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Melatonin suppression of heat-induced leaf senescence involves changes in abscisic acid and cytokinin biosynthesis and signaling pathways in perennial ryegrass (*Lolium perenne* L.)



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ABSTRACT

Leaf senescence is a typical symptom of heat damage in cool-season plant species. The objective of this study was to determine whether melatonin could suppress heat-induced leaf senescence in perennial ryegrass (*Lolium perenne* L.) and whether melatonin interacted with abscisic acid (ABA) and cytokinin (CK) to exert its biological function. Perennial ryegrass (cv. 'Pinnacle') plants were foliar sprayed with melatonin or water and exposed to heat stress at 38/33 °C (day/night) and non-stress condition at 22/17 °C for 28 d in growth chambers. Exogenous application of melatonin alleviated growth inhibition and leaf senescence induced by heat stress, as manifested by significant higher tiller number, above-ground dry weight, plant height, turf quality, leaf chlorophyll (Chl) content, photochemical efficiency (Fv/Fm), net photosynthesis rate, and cell membrane stability in melatonin-treated plants compared to non-melatonin treatment under heat stress. The suppression of heat-induced leaf senescence by melatonin was also reflected by the reduction of transcript levels of senescence-associated genes (*LpSAG12.1* and *LpH3G*) in plants exposed to heat stress. Melatonin treatment increased the endogenous content of melatonin and CK content, whereas it decreased ABA content under heat stress. The expression of CK biosynthesis genes and its signaling response transcription factors (type B ARRs) were up-regulated, while the biosynthesis and signaling genes involved in ABA were down-regulated by melatonin treatment under heat stress. These results indicate that the suppression of heat-induced leaf senescence by exogenous melatonin could be associated with activating CK synthesis and signaling while inhibiting ABA synthesis and signaling in perennial ryegrass.

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1. Introduction

Traditional plant hormones, such as cytokinins (CK) and abscisic acid (ABA), are known to play critical roles in regulating plant growth and development, as well as plant responses to abiotic stresses (Kirkham, 1983; Li et al., 1992). Melatonin (N-acetyl-5-methoxytryptamine), an important neurohormone for mammals, was first identified in the pineal gland of bovine in 1958 (Lerner et al., 1958), and also in plants (Dubbels et al., 1995;

Hattori et al., 1995). It acts in various plant cellular metabolic and biological processes, including rooting (Park and Back, 2012), photosynthesis (Lazár et al., 2013), chlorophyll catabolism (Arnao and Hernández-Ruiz, 2009), and stress tolerance (Liang et al., 2015; Zhang et al., 2016a). In particular, either exogenous applying melatonin or increasing the endogenous melatonin content by overexpressing its biosynthetic gene(s) can significantly improve plant tolerance against stresses caused by cold or high temperature, drought, UV irradiation, and salt by acting as an effective antioxidant, membrane stabilizer, and biostimulator in modifying the expression of redox network genes (Arnao and Hernández-Ruiz, 2014). Exogenous melatonin treatment leads to improved drought tolerance and delayed leaf senescence, which has been associated with decreased ABA content and down-regulated gene expression of the ABA pathway (Li et al., 2015). Arnao and

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ORIGINAL ARTICLE

A cold responsive ethylene responsive factor from *Medicago falcata* confers cold tolerance by up-regulation of polyamine turnover, antioxidant protection, and proline accumulation

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Abstract

Ethylene responsive factor (ERF) subfamily transcription factors play an important role in plant abiotic and biotic stress tolerance. A cold responsive ERF, *MfERF1*, was isolated from *Medicago falcata*, an important forage legume that has great cold tolerance. Overexpression of *MfERF1* resulted in an increased tolerance to freezing and chilling in transgenic tobacco plants, whereas down-regulation of the ortholog of *MfERF1* in *Medicago truncatula* resulted in reduced freezing tolerance in RNAi plants. Higher transcript levels of some stress responsive genes (*CHN50*, *OSM*, *ERD10C*, and *SAMS*) and those involved in spermidine (Spd) and spermine (Spm) synthesis (*SAMDC1*, *SAMDC2*, *SPDS1*, *SPDS2*, and *SPMS*) and catabolism (*PAO*) were observed in transgenic plants than in wild type. However, neither Spd nor Spm level was accumulated in transgenic plants as a result of promoted polyamine oxidase activity. Transgenic plants had higher activities of antioxidants associated with the induced encoding genes including Cu, Zn-SOD, CAT1, CAT2, CAT3, and cpAPX and accumulated more proline associated with induced P5CS and reduced PROX2 transcription as compared with wild type. The results suggest that *MfERF1* confers cold tolerance through promoted polyamine turnover, antioxidant protection, and proline accumulation.

KEYWORDS

polyamine oxidation, spermidine, spermine

1 | INTRODUCTION

Cold stress has adverse effects on plant growth and crop yields. Temperate plants have evolved a mechanism called cold acclimation, by which they respond to a period of low but non-freezing temperatures to increase their capacity to survive to the subsequent freezing temperatures. Thousands of genes are reprogrammed in expression, and multiple metabolic pathways are modified during cold acclimation (Krasensky & Jonak, 2012). The common responses included at least accumulated cryoprotectant molecules such as soluble sugars, sugar alcohols, and low molecular weight nitrogenous compounds (proline and glycine betaine) and activated antioxidant defence system (Keunen, Peshev, Vangronsveld, Van den Ende, & Cuyppers, 2013; Szabados & Savouré, 2010). Antioxidant defence system functions to scavenge the accumulated reactive oxygen species (ROS) in plant cells (Suzuki, Koussevitzky, Mittler, & Miller, 2012), whereas the cryoprotectant molecules function to

maintain stability of membrane, proteins, and ion homeostasis and to scavenge ROS (Keunen et al., 2013; Szabados & Savouré, 2010). Transcription factors play a pivotal role in regulation of downstream defence gene expression and metabolic pathway rearrangement.

Ethylene responsive factors (ERFs) belong to AP2/ERF superfamily transcription factors and are involved in plant responses to multiple environmental stresses. In addition to the important role of ERFs in regulation of plant pathogen resistance through binding with GCC box (AGCCGCC) and modulating the expression of ethylene/salicylic acid/jasmonic acid-regulated pathogenesis-related (PR) genes (Zarei et al., 2011; Zhu et al., 2014), some ERFs regulate plant tolerance to abiotic stress, such as drought, salt, and cold. Overexpression of pepper transcription factor (*CaPF1*), which encodes a group VII family protein in pepper (*Capsicum annuum*), resulted in elevated tolerance to pathogen and freezing stresses in transgenic *Arabidopsis* as a result of induced expression of PR and cold-regulated genes (Yi et al., 2004) and enhanced tolerance to drought, salinity, and freezing in transgenic



Ensiling as pretreatment of rice straw: The effect of hemicellulase and *Lactobacillus plantarum* on hemicellulose degradation and cellulose conversion



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ABSTRACT

The fermentation characteristics, structural carbohydrate degradation and enzymatic hydrolysis of rice straw ensiled with hemicellulase and *Lactobacillus plantarum* were examined. Fresh rice straw was ensiled in 1-L laboratory silos with no additive control (CK), *L. plantarum* (L), hemicellulase (HC) and hemicellulase + *L. plantarum* (HCL) for 6, 15, 30 and 60 days. All additives increased lactic acid concentration, and reduced pH and lignocellulosic content of the resulting silage relative to the control. The highest organic acid and residual sugar contents and lignocellulose degradation were observed in HCL silage. Hemicellulase alone or combined with *L. plantarum* improved the enzymatic hydrolysis with higher glucose yield and cellulose convertibility. Fresh rice straw ensiled with the combined additives increased feedstock preservation and cellulose conversion, and is thus recommended as a biological pretreatment for subsequent biofuel production.

1. Introduction

With the depletion of fossil resources and increasing concerns regarding climate change, clean and renewable biofuels as alternatives have attracted extensive attention. Lignocellulosic biomass, which primarily consists of cellulose, hemicellulose and lignin, is a potential feedstock for biofuel production due to its high availability and low cost (Nguyen et al., 2010). Cereal straw is a common type of lignocellulosic material that is generated in large quantities worldwide every year. Approximately 21 MT yr⁻¹ of rice straw was produced after rice harvesting accounting for 47% of the total crop residue in China (Wang et al., 2010; Chen, 2016). However, plenty of rice straw has been left unused, improperly disposed or burnt directly, wasting resource and causing environmental pollution (Murali et al., 2010), indicating a need for better rice straw disposal methodologies.

Rice straw is recalcitrant to chemical and biological degradation with its complicated structure, thus pretreatment of this lignocellulosic biomass is necessary prior to its subsequent transformation and comprehensive utilization. In addition, because of the seasonality of straw harvesting and annual supply of feedstock needed, long-term effective storage of harvested straw is required. Ensiling is a promising technology for supplying year-round availability of feedstock as well as

being effective pretreatment, since ensiling the process preserves more than 90% of a plant's energy (Egg et al., 1993) and improves the enzymatic hydrolysis compared with the raw material (Li et al., 2018). Ambyejensen et al. (2013) reported that ensiling process boosted the cellulose convertibility in green biomass and provided new insights into biomass conversion. Gallegos et al. (2017) also observed that ensiling fermentation was a successful biological pretreatment for straw-like biomass and effectively increased biogas production in wheat straw silage.

Owing to the limitations of straw material, various additives, including lactic acid bacteria (LAB) and enzymes, are commonly applied to improve its fermentation quality, silage preservation and fibre utilization. *Lactobacillus plantarum*, a facultative homofermentation LAB, has often been applied to rice straw silage (Fang et al., 2012). Hemicellulose is the second most plentiful organic material and is known to generally hydrolyse better for biogas production than cellulose, possibly due to its amorphous structure and much lower polymerization level compared to cellulose. Thus, in this study, exogenous hemicellulase and *L. plantarum* were used to improve the efficiency of rice straw utilization. Hemicellulase is a complex enzyme that breaks down the backbone of xylan and arabinose side chains (Yang et al., 2017), and release pentose (xylose and arabinose). Tanjore et al. (2012)

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Dynamics of microbial community and fermentation quality during ensiling of sterile and nonsterile alfalfa with or without *Lactobacillus plantarum* inoculant



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ARTICLE INFO

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Alfalfa
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ABSTRACT

To reveal the mechanism of the survival and adaption of inoculated *Lactobacillus plantarum* during ensiling. Alfalfa was ensiled directly (A1), after γ-ray irradiation (A0), and after inoculation of the sterile (A0L) or fresh alfalfa (A1L) with *Lactobacillus plantarum*. The A0L had the higher lactic acid content and lower pH than that in A1L from 3 days of ensiling. *Pediococcus* was the dominant microbes in A1 silage, followed by *Enterococcus* and *Lactobacillus*, while *Lactobacillus* in A1L outnumbered all other genera at 3 d. In A0L silage, the relative abundance of *Lactobacillus* increased to 99.13% at day 3. It indicated that *Lactobacillus* could dominated the fermentation of inoculated silages regardless of the γ-ray irradiation, although there was a short lag period for irradiated alfalfa.

1. Introduction

As a traditional forage preservation method, ensiling is a microbial-based and anaerobic fermentation process dominated by lactic acid bacteria (LAB), which convert water soluble carbohydrates (WSC) into organic acids, mainly lactic acid, resulting in the decline of pH and inhibition of undesirable microorganisms (Dunière et al., 2013; Eikmeyer et al., 2013). Ensiling takes place by complex microbial communities enclosed in silos, once sealed, the microorganisms capable of anaerobic growth begin to grow and compete for available nutrients, the relative abundance of their members may vary and the communities tend to establish itself, which is decisive for the later performance of silages. If LAB will quickly dominate the initial silage fermentation, the competing microorganisms will not survive and the end result will be a stable, low pH silage, otherwise, the end result will be a poorly fermented silage.

Alfalfa is one of the most important forage crops used for ensiling worldwide (Dunière et al., 2013), however, alfalfa is recognized as more difficult to ensile than other forages because of high buffering capacity and low WSC content (Nkosi et al., 2016). Besides, the microbial composition also plays important role in the fermentation during alfalfa ensiling, McAllister et al. (2018) claimed that microbial populations associated with alfalfa silages appeared to be more diverse than those associated with cereal silages, resulted in the growth of undesirable microbes and a worse fermentation quality. *Lactobacillus*

plantarum (*L. plantarum*) has been used to enhance the lactic acid fermentation and improve the alfalfa silage quality (Ogunade et al., 2018). However, the response to inoculants varies with many factors, including the epiphytic microorganisms in fresh materials and the proliferated prosperity of the inoculants, and few studies have examined the effects of epiphytic microorganisms on the survival of inoculated bacteria.

Actually, it is difficult to reveal the respective dynamics of exogenous bacteria and epiphytic microorganisms during alfalfa ensiling, since both occur in the silos. Some techniques have been used to obtain sterile substrates in silage research, including autoclaving (Graham et al., 1985), heating (121 °C for 20 min) (Mogodiniyai Kasmaei et al., 2014) and γ-ray radiation (Heron et al., 1986). Autoclaving and heating could destroy plant enzymes and physical structure, which affected the fermentation dynamics of silages. Sterilization by γ-ray irradiation has been used to differentiate the effects of plant enzymes from those of microbial activity on lipolysis and proteolysis in ensiled alfalfa (Ding et al., 2013).

The objective of this study was to reveal the mechanism of the survival and adaption of inoculated *L. plantarum* during ensiling of alfalfa, the changes in microbial community composition during the early stage of alfalfa silage excluding the effect of epiphytic microorganisms by γ-ray irradiation were determined by high throughput sequencing.

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Characterization of *Enterococcus faecalis* JF85 and *Enterococcus faecium* Y83 isolated from Tibetan yak (*Bos grunniens*) for ensiling *Pennisetum sinense*



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ABSTRACT

Two bacteria strains with cellulolytic potential isolated from Tibetan yak (*Bos grunniens*) rumen were identified as *Enterococcus faecalis* (JF85) and *Enterococcus faecium* (Y83). Isolates grow well within a range of temperature 15 to 55 °C and pH 3.0–7.0, respectively. Two strains were inoculated with or without *Lactobacillus plantarum* (Lp) to *Pennisetum sinense* silage for 90 days. All inoculants increased lactic acid content, decreased pH and lignocellulose contents compared with silage without additives (control). The lowest pH, highest lactic acid and largest reduction in lignocellulose contents were observed in JF85 + Lp and Y83 + Lp silages. Isolates alone or in combination with Lp significantly increased WSC, mono- and disaccharides contents as compared to the control. Combined addition efficiently improved enzymatic hydrolysis of *Pennisetum sinense* silage, indicated by higher glucose yield and cellulose convertibility. *Pennisetum sinense* ensiled with combined additives is a suitable storage and pretreatment method prior to sugars production from energy crop.

1. Introduction

The progressive depletion of fossil fuels, environmental pollution and climate change have triggered the global demand for renewable and sustainable energy. Lignocellulosic biomasses, including energy crops and agricultural residues offer potential substrates for the production of renewable energy through bioconversion (enzymatic hydrolysis and fermentation). Lignocellulosic biomass is the most abundant polymeric carbohydrates in the world and can be used as feedstock to generate fermentable sugars for sustainable biofuel production. *Pennisetum sinense*, a hybrid of *Pennisetum purpureum* and *Pennisetum americanum*, is a monocot C4 perennial grass and has been widely used as an energy crop (Li et al., 2014). *P. sinense* is well adapted to a wide variety of soils types, fertility levels, and weather conditions, and capable of yielding high biomass about 40 t DM per hectare per year (Lu et al., 2014). Thus, it has become an attractive renewable resource for the production of biofuel, feed, and chemical due to its low energy input, high yield potential, and wide availability in tropics and subtropics of Asia (Peng et al., 2017).

In the tropical and some subtropical regions, including south of China, the temperatures are suitable for *P. sinense* growth in early spring and later autumn. However, fresh grasses are not available during the winter months (Chou et al., 2009) hence constraining the supply patterns. The efficient conservation of fresh grasses could ensure yearly-

round supply of carbohydrates for maintaining viable bioenergy supply chains. Ensiling is not only an appropriate method of storing feedstock for biofuel production with the potentially very low loss of carbohydrates but also a biological pretreatment method (Herrmann et al., 2011). Ensiling is widely used to preserve animal feed, and applicable to conserve lignocellulosic biomass such as *P. sinense* for biofuel production. Ensilage has proven to be better than fungal pretreatment for preserving giant reed harvested from August through December, since it could result in higher glucose and methane yields than untreated and fungal pretreated giant reed for all harvested times (Liu et al., 2016). Zheng et al. (2012) also reported that the ensiling process significantly improved the enzymatic digestibility of sugar beet pulp as compared to raw sugar beet pulp.

P. sinense demonstrates difficulty to ensiling due to its coarse and stemmy structures alongside low water soluble carbohydrate (WSC) and high fiber contents. Exogenous fibrolytic enzyme has been explored to induce direct conversion of structural carbohydrates into soluble sugars for LAB fermentation (Wang et al., 2002; Colombatto et al., 2004), but, high cost and instability of commercially enzymes limited their widespread application in silage. Microorganisms action altogether presents a combined storage and pretreatment benefits which require less energy and affords easy handling (Adekunle et al., 2016). Therefore, screening and isolating fibrolytic microorganism lineages with high substrate specific activities and stability is very crucial.

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The effects of fibrolytic enzymes, cellulolytic fungi and bacteria on the fermentation characteristics, structural carbohydrates degradation, and enzymatic conversion yields of *Pennisetum sinense* silage



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ARTICLE INFO

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ABSTRACT

Biological inoculants were tested on *Pennisetum sinense* for their effects on fermentation characteristics, structural carbohydrates degradation, and enzymatic conversion yields. *Pennisetum sinense* was ensiled without additive, *Lactobacillus plantarum* (Lp), *Trichoderma reesei* (Tr), fibrolytic enzymes (E), and *Enterococcus faecium* (Y83) for 90 days. Y83 silages had higher LA and lower AA, ammonia-N and DM loss as compared to E and Tr silages. Tr and E had superior effects for degrading lignocellulose while Y83 had intermediate effects. The first-order exponential decay models ($R^2 = 0.928\text{--}0.998$) predicted nonstructural carbohydrates kinetics and demonstrated high water soluble carbohydrate (g/kg DM) preservation potential in Y83 (21.40), followed by Tr (18.94) and E (16.74). Addition of Y83 improved the conversion efficiency of *P. sinense* silage than Tr and E, indicated by higher glucose and total reducing sugars yield (22.49 and 36.89 w/w % DM, respectively). In conclusion, Y83 can be exploited for the ensiling lignocellulosic biomass before grass processing.

1. Introduction

The high global dependency on fossil fuels has led to the uncertain future on the use of petroleum resources. Concerns about climate change and environmental pollution have led to the intense search for sustainable and eco-friendly energy sources. Lignocellulosic materials are the most abundant renewable organic resources (~200 billion tons annually) on earth and are readily available for conversion to biofuels (Chandel and Singh, 2011). C4 grasses including *Pennisetum sinense*, a hybrid of *Pennisetum purpureum* and *Pennisetum americanum*, are promising feedstocks for renewable biofuel production. *P. sinense* like other lignocellulose biomass has limitations to biofuel production including the high degree of polymerization and complex lignocellulose structure as established in previous studies (Lu et al., 2014). Furthermore, the bioprocessing of grasses to biofuels is hampered by availability due to short harvest time and the poor storability of the green crops since they require large capacity presses or bioreactors for immediate processing (Schmidt et al., 1997).

The advances in biofuel production have outlined the importance of substrate pretreatment and preservation. According to Herrmann et al. (2011) ensiling is an efficient way that curbs the limitation of supply since feedstocks can be preserved for extended periods of time and provides the medium for potential pretreatment. *P. sinense* presents

difficulty to ensiling due to its low water soluble carbohydrate (WSC) and high lignocellulosic contents. Various chemicals, fibrolytic enzymes, and inoculants have been used to improve silage fermentation by enhancing structural carbohydrate degradation and release of the fermentable substrate for microbial fermentation. The application of cellulolytic microorganisms as silage additives could be feasible due to the economic and environmental benefits when placed alongside other additives. Exogenous fibrolytic enzymes are often added to lignocellulosic materials before ensiling, however contradiction and inconsistencies have been shown in different studies, relating to their effects on fermentation constituent especially dry matter (DM), neutral detergent fiber (NDF) disappearance and degradation of organic matter (Mandevu et al., 1999; Colomatto et al., 2004; Khota et al., 2016). These inconsistencies were due to various factors such as enzyme types, concentrations and activity, application methods and the targeted substrates, which limited its widespread application in silages. Nolan et al. (2018) demonstrated that fibrolytic enzymes performances impacted on fibers and methane yields differently depending on grass species and stage at harvest. Thus no single enzyme is consistently superior. Fungi have been primarily used commercially for cellulase production based on their ability to secrete cellulase in substrate medium. Among the cellulolytic fungi, *Trichoderma reesei* has gained attention based on its capacity to produce cellulolytic enzymes

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Effects of arbuscular mycorrhizal fungi, biochar and cadmium on the yield and element uptake of *Medicago sativa*



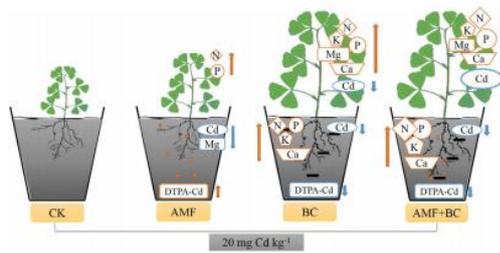
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HIGHLIGHTS

- AMF only promoted N and P uptake of plant shoots.
- Biochar facilitated N, P, K and Ca contents of plants grown in Cd-contaminated soils.
- Biochar was more effective at increasing plant nutrient uptake.
- Both AMF and biochar could decrease plant Cd concentration.

GRAPHICAL ABSTRACT



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ABSTRACT

The synergistic effects of arbuscular mycorrhizal fungi (AMF) inoculation and biochar application on plant growth and heavy metal uptake remain unclear. A pot experiment was carried out to investigate the influence of AMF inoculation, biochar and cadmium (Cd) addition on the growth, nutrient and cadmium uptake of *Medicago sativa*, as well as soil biological and chemical characteristics. In comparison to the non-Cd pollution treatment, Cd addition significantly decreased mycorrhizal colonization, biomass, and N, P, Ca and Mg contents of shoots and roots in the absence of biochar. Biochar amendment did not increase mycorrhizal colonization at either Cd levels. Regardless of the biochar amendment, AMF inoculation significantly promoted contents of N and P in plant shoots grown in the Cd-contaminated soils. Nevertheless, in the presence of Cd pollution, biochar dramatically elevated the biomass and N, P, K and Ca contents of plant tissues in both AMF inoculation treatments. Biochar addition significantly reduced soil DTPA-extracted Cd. The treatments with AMF inoculation and biochar amendment showed the lowest shoot Cd concentrations and contents, highest plant tissue N and P contents in the Cd addition group. These results suggested that combined use of AMF inoculation and biochar amendment had significant synergistic effects not only on nutrient uptake but also on the reduction in cadmium uptake of alfalfa grown in Cd-polluted soil.

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1. Introduction

Cadmium (Cd) is a common heavy metal contaminant in agricultural ecosystems due to industrial practices, overuse of fertilizer, irrigation by wastewater, and improper disposal of waste (Yi et al., 2011). Cd is a toxic metal for both plant and human health, and a low level of Cd

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Original article

Drought inhibition of tillering in *Festuca arundinacea* associated with axillary bud development and strigolactone signalingLili Zhuang^{a,*}, Jian Wang^{a,1}, Bingru Huang^{b,*}^a College of Agro-Grassland Science, Nanjing Agricultural University, Nanjing, Jiangsu, PR China^b Department of Plant Biology and Pathology, Rutgers, The State University of New Jersey, New Brunswick, NJ 08901, USA

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 Drought stress

ABSTRACT

Drought stress inhibits tiller formation and growth, but the underlying mechanism is not well understood. Tiller development and lateral branch growth in monocot and dicot species respectively involve two stages: axillary bud initiation and subsequent outgrowth. The objective of this study was to investigate whether drought-inhibition of tiller growth is mainly due to the suppression of axillary bud initiation or subsequent outgrowth in perennial grass species and to determine whether drought-inhibition of tiller development and growth in grass species are associated with strigolactone (SL) accumulation and signaling. Seedlings with one fully-expanded leaf without axillary buds and those with three-fully expanded leaves and two axillary buds were grown in 20% polyethylene glycol (PEG) solution to induce drought stress. Plant height, number of leaves, axillary buds, tillers and length of axillary buds were monitored during 21 d of stress. Both axillary bud initiation and outgrowth were inhibited by drought stress, with outgrowth being more sensitive to drought stress. qRT-PCR analysis showed that expression level of genes involved in axillary bud activity was down-regulated at 14 d of drought stress while genes involved in axillary bud dormancy was up-regulated. Strigolactone (SL) content was elevated under drought stress in crowns. qRT-PCR analysis showed that expression level of genes involved in SL biosynthesis and signaling transduction were up-regulated during drought stress. Axillary bud outgrowth was sensitive to drought stress and could be associated with SL signaling, contributing to drought-inhibition of tillering in perennial grass species.

1. Introduction

Tillering is a critical trait controlling plant density for monocotyledonous grass species, which affects plant establishment and recuperative ability from stress damage, and it is a determinant factor for the perenniality for perennial grass species (Busso et al., 1989; Busso and Richards, 1995). Tillers in grass species arise from nodes of non-elongated internodes (named crown) at the base of the parent shoot. Tiller development in monocot species and lateral branch growth in dicot species involve two stages: axillary bud initiation and subsequent outgrowth (Li et al., 2003; Tantikanjana et al., 2001). Axillary bud formation is largely genetically controlled (Kebrom et al., 2013), but can be affected by environmental factors (Kebrom et al., 2013; Rameau et al., 2015). Tiller development is very sensitive to water stress which can inhibit tiller bud number and outgrowth (Busso et al., 1989). However, whether drought-inhibition of tiller growth is due to the suppression of axillary bud initiation or outgrowth or both developmental processes in perennial grass species are not well documented,

and the underlying mechanisms are also poorly understood.

Several transcription factors are found to play roles in regulating axillary meristem initiation, which is pivotal for axillary bud formation. Mutations in LATERAL SUPPRESSOR (LAS) or its ortholog in rice (*Oryza sativa*) and tomato (*Lycopersicon esculentum*), which belong to GRAS family (named after GIBBERELIC ACID INSENSITIVE (GAI), REPRESSOR OF GAI1 (RGA), and SCARECROW (SCR)), result in defects in axillary meristem initiation (Schumacher et al., 1999; Greb et al., 2003; Li et al., 2003). MYB-like transcription factors REGULATOR OF AXILLARY MERISTEMS 1 (RAX1), RAX2 and RAX3 function redundantly to positionally specify a stem cell niche for axillary meristem formation in *Arabidopsis thaliana* and in tomato (Schmitz et al., 2002; Keller et al., 2006a; Müller et al., 2006). Recent research shows that EXCESSIVE BRANCHES1 (EXB1) in *Arabidopsis*, encoding a member of WRKY protein, controls axillary meristem initiation by positively regulating the transcription of RAX1, RAX2, and RAX3 (Guo et al., 2015). In addition, several genes regulating bud activation and bud dormancy related to cell division have been identified (Gonzalez-

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Metabolic Pathways Involved in Carbon Dioxide Enhanced Heat Tolerance in Bermudagrass

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Front. Plant Sci. 8:1506.
doi: 10.3389/fpls.2017.01506

Global climate changes involve elevated temperature and CO₂ concentration, imposing significant impact on plant growth of various plant species. Elevated temperature exacerbates heat damages, but elevated CO₂ has positive effects on promoting plant growth and heat tolerance. The objective of this study was to identify metabolic pathways affected by elevated CO₂ conferring the improvement of heat tolerance in a C₄ perennial grass species, bermudagrass (*Cynodon dactylon* Pers.). Plants were planted under either ambient CO₂ concentration (400 μmol·mol⁻¹) or elevated CO₂ concentration (800 μmol·mol⁻¹) and subjected to ambient temperature (30/25°C, day/night) or heat stress (45/40°C, day/night). Elevated CO₂ concentration suppressed heat-induced damages and improved heat tolerance in bermudagrass. The enhanced heat tolerance under elevated CO₂ was attributed to some important metabolic pathways during which proteins and metabolites were up-regulated, including light reaction (ATP synthase subunit and photosystem I reaction center subunit) and carbon fixation [(glyceraldehyde-3-phosphate dehydrogenase, GAPDH), fructose-bisphosphate aldolase, phosphoglycerate kinase, sedoheptulose-1,7-bisphosphatase and sugars] of photosynthesis, glycolysis (GAPDH, glucose, fructose, and galactose) and TCA cycle (pyruvic acid, malic acid and malate dehydrogenase) of respiration, amino acid metabolism (aspartic acid, methionine, threonine, isoleucine, lysine, valine, alanine, and isoleucine) as well as the GABA shunt (GABA, glutamic acid, alanine, proline and 5-oxoproline). The up-regulation of those metabolic processes by elevated CO₂ could at least partially contribute to the improvement of heat tolerance in perennial grass species.

Keywords: bermudagrass, elevated CO₂, heat stress, metabolites, protein

INTRODUCTION

Global climate changes involve elevated temperature and CO₂ concentration, imposing significant impact on plant growth (Kirkham, 2011). During this century, global temperatures are predicted to rise by 2–5°C; atmospheric CO₂ concentration has increased by 100 μmol mol⁻¹ since the beginning of the industrialized era and the concentration is predicted to continue rising at a rate of approximately 2 μmol mol⁻¹ per year (Intergovernmental Panel on Climate Change [IPCC], 2007). Previous research has shown that elevated CO₂ promotes plant growth under optimal growing temperatures in various plant species (Hamerlynck et al., 2000; Prasad et al., 2002; Qaderi et al., 2006). Recent research also found that elevated CO₂ has positive effects on promoting heat

Lipidomic reprogramming associated with drought stress priming-enhanced heat tolerance in tall fescue (*Festuca arundinacea*)

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Abstract

Stress priming by exposing plants to a mild or moderate drought could enhance plant tolerance to subsequent heat stress. Lipids play vital roles in stress adaptation, but how lipidomic profiles change, affecting the cross-stress tolerance, is largely unknown. The objectives of this study were to perform lipidomics, to analyse the content, composition, and saturation levels of lipids in leaves of tall fescue (*Festuca arundinacea*) following drought priming and subsequent heat stress, and to identify major lipids and molecular species associated with priming-enhanced heat tolerance. Plants were initially exposed to drought for 8 days by withholding irrigation and subsequently subjected to 25 days of heat stress (38/33°C day/night) in growth chambers. Drought-primed plants maintained significantly higher leaf relative water content, chlorophyll content, photochemical efficiency, and lower electrolyte leakage than nonprimed plants under heat stress. Drought priming enhanced the accumulation of phospholipids and glycolipids involved in membrane stabilization and stress signalling (phosphatidic acid, phosphatidylcholine, phosphatidylinositol, phosphatidylglycerol, and digalactosyl diacylglycerol) during subsequent exposure to heat stress. The reprogramming of lipid metabolism for membrane stabilization and signalling in response to drought priming and subsequent exposure to heat stress could contribute to drought priming-enhanced heat tolerance in cool-season grass species.

KEYWORDS

drought priming, glycolipids, heat tolerance, lipidomics, phospholipids, tall fescue (*Festuca arundinacea*)

1 | INTRODUCTION

High temperature is a major abiotic stress limiting the growth and productivity of temperate plant species, especially during summer months (Missaoui, Malinowski, Pinchak, & Kigel, 2017; Mittler, Finka, & Gouubino, 2012). The frequency and severity of heat stress are likely to increase due to global warming, as the global mean air temperature is predicted to increase by 1.4–3.1°C by the end of the 21st century (IPCC, 2013; Long & Ort, 2010). Approaches to improving heat tolerance of plants are critically important to maintain plant

growth and productivity, particularly in areas with prolonged periods of high temperatures (Bita & Gerats, 2013; Varshney, Bansal, Aggarwal, Datta, & Craufurd, 2011). Stress priming by exposure of plants to mild drought stress or water deficit has been reported to be a viable method for improving heat tolerance in various plant species (Ashoub, Baeumisberger, Neupaertl, Karas, & Brüggemann, 2015; Bruce, Matthes, Napier, & Pickett, 2007; Wang et al., 2014). Drought priming-enhanced heat tolerance has been associated with osmotic adjustment and development of deep roots (Jiang & Huang, 2001) and is also related to the induction of stress-responsive proteins and

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论文收录和引用 检索报告

委托内容：江苏省重点实验室草种质资源创新与利用验收

委托单位：南京农业大学

委托日期：2020年6月16日

检索机构（盖章）南京农业大学查新站

完成日期：2020年6月18日

南京农业大学科技查新站

论文收录引用检索报告

一、 检索要求

1. 被检作者：郭振飞 (Guo Zhenfei; Guo ZF)、张敬 (Zhang Jing; Zhang J)、邵涛 (Shao Tao; Shao T)、肖燕 (Xiao Yan)、庄黎丽 (Zhuang Lili; Zhuang LL)、于景金 (Yu Jingjin; Yu JJ)、张夏香 (Zhang Xiaxiang; Zhang XX)
2. 作者单位：南京农业大学 (Nanjing Agricultural University, China)
3. 检索目的：江苏省重点实验室草种质资源创新与利用验收
4. 论文发表年限：2017-2019 年
5. 提供待检索论文篇数：10 篇英文论文

二、 检索范围：

Science Citation Index Expanded (SCI-EXPANDED) 2017-2020/06
Journal Citation Reports (JCR) 2017-2018

三、 检索结果

SCI 论文收录引用、影响因子及 JCR 分区情况：论文作者郭振飞等提供的 10 篇英文论文均被 SCI 收录，该 10 篇论文被 SCI 总引用 172 次，他引 140 次。该 10 篇论文的收录引用、期刊发表当年影响因子及 JCR 分区详情见附件 1。

高被引论文情况：论文作者郭振飞等提供的 10 篇论文中的 1 篇为高被引论文，详情见附件 2。

注：他引：如果引用文献与被引文献作者有相同者为自引，否则为他引。

本报告已获得本委托方的认可。

附件 1：10 篇 SCI 论文收录引用、期刊发表当年影响因子及 JCR 分区情况

附件 2：1 篇高被引论文情况

检索报告人：何群

审核人：张已慧

检索单位：南京农业大学科技查新站

完成时间：2020 年 6 月 18 日

南京农业大学科技查新站
农业部查新单位南京农业大学科技查新站



电话 (传真)：025-84396016
Email: chayin@njau.edu.cn

附件 1: 10 篇 SCI 论文收录引用、期刊发表当年影响因子及 JCR 分区情况

第 1 条, 共 10 条

标题: Melatonin suppression of heat-induced leaf senescence involves changes in abscisic acid and cytokinin biosynthesis and signaling pathways in perennial ryegrass (*Lolium perenne* L.)

作者: Zhang, J (Zhang, Jing); Shi, Y (Shi, Yi); Zhang, XZ (Zhang, Xunzhong); Du, HM (Du, Hongmei); Xu, B (Xu, Bin); Huang, BR (Huang, Bingru)

来源出版物: ENVIRONMENTAL AND EXPERIMENTAL BOTANY 卷: 138 页: 36-45 DOI:

10.1016/j.envexpbot.2017.02.012 出版年: JUN 2017

Web of Science 核心合集中的 "被引频次": 53

被引频次合计: 58

地址: [Zhang, Jing; Xu, Bin] Nanjing Agr Univ, Coll Agrograssland Sci, Nanjing 210095, Jiangsu, Peoples R China.

[Zhang, Jing; Shi, Yi; Du, Hongmei; Huang, Bingru] Rutgers State Univ, Dept Plant Biol & Pathol, New Brunswick, NJ 08901 USA.

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binxu@njau.edu.cn; huang@aesop.rutgers.edu

SCI 引用 53 次, 他引 52 次

2017 年期刊影响因子为: 3.666

JCR 分区为:

| JCR® 类别 | 类别中的排序 | JCR 分区 |
|------------------------|--------|--------|
| ENVIRONMENTAL SCIENCES | 56/242 | Q1 |
| PLANT SCIENCES | 25/232 | Q1 |

第 2 条, 共 10 条

标题: A cold responsive ethylene responsive factor from *Medicago falcata* confers cold tolerance by up-regulation of polyamine turnover, antioxidant protection, and proline accumulation

作者: Zhuo, CL (Zhuo, Chunliu); Liang, L (Liang, Lu); Zhao, YQ (Zhao, Yaqing); Guo, ZF (Guo, Zhenfei); Lu, SY (Lu, Shaoyun)

来源出版物: PLANT CELL AND ENVIRONMENT 卷: 41 期: 9 特刊: SI 页: 2021-2032 DOI:

10.1111/pce.13114 出版年: SEP 2018

Web of Science 核心合集中的 "被引频次": 22

被引频次合计: 25

地址: [Zhuo, Chunliu; Liang, Lu; Zhao, Yaqing; Lu, Shaoyun] South China Agr Univ, Coll Life Sci, Guangdong Engn Res Ctr Grassland Sci, State Key Lab Conservat & Utilizat Subtrop Agrobi, Guangzhou 510642, Guangdong, Peoples R China.

[Guo, Zhenfei] Nanjing Agr Univ, Coll Grassland Sci, Nanjing 210095, Jiangsu, Peoples R China.

[Zhuo, Chunliu] Univ North Texas, BioDiscovery Inst, Dept Biol Sci, Denton, TX 76203 USA.

通讯作者地址: Guo, ZF (通讯作者), Nanjing Agr Univ, Coll Grassland Sci, Nanjing 210095, Jiangsu, Peoples R China.

Lu, SY (通讯作者), South China Agr Univ, Coll Life Sci, Guangzhou 510642, Guangdong, Peoples R China.

电子邮件地址: zfguo@njau.edu.cn; turflab@scau.edu.cn

SCI 引用 22 次, 他引 19 次

PLANT CELL AND ENVIRONMENT

Impact factor
5.624 6.026
2018 5年

| JCR # 类别 | 类别中的排名 | JCR 分区 |
|----------------|--------|--------|
| PLANT SCIENCES | 13/228 | Q1 |

数据来自第 2018 版 Journal Citation Reports

第 3 条, 共 10 条

标题: Ensiling as pretreatment of rice straw: The effect of hemicellulase and Lactobacillus plantarum on hemicellulose degradation and cellulose conversion

作者: Zhao, J (Zhao, Jie); Dong, ZH (Dong, Zhihao); Li, JF (Li, Junfeng); Chen, L (Chen, Lei); Bai, YF (Bai, Yunfeng); Jia, YS (Jia, Yushan); Shao, T (Shao, Tao)

来源出版物: BIORESOURCE TECHNOLOGY 卷: 266 页: 158-165 DOI: 10.1016/j.biortech.2018.06.058 出版年: OCT 2018

Web of Science 核心合集中的 "被引频次": 17

被引频次合计: 19

地址: [Zhao, Jie; Dong, Zhihao; Li, Junfeng; Chen, Lei; Shao, Tao] Nanjing Agr Univ, Coll Agrograssland Sci, Inst Ensiling & Proc Grass, Nanjing 210095, Jiangsu, Peoples R China.

[Bai, Yunfeng] Jiangsu Acad Agr Sci, Nanjing 210014, Jiangsu, Peoples R China.

[Jia, Yushan] Inner Mongolia Agr Univ, Minist Agr, Key Lab Forage Cultivat Proc & High Efficient Uti, Hohhot 010018, Peoples R China.

通讯作者地址: Shao, T (通讯作者), Nanjing Agr Univ, Coll Agrograssland Sci, Inst Ensiling & Proc Grass, Nanjing 210095, Jiangsu, Peoples R China.

电子邮件地址: taoshaolan@163.com

SCI 引用 17 次, 他引 13 次

BIORESOURCE TECHNOLOGY

Impact factor
6.669 6.589
2018 5年

| JCR® 类别 | 期刊中的排名 | JCR分区 |
|--------------------------------------|--------|-------|
| AGRICULTURAL ENGINEERING | 1/13 | Q1 |
| BIOTECHNOLOGY & APPLIED MICROBIOLOGY | 13/162 | Q1 |
| ENERGY & FUELS | 13/103 | Q1 |

数据源自 2018 JCR Journal Citation Reports

第 4 条, 共 10 条

标题: Dynamics of microbial community and fermentation quality during ensiling of sterile and nonsterile alfalfa with or without *Lactobacillus plantarum* inoculant

作者: Yang, LL (Yang, Lili); Yuan, XJ (Yuan, Xianjun); Li, JF (Li, Junfeng); Dong, ZH (Dong, Zhihao); Shao, T (Shao, Tao)

来源出版物: BIORESOURCE TECHNOLOGY 卷: 275 页: 280-287 DOI: 10.1016/j.biortech.2018.12.067 出

版年: MAR 2019

Web of Science 核心合集中的 "被引频次": 17

被引频次合计: 17

地址: [Yang, Lili; Yuan, Xianjun; Li, Junfeng; Dong, Zhihao; Shao, Tao] Nanjing Agr Univ, Coll Agrograssland Sci, Inst Ensiling & Proc Grass, Nanjing 210095, Jiangsu, Peoples R China.

通讯作者地址: Shao, T (通讯作者), Nanjing Agr Univ, Coll Agrograssland Sci, Inst Ensiling & Proc Grass, Nanjing 210095, Jiangsu, Peoples R China.

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SCI 引用 17 次, 他引 13 次

由于 2019 年期刊影响因子和分区未出来, 因此记录为 2018 年期刊影响因子和分区:

BIORESOURCE TECHNOLOGY

Impact factor
6.669 6.589
2018 5年

| JCR® 类别 | 期刊中的排名 | JCR分区 |
|--------------------------------------|--------|-------|
| AGRICULTURAL ENGINEERING | 1/13 | Q1 |
| BIOTECHNOLOGY & APPLIED MICROBIOLOGY | 13/162 | Q1 |
| ENERGY & FUELS | 13/103 | Q1 |

数据源自 2018 JCR Journal Citation Reports

第 5 条, 共 10 条

标题: Characterization of *Enterococcus faecalis* JF85 and *Enterococcus faecium* Y83 isolated from Tibetan yak (*Bos grunniens*) for ensiling *Pennisetum sinense*

作者: Li, JF (Li, Junfeng); Yuan, XJ (Yuan, Xianjun); Desta, ST (Desta, Seare T.); Dong, ZH (Dong, Zhihao); Mugabe, W (Mugabe, Wazha); Shao, T (Shao, Tao)

来源出版物: BIORESOURCE TECHNOLOGY 卷: 257 页: 76-83 DOI: 10.1016/j.biortech.2018.02.070 出版

年: JUN 2018



Web of Science 核心合集中的 "被引频次": 15

被引频次合计: 16

地址: [Li, Junfeng; Yuan, Xianjun; Desta, Seare T.; Dong, Zhihao; Mugabe, Wazha; Shao, Tao] Nanjing Agr Univ, Coll Prataculture Sci, Inst Ensiling & Proc Grass, Nanjing 210095, Jiangsu, Peoples R China.

通讯作者地址: Shao, T (通讯作者), Nanjing Agr Univ, Coll Prataculture Sci, Inst Ensiling & Proc Grass, Nanjing 210095, Jiangsu, Peoples R China.

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SCI 引用 15 次, 他引 8 次

BIORESOURTE TECHNOLOGY

Impact factor
6.669 6.589
2018 5 年

| JCR 主题 | 期刊中的排名 | JCR 分区 |
|--------------------------------------|--------|--------|
| AGRICULTURAL ENGINEERING | 1/13 | Q1 |
| BIOTECHNOLOGY & APPLIED MICROBIOLOGY | 13/162 | Q1 |
| ENERGY & FUELS | 13/103 | Q1 |

数据源自 2018 版 Journal Citation Reports

第 6 条, 共 10 条

标题: The effects of fibrolytic enzymes, cellulolytic fungi and bacteria on the fermentation characteristics, structural carbohydrates degradation, and enzymatic conversion yields of Pennisetum sinense silage

作者: Li, JF (Li, Junfeng); Yuan, XJ (Yuan, Xianjun); Dong, ZH (Dong, Zhihao); Mugabe, W (Mugabe, Wazha); Shao, T (Shao, Tao)

来源出版物: BIORESOURTE TECHNOLOGY 卷: 264 页: 123-130 DOI: 10.1016/j.biortech.2018.05.059 出版年: SEP 2018

Web of Science 核心合集中的 "被引频次": 13

被引频次合计: 14

地址: [Li, Junfeng; Yuan, Xianjun; Dong, Zhihao; Mugabe, Wazha; Shao, Tao] Nanjing Agr Univ, Coll Agrograssland Sci, Inst Ensiling & Proc Grass, Nanjing 210095, Jiangsu, Peoples R China.

通讯作者地址: Shao, T (通讯作者), Nanjing Agr Univ, Coll Prataculture Sci, Inst Ensiling & Proc Grass, Nanjing 210095, Jiangsu, Peoples R China.

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SCI 引用 13 次, 他引 12 次

BIORESOURTE TECHNOLOGY

Impact factor
6.669 6.589
2018 5 年

| JCR 主题 | 期刊中的排名 | JCR 分区 |
|--------------------------------------|--------|--------|
| AGRICULTURAL ENGINEERING | 1/13 | Q1 |
| BIOTECHNOLOGY & APPLIED MICROBIOLOGY | 13/162 | Q1 |
| ENERGY & FUELS | 13/103 | Q1 |

数据源自 2018 版 Journal Citation Reports

检索证明报告

第 7 条, 共 10 条

标题: Effects of arbuscular mycorrhizal fungi, biochar and cadmium on the yield and element uptake of *Medicago sativa*

作者: Zhang, FG (Zhang, Fengge); Liu, MH (Liu, Mohan); Li, Y (Li, Yang); Che, YY (Che, Yeye); Xiao, Y (Xiao, Yan)

来源出版物: SCIENCE OF THE TOTAL ENVIRONMENT 卷: 655 页: 1150-1158 DOI:

10.1016/j.scitotenv.2018.11.317 出版年: MAR 10 2019

Web of Science 核心合集中的 "被引频次": 11

被引频次合计: 12

地址: [Zhang, Fengge; Liu, Mohan; Li, Yang; Che, Yeye; Xiao, Yan] Nanjing Agr Univ, Coll Agrograssland Sci, Nanjing 210095, Jiangsu, Peoples R China.

通讯作者地址: Xiao, Y (通讯作者), Nanjing Agr Univ, Coll Agrograssland Sci, Nanjing 210095, Jiangsu, Peoples R China.

电子邮件地址: xiaoyan@njau.edu.cn

SCI 引用 11 次, 他引 6 次

由于 2019 年期刊影响因子和分区未出来, 因此记录为 2018 年期刊影响因子和分区:

SCIENCE OF THE TOTAL ENVIRONMENT

Impact factor
5.589 5.727
2018 5 年

| JCR®类别 | 类别中的排名 | JCR分区 |
|------------------------|--------|-------|
| ENVIRONMENTAL SCIENCES | 27/251 | Q1 |

数据来自第 2018 版 Journal Citation Reports

第 8 条, 共 10 条

标题: Drought inhibition of tillering in *Festuca arundinacea* associated with axillary bud development and strigolactone signaling

作者: Zhuang, LL (Zhuang, Lili); Wang, J (Wang, Jian); Huang, BR (Huang, Bingru)

来源出版物: ENVIRONMENTAL AND EXPERIMENTAL BOTANY 卷: 142 页: 15-23 DOI:

10.1016/j.envexpbot.2017.07.017 出版年: OCT 2017

Web of Science 核心合集中的 "被引频次": 7

被引频次合计: 10

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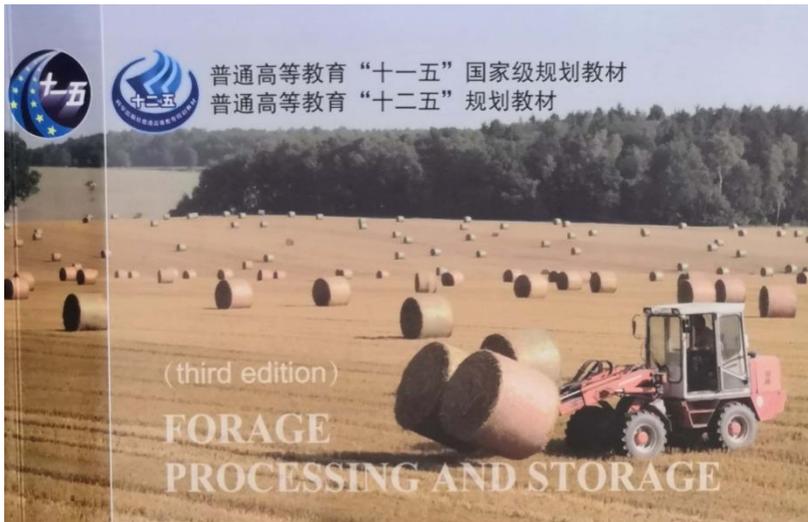
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互花米草 生态工程

钦 佩 张焕仕 覃凤飞 编著



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