxidant enzyme activity [20]. However, the mechanism of induction of the antioxidant enzymes by ABA has not been elucidated in turfgrass species.

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In this study, we found that application of 19 μM ABA had the best effects on drought-tolerance improvement of 'TifEagle'. The enhanced induction of superoxide dismutase (SOD) and catalase (CAT) activities by ABA, and its association with the signal molecules H_2O_2 and NO, were further investigated. The results revealed that ABA induced the production of H_2O_2 and NO, which, in turn, mediated the enhanced antioxidant enzyme activities.

2. Results

2.1. ABA increased drought tolerance of triploid bermudagrass

In a previous report, 5 mg L^{-1} (19 μM) ABA exhibited better effect on drought tolerance of triploid bermudagrass cultivars 'Tifdwarf' and 'Tifway', compared to 1 and 2 mg L^{-1} ABA [20]. In this study, we tested 19 μM and two higher concentrations of ABA (38 and 57 μM) on drought tolerance of the triploid bermudagrass cultivar 'TifEagle', and evaluated their protection effects based on relative water content (RWC), ion leakage, and the death rate of the plants. All treatments with ABA significantly increased the RWC and decreased the ion leakage and the death rate under drought stress, when compared to the control, while 19 μM ABA showed the best protection against drought injury among the three treatments (Fig. 1).

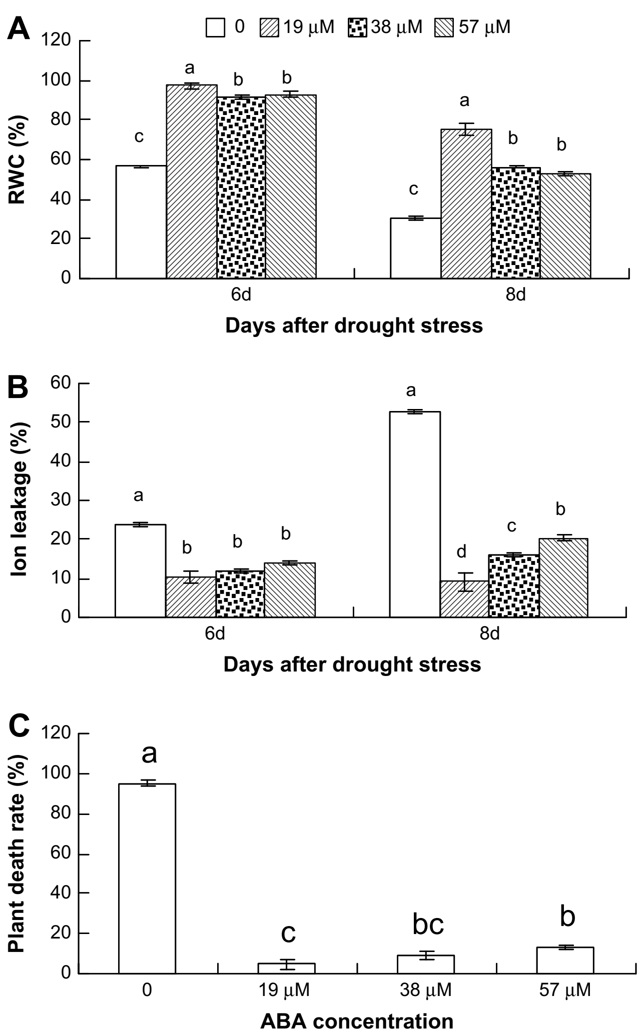

Fig. 1. Effect of ABA treatment on drought tolerance of triploid bermudagrass. RWC (A) and ion leakage (B) were measured at days 6 and 8 after treatments with different concentrations of ABA, while the dead plants were counted at day 8 (C). Means of three independent samples and standard errors are presented. The same letter above the columns indicates no significant difference at $P = 0.05$ using the Tukey test.

The time-course changes of RWC and ion leakage as affected by 19 μM ABA during drought stress are presented in Fig. 2. Plant leaves still remained turgid in both ABA-treated and control plants within 2 days after water withholding. From Day 4 to Day 8, RWC decrease and ion leakage increase were remarkable in the control plants, and significantly different from the ABA-treated plants. At Day 8, control plants had a RWC of 47.6% and an ion leakage of 41.5%, whereas the RWC and ion leakage in ABA-treated plants were 76.9% and 15%, respectively (Fig. 2).

2.2. ABA-induced activities of SOD and CAT

SOD and CAT are two major enzymes in plant antioxidant defense systems, and their activities are generally enhanced as early responses of plants to drought stress. In our study, both enzymes had increases in their activities 4 days after water withholding in ABA-treated and control plants while ABA-treated plants maintained significantly higher activities of SOD and CAT at days 6 and 8 than the control plants (Fig. 3A and B). Another important parameter to measure oxidative injury of plant cells during drought stress is malondialdehyde (MDA) level, which is an indicator of plant lipid peroxidation. In this study, MDA contents in both ABA-treated and control plants elevated gradually during drought stress. However, ABA-treated plants had consistently less MDA than the control plants from day 2 onwards (Fig. 3C), indicating that ABA treatment alleviated oxidative injury induced by drought.

2.3. ABA-induced SOD and CAT activities were dependent upon H_2O_2 and NO

Concentration effects and time course of ABA treatments on the elevated activities of SOD and CAT were studied. Three concentrations of ABA (25, 50, and 100 μM) treatments exhibited significant enhancement on the enzyme activities. Among them, 100 μM ABA

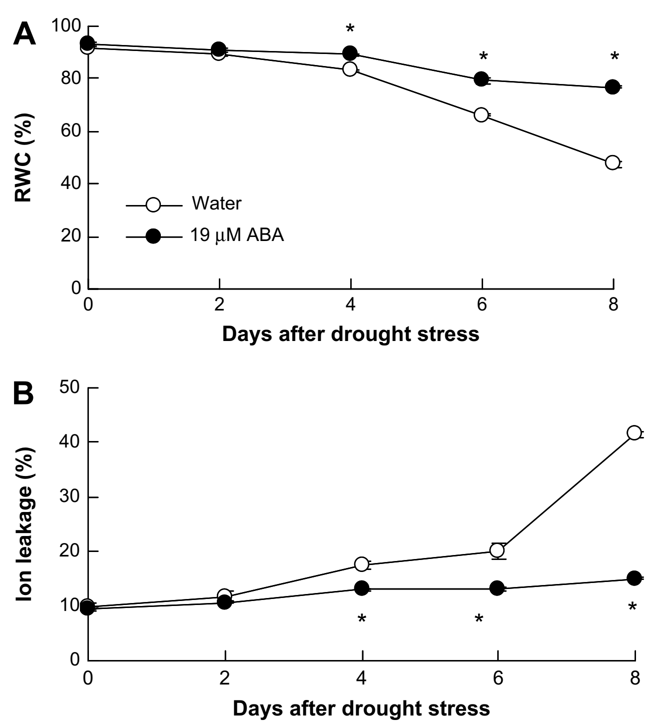

Fig. 2. Changes of RWC and ion leakage of bermudagrass as affected by ABA (19 μM) under drought stress. Means of three independent samples and standard errors are presented. The symbol * indicates significant difference between ABA treatment and the control at $P = 0.05$ using the Tukey test at a given day.