Effects of Physiological Protection on Compensatory Growth of Ryegrass After Mowing: Postprint

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Abstract

Through analysis of growth rates of residual leaves and leaf regrowth portions, activities of superoxide dismutase (SOD), peroxidase (POD), and catalase (CAT), and contents of malondialdehyde, soluble sugars, and proline in ryegrass (Lolium perenne L) under light, moderate, severe, and complete mowing treatments at 6 d and 12 d post-mowing, this study aimed to reveal the relationship between leaf antioxidant enzyme activities and osmotic regulator contents with compensatory growth following mowing stress, as well as the physiological regulatory mechanisms of forage tolerance to mowing. Results showed that leaf growth rates after light, moderate, and complete mowing were higher than the control, while severe mowing was lower than the control. Compensatory growth was most pronounced after complete mowing, followed by light and moderate mowing, while no compensatory growth occurred under severe mowing. In control ryegrass leaves, antioxidant enzyme activities and osmotic regulator contents varied among leaf parts, with higher MDA content in leaf tips, accompanied by higher SOD and CAT activities and higher proline content; leaf bases had the lowest MDA content, with lower SOD and CAT activities and proline content. Compared with the control, at 6 d post-mowing under different mowing intensities, the average MDA content, SOD and CAT activities, and soluble sugar and proline contents in regrown leaves and overall leaves were lower. However, at 12 d post-mowing under different intensities, while average MDA content in regrown leaves and overall leaves remained low, SOD and CAT activities increased, proline content increased, but POD activity and soluble sugar content were lower than the control. This indicates that while mowing reduced leaf area and photosynthetic capacity, mowing injury stress initiated forage compensatory growth, causing rapid growth of residual leaves, and residual leaf area was positively correlated with compensatory growth rate. Additionally, although leaf compensatory growth rates differed under different mowing intensities, all mowing intensities (at 12 d) activated the antioxidant protective enzyme system in residual leaves and promoted proline accumulation. During the compensatory growth process, CAT and SOD could promptly scavenge oxygen free radicals accumulated in residual leaves, maintaining low membrane lipid peroxidation and cell membrane integrity, while accumulated proline could maintain cellular water balance. Therefore, antioxidant enzymes (SOD and CAT) and osmotic regulators (proline) play important physiological protective roles in rapid self-healing of injured tissues and rapid compensatory growth of residual leaves in ryegrass after mowing.

Full Text

Preamble

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Relationship between Physiological Protection Mechanisms and the Compensatory Growth of *Lolium perenne* L. at Different Cutting Treatment Levels

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Abstract

Grazing and cutting can promote compensatory growth in forage grasses, which plays an important role in maintaining growth and resistance to mowing, grazing, and trampling. However, little is known about the physiological mechanisms involved in the compensatory growth of grasses. In this study, the growth rate, superoxide dismutase (SOD), peroxidase (POD), and catalase (CAT) activities, as well as soluble sugar, proline, and malondialdehyde (MDA) contents were investigated in the leaves of *Lolium perenne* under light, moderate, severe, and whole cutting levels to determine the relationships between antioxidant enzyme activities, osmoregulation and compensatory growth, and the physiological mechanisms of compensatory growth in grasses after cutting.

The results showed that the growth rate was higher in leaves after light, moderate, and whole cutting treatments compared to the control, but lower under severe cutting. Compared to the control, *L. perenne* showed significant compensatory growth under light, moderate, and whole cutting levels, while no compensatory growth occurred under severe cutting. Normally, the top of the leaves had higher MDA contents, SOD and CAT activities, while the base of the leaves had lower MDA, proline contents, SOD and CAT activities. At 6 days after different cutting levels, the regrowth of *L. perenne* leaves had lower MDA, soluble sugar, and proline contents, as well as lower SOD and CAT activities compared to the control. However, at 12 days after cutting, the regrowth leaves still had lower MDA contents, but higher SOD and CAT activities and proline content.

This indicated that cutting decreased leaf area, reduced photosynthetic energy availability, and enhanced the compensatory growth function of residual leaves. Therefore, cutting damage was an internal factor resulting in compensatory growth. The compensatory growth rate was positively correlated with residual leaf size. In addition, although there were differences in the compensatory growth rate among different cutting levels, all cutting levels activated antioxidant enzymes and enhanced proline accumulation. During the compensatory growth of residual leaves, SOD and CAT could scavenge active oxygen free radicals produced during photosynthetic metabolism, inhibit membrane lipid peroxidation, and maintain the balance of oxygen free radicals metabolism. Accumulated proline could maintain water balance. Therefore, antioxidant enzymes and osmoregulation play an important role in physiological protection, including photosynthesis and compensatory growth, during rapid self-healing after cutting of residual leaves in *L. perenne*.

Keywords: *Lolium perenne* L.; antioxidant enzymes; osmoregulation; compensatory growth; different cutting treatments

Introduction

Mowing tolerance is a characteristic of perennial forage grasses that enables self-recovery and protection after mowing stress, and it is fundamental for timed harvesting of forage for livestock production and landscaping. Mowing tolerance plays an important role in the development of horticulture and animal husbandry. Some studies have found that mowing tolerance is related to compensatory growth after cutting, and moderate cutting can not only improve leaf light energy conversion efficiency and photosynthetic rate but also increase forage and seed yield. Forage regeneration is essentially a reconstruction process of tissues and organs, and compensatory photosynthesis triggered by enhanced carbon assimilation after cutting may be key to accelerated growth. Current domestic research on cutting mainly focuses on the effects of cutting intensity, timing, and fertilization on forage yield and quality. For forage grasses, cutting causes mechanical damage to leaves, triggering cell sap leakage and disrupting plant water balance. However, why forages can still perform compensatory photosynthesis and compensatory growth under mowing stress, and the physiological regulation mechanisms involved, remain unclear.

Research on plant adaptation mechanisms to stress is extensive. Under low temperature, drought, and salt stress, forage leaf antioxidant enzyme activities and malondialdehyde content increase. During autumn cold acclimation in some alpine perennial forages, root antioxidant enzyme activities increase. Under stress conditions, maintaining high antioxidant enzyme activities in forage cells plays an important role in inhibiting cell membrane lipid peroxidation, maintaining oxygen free radical metabolism balance, and cell membrane integrity. Studies have also found that under drought, low temperature, and salt stress, forage leaves accumulate osmotic adjustment substances such as proline and soluble sugars, which help increase cell osmotic pressure and maintain cell water-holding capacity and water metabolism balance. Forage stress resistance is positively correlated with antioxidant enzyme activities and osmotic adjustment substance content, and stress-resistant plants can improve stress tolerance by enhancing antioxidant defense systems and osmotic adjustment capacity.

Whether compensatory photosynthesis and compensatory growth after injury are related to high antioxidant capacity, and whether osmotic adjustment substances are involved in maintaining cell water metabolism balance under leaf dehydration after cutting, remain unclear. *Lolium perenne* is a widely introduced and cultivated excellent forage grass. Studies on this plant have found that cutting can significantly trigger compensatory growth, carbohydrates in stubble play a key role in regeneration, and changes in light environment of grassland canopy after cutting are closely related to compensatory growth. Cutting can significantly increase hay yield and protein content, and compensatory capacity depends on the photosynthetic efficiency of remaining leaves after cutting. Most research has focused on the relationship between substances and energy conversion in residual leaves and leaf regeneration after cutting, with less research on physiological changes in stress resistance of residual leaves in gramineous plants, and results are typically obtained from analysis of entire residual leaves.

In grazing and cutting, upper leaves are typically removed, leaving lower leaves that become key for grass recovery. What physiological changes occur in these remaining leaves to maintain compensatory growth? Are there differences in stress resistance physiological regulation between cut and non-cut parts? This question has been rarely addressed in similar studies. This study used artificially planted *L. perenne* lawn green belts as experimental sites, with *L. perenne* as experimental material. Cutting treatments were conducted in autumn when cool temperatures were suitable for grass growth. By analyzing antioxidant enzyme activities, membrane lipid peroxidation products, and osmotic adjustment substance contents in different parts of *L. perenne* leaves at 6 and 12 days after cutting, this study aimed to reveal the relationship between changes in antioxidant enzyme activities and adjustment substance contents and compensatory growth after cutting stress, as well as their physiological protective roles, to provide theoretical guidance for forage stress resistance breeding and grassland scientific management.

1. Study Site Overview

The experimental site was located on green belts within Ludong University campus in Yantai City (119°34 -121°57 E, 36°16 -38°23 N). The region has a temperate monsoon climate with an average annual temperature of 11.8°C, extreme maximum temperature of 38.4°C, and average annual precipitation of 651.9 mm, concentrated in June-September (accounting for 65% of annual rainfall). The soil is brown loam.

2. Experimental Treatments

The *L. perenne* green belts on Ludong University campus were established in 2015 and grew well under campus forestry management, being in the vegetative growth stage. Uniform, weed-free *L. perenne* plots were selected as experimental sites, each measuring approximately 1.5 m × 1.5 m. Each treatment had three replicates arranged sequentially with the control. When plants reached 30-35 cm height, leaves were divided from top to bottom into four sections: (30-22 cm), (22-15 cm), (15-7 cm), and (7-0 cm). Light cutting removed the top 8 cm (30-22 cm), moderate cutting removed the top 15 cm (30-15 cm), severe cutting removed the top 23 cm (30-7 cm), and whole cutting removed all aboveground parts (30-0 cm). The remaining stubble heights were marked with bamboo sticks for later growth rate measurements. Plant height was measured every two days after cutting to determine growth rate.

3. Experimental Sampling

To better understand the effects of cutting injury on different parts of residual *L. perenne* leaves, samples were taken from different sections of residual leaves and regrown leaves at 6 and 12 days after cutting for determination of stress resistance physiological indicators. The clipped leaf portions were quickly wrapped and fixed in liquid nitrogen, then stored in an ultra-low temperature freezer in the laboratory. For sampling, leaves were first straightened, then the remaining portions were cut according to the marked cutting heights on bamboo sticks. The base sections were labeled as , , , , and the regrown portions were labeled as regenerated leaves. Sampling was conducted on two plots per cutting treatment at 10:00 am.

4. Experimental Methods

Growth rate was measured using a ruler every two days after cutting. Enzyme extraction was performed at 4°C. Liquid nitrogen-fixed leaves were ground in a pre-cooled mortar with enzyme extraction buffer (phosphate buffer) on ice to form a homogenate, then centrifuged at 15,000 r/min for 15 min at 4°C. The supernatant was used for antioxidant enzyme activity and proline content determination. Soluble protein content was determined by the Coomassie brilliant blue method. POD activity was measured by the guaiacol method, SOD activity by the nitroblue tetrazolium (NBT) photoreduction method, and CAT activity by the hydrogen peroxide method. Free proline content was determined by the ninhydrin colorimetric method, soluble sugar content by the anthrone method, and malondialdehyde content by the thiobarbituric acid method.

Experimental data were expressed as means of three or more replicates (mean ± SD) and analyzed using SPSS 11.5 software.

Results

1. Comparison of Leaf Growth Rate in *L. perenne* Under Different Cutting Intensities

After different cutting intensities, the net growth of leaves in light and moderate cutting treatments increased by 46.3% and 65.7% compared to the control, while severe cutting decreased growth rate. Whole cutting increased leaf growth by 289% compared to the control, with growth rate much higher than light and moderate cutting. These results showed obvious compensatory growth after cutting.

2. Membrane Lipid Peroxidation Products (MDA) in Residual and Regenerated Leaves of *L. perenne* Under Different Cutting Intensities

Under normal growth conditions, MDA content in *L. perenne* leaves was higher in the upper portion and lower in the lower portion, though differences were not significant. At 6 days after cutting, MDA content in the regrowth portion of cut leaves was lower than the control, decreasing with increasing cutting intensity. At 12 days, MDA content remained lower than the control and differed significantly. Cutting treatment did not increase intracellular membrane lipid peroxidation, consistent with results from He et al. on alfalfa.

The effect of different cutting intensities on MDA content in the leaves of *Lolium perenne* L. (mol/g FW)

3. Comparison of Antioxidant Enzyme Activities in Residual and Regenerated Leaves of *L. perenne* Under Different Cutting Intensities

In control leaves, SOD activity tended to increase from leaf base to apex, with highest enzyme activity at the top. Compared to the control, average SOD activity across the whole leaf tended to decrease after cutting, except under light cutting. At 6 days, SOD activity in the regrowth portion was lower than the control. At 12 days, SOD activity in regrown leaves increased, especially under moderate cutting (increased by 54.9%). POD activity increased from leaf base to apex in control leaves. At 6 days, average POD activity increased slightly under different cutting treatments. At 12 days, POD activity in regrown leaves increased significantly under different cutting treatments, with increases of 13.6%, 23.9%, and 23.9% for light, moderate, and severe cutting, respectively. CAT activity in control leaves gradually decreased from base to apex. At 6 days, average CAT activity decreased under all cutting treatments. At 12 days, CAT activity in regrown leaves increased, with increases of 6.8%, 40.2%, and 39.8% under light, moderate, and severe cutting, respectively.

The effect of different cutting intensities on SOD activity in the leaves of *Lolium perenne* L. (U/g FW)
The effect of different cutting intensities on POD activity in the leaves of *Lolium perenne* L. (g H O /g FW/min)

The effect of different cutting intensities on CAT activity in the leaves of *Lolium perenne* L. (g H O /g FW/min)

4. Comparison of Osmotic Adjustment Substance Contents in Residual and Regenerated Leaves of *L. perenne* Under Different Cutting Intensities

Soluble sugar content in *L. perenne* leaves was concentrated in the middle portion, lower at the top and base. Compared to the control, average soluble sugar content decreased with increasing cutting intensity, with decreases of 22.2%, 22.2%, 57.1%, and 46.7% under different cutting treatments. At 12 days, soluble sugar content in the top regrown leaves decreased significantly, with decreases of 16.7%, 110.3%, 43.5%, and 45.5%.

Proline content was concentrated in the upper-middle portion of leaves, lower in the lower portion. Compared to the control, average proline content decreased under different cutting intensities, with decreases of 10.1%, 21.5%, and 14.5% under all cutting treatments. At 12 days, proline content in leaves showed an increasing trend, with increases of 37.2%, 29.6%, and 43.8% under different cutting treatments. Proline content in regenerated leaves increased significantly, with increases of 24.5%, 23.5%, and 14.2% under whole cutting treatment.

The effect of different cutting intensities on soluble sugar contents in the leaves of *Lolium perenne* L. (g/g FW)
The effect of different cutting intensities on proline contents in the leaves of *Lolium perenne* L. (g/g FW)

Discussion and Conclusion

Mowing tolerance plays an important role in the development of animal husbandry and horticulture. Cutting promotes compensatory growth in forage grasses, which is key to their survival and grazing tolerance. However, the physiological protective regulation mechanisms maintaining compensatory growth after cutting remain unclear. Measurements of stress resistance physiological indicators in different leaf parts after cutting showed that under normal conditions without cutting, different parts of *L. perenne* leaves had different antioxidant enzyme and osmotic adjustment substance contents. The leaf top had higher membrane lipid peroxidation, accompanied by higher SOD and CAT activities and proline content, while the leaf base had the lowest membrane lipid peroxidation and correspondingly lower SOD, CAT activities and proline content.

During normal growth, there was a significant positive correlation between membrane lipid peroxidation levels and antioxidant enzyme activities in different leaf parts, which was related to their environmental conditions. *Lolium perenne* has erect linear leaves with strong light at the top and rapid water loss, which induces oxygen free radical accumulation and membrane lipid peroxidation. Accumulated oxygen free radicals can activate the antioxidant enzyme system, increasing enzyme activities, while water deficit also induces proline accumulation. Therefore, higher antioxidant enzyme activities and proline content at the leaf top effectively maintain oxygen free radical metabolism balance and water balance, playing an important role in leaf top survival. Compared to the leaf top, the leaf middle is in a relatively suitable environment with less water deficit, weaker photosynthetic and respiratory metabolism, and lower antioxidant enzyme activities. The leaf base at the bottom of the canopy has minimal oxygen free radical accumulation and thus low membrane lipid peroxidation and antioxidant enzyme activities.

This study found that compensatory growth rates differed under different cutting intensities. Light and moderate cutting showed obvious compensatory growth, while whole cutting showed the most significant compensatory growth. The reason may be that light and moderate cutting mainly removed leaf tops, leaving the middle-lower portions that depend on the upper-middle and lower-middle leaf parts for growth. The middle leaf parts are relatively fast-growing and in suitable environmental conditions within the canopy, so their photosynthetic rate increased rapidly after cutting, leading to obvious compensatory growth. Severe cutting left only old leaves at the base, which have weak photosynthesis and vitality, insufficient to compensate for respiratory consumption, resulting in reduced growth rate and no compensatory growth in a short time. Whole cutting removed all aboveground leaves, so regeneration could only depend on carbohydrate and nitrogen reserves in the stem base and roots, which play important roles in initiating regrowth and early growth. Whole cutting also provided open space, flowing air, and strong solar radiation for new leaf growth, while underground root nutrients had short transport distances and no respiratory consumption from base leaves, allowing all root nutrients to be used for new leaf growth. This created favorable conditions for rapid new leaf growth and significant compensatory growth, though frequent whole cutting can lead to nutrient output exceeding input and cause plant death.

The results also showed that in a short time (6 days) after cutting, MDA, soluble sugar, and proline contents in regenerated leaves were lower than the control. However, in a longer time (12 days), SOD and CAT activities and proline content increased and were higher than the control. On one hand, the ability to maintain low membrane lipid peroxidation levels is related to compensatory growth after cutting. Many studies have found that plants with strong stress resistance have lower MDA content. Lower membrane lipid peroxidation indicates balanced oxygen free radical metabolism, which may be an important physiological guarantee for rapid self-healing of injured parts and rapid compensatory growth of the whole leaf. On the other hand, low membrane lipid peroxidation levels are related to antioxidant enzyme activities and osmotic adjustment substance contents.

Cutting rapidly reduces photosynthetic leaf area and energy synthesis capacity, causing energy imbalance that may stimulate rapid growth of residual leaves to compensate for energy loss, thereby initiating compensatory growth. Compensatory growth after cutting depends on photosynthetic products, and increased photosynthetic rate in residual leaves after cutting is key to compensatory growth. Since photosynthesis and respiration induce oxygen free radical accumulation, and antioxidant enzymes are inducible enzymes, oxygen free radicals accumulated during photosynthesis can activate the antioxidant protection system, increasing SOD and CAT activities to inhibit membrane lipid peroxidation. Antioxidant enzymes maintain residual leaf growth by rapidly scavenging oxygen free radicals and maintaining their metabolism balance. Under whole cutting treatment, although root reserves provide material basis for new leaf growth, maintaining higher SOD, CAT activities and proline content during new leaf growth may be the reason why *L. perenne* tolerates whole cutting, as they provide strong anti-membrane lipid peroxidation capacity and water retention ability.

Since life is a balance between free radical production and antioxidant action, rapidly increasing antioxidant enzyme activities in residual leaves after cutting to timely scavenge oxygen free radicals produced during photosynthetic metabolism, maintaining a balance between production and scavenging, plays an important physiological protective role in rapid compensatory growth of residual leaves. Cutting causes leaf wounds and water loss, which can increase proline content. Proline has strong hydrophilicity, can stabilize protoplasm colloids and metabolic processes, and acts as an important water stabilizer during rapid compensatory growth of stubble leaves.

Although compensatory growth rates differed under different cutting intensities, all cutting treatments activated the antioxidant protection enzyme system and promoted accumulation of osmotic adjustment substances. During compensatory growth, these could timely scavenge accumulated oxygen free radicals, inhibit membrane lipid peroxidation, and maintain cell water balance, thus playing important physiological protective roles in *L. perenne* compensatory growth.

Conclusion

Compensatory growth rates in *L. perenne* leaves differed significantly after different cutting intensities. Light and moderate cutting left the vigorous middle leaf parts, resulting in obvious compensatory growth, while severe cutting left weak basal old leaves with no obvious compensatory growth. Cutting reduced photosynthetic leaf area and energy income, causing plant energy imbalance that triggered compensatory growth, and the compensatory growth rate was positively correlated with residual leaf vigor. After different cutting intensities, SOD, CAT activities and proline content increased while MDA content remained low. All cutting treatments activated the antioxidant protection enzyme system and promoted accumulation of osmotic adjustment substances. During compensatory growth, these could timely scavenge accumulated oxygen free radicals, inhibit membrane lipid peroxidation, protect cell membrane integrity, and maintain water balance. Therefore, antioxidant enzymes and osmotic adjustment substances play important physiological protective roles in maintaining low membrane lipid peroxidation levels and rapid compensatory growth after cutting in *L. perenne*.

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Note: Figure translations are in progress. See original paper for figures.