

# Dwarfing and the underlying morphological changes of *Poa alpigena* plants in response to overgrazing conditions

Shi Hongxiao<sup>1</sup>, Hou Xiangyang<sup>1</sup>, Wu Xinhong<sup>1</sup>, Song haiqun<sup>2</sup>, Yang Tingting<sup>1</sup>

<sup>1</sup>Institute of Grassland Research, Chinese Academy of Agricultural Sciences, Hohhot, Inner Mongolia China

<sup>2</sup>College of Agricultural and Animal Husbandry, Qinghai University, Xining Qinghai, China

Corresponding Author:

Shi Hongxiao<sup>1</sup>

Street Address, Hohhot, Inner Mongolia, 010010, China

Email address: axiao8003@sina.com

## Abstract

*Poa alpigena* as the research object on alpine meadow in this paper, analyzed the change characteristics of the stem and leaf anatomical structures of *Poa alpigena* plants under the overgrazing and enclosed conditions aims to revealed the dwarfing of morphological mechanism in overgrazing. the results show that that leaf thickness, leaf epidermal thickness, epidermal cell area, and phloem thickness increased with increasing grazing intensity ( $p < 0.05$ ). In contrast, xylem thickness, mesophyll cell area, and guide wall thickness decreased with increasing grazing intensity ( $p < 0.05$ ). Mesophyll cell density was relatively unaffected by grazing intensity. Additionally, the plasticity indices were high (i.e., greater than 0.5) for leaf area, upper epidermal cutin layer thickness, and leaf xylem thickness. The plasticity indices were greater than 0.4 for stem tube diameter, epidermal cell size, and epidermal cuticle thickness. These results reflected the *Poa alpigena* stem and leaf structural changes induced by the water and mechanical stresses caused by grazing livestock. Thus, plateau plants adapt to grazing stress by increasing the thickness of their leaves, cuticles, and phloem. The *Poa alpigena* mesophyll cell area as well as the stem epidermal cell area and density decrease in response to minor changes in grazing intensity, which ultimately result in the shortened leaves and stems of dwarf plants.

Key words: grazing; *Poa alpigena*; anatomical structure

## Introduction

Dwarfing is a common adaptive response of plants to environmental stresses (Saito *et al.* 2010; Gell *et al.* 2011; Peng *et al.* 2011; Yang *et al.* 2011; Leeds *et al.* 2012). Dwarf grassland plants exhibit several traits, including shortened stature under overgrazing conditions, narrow and short leaves, short internodes, stiff leaves, narrow thickets, and a shallow root distribution (Wangwei *et al.* 2000a, 2000b). Changes to the main plant characteristics and the mechanism regulating the development of the dwarf phenotype of grassland plants have not been fully characterized. Thus, a thorough analysis of the mechanism responsible for the dwarfing of grassland plants is necessary.

Plant morphological and anatomical structures are sensitive to environmental stresses. Elucidating the structural changes of plants exposed to environmental stresses may provide important cytological information regarding the mechanism underlying the development of stress-induced damages and how plants can tolerate adverse environments (Wukai *et al.* 2007). To date, studies on the effects of environmental factors on plant anatomy have mainly focused on the effects of water, temperature, light, and salt stresses (Zhengxuepin *et al.* 1993; Lizhengli *et al.* 1981; Hejinsheng *et al.* 1994; Boardman N K *et al.* 1997). Additionally, plant anatomical changes in response to ecological conditions in specific habitats have been investigated (Gaoqiang *et al.* 2008). Studies regarding environment-induced plant structural changes were initially conducted outside of China (Boardman N K *et al.* 1977; Wylie R B *et al.* 1946; Chabot B F *et al.*; Jurid T W *et al.* 1979), but have since been completed at various sites in China (Linzhi *et al.* 1989; Zhongzhangchen *et al.* 1992; Zhenxueping *et al.* 1993). However, there have been relatively few studies on plant morphology and anatomy in the grazing ecosystems of China, especially regarding changes to the dominant species in the alpine meadow grazing ecosystems of the Qinghai–Tibet Plateau under different grazing intensities.

The Qinghai–Tibet Plateau mainly comprises alpine meadows, which are important for maintaining the ecological functions of the region (Shi *et al.* 2016). Determining how alpine meadow plants develop is vital to clarifying how they are damaged by environmental stresses. Clarifying the important morphological changes responsible for the dwarfing of *Poa alpigena* plants is warranted. *Poa alpigena* is a gramineous angiosperm that serves as a perennial forage grass species. It is the dominant plant species in the Qinghai–Tibet Plateau alpine meadows (Wang *et al.* 1990). Thus, to characterize the mechanism regulating *Poa alpigena* morphology, we analyzed the changes to the stem and leaf microstructural characteristics affected by overgrowth and restoration.

## Materials and methods

## Research overview

This study was conducted at the Ministry of Agriculture Yushu Alpine Grassland Resource and Ecological Environment at the Key Field Scientific Observation Station(N33°24' 30" , E97°18' 00" ). the study region is part of the Qinghai–Tibet Plateau, with an average altitude of 4,250 m above sea level, an annual average temperature is-6.4-4.3 °C, and an average annual rainfall of 374.2–721.2 mm. Grassland type is *alpine kobresia* weeds meadow, the main advantage of pasture is *Kobresia pygmaea*, a dominant species is *Kobresia kansuensis* , *Stipa Aliena* , *Poa crymophila* , *Elymus natans* , *Potehtilla saundersiana* , *Anaphalis lactea* , *Thalictrum alpinum*.

## Plot conditions and sampling

the following three types of grassland test plots were prepared: whole-year grazing (YG) (i.e., open grazing), fenced for 3 years (UG3), and fenced for 5 years (UG5). Three plots were prepared for each type (i.e., three replicates)The detailed characteristics of the sample are shown in the following table(table 1):

Table 1 The basic characteristics test sample

Plot	Latitude		Altitude (m)	Grazing intensity	Land-use-type	Dominant species
	Longitude	Latitude				
YG	33°0'27.72 "	97°18'13.32 "	4279.9	Heavy grazing	Annul grazing from January to December	<i>Kobresia pygmaea</i> , <i>Kobresia kansuensis</i>
UG3	33°21'38.25 "	97°18'6.65 "	4277.4	No grazing	Fencdd and ungrazing in 2011	<i>Elymus natans</i> , <i>Poa crymophila</i> , <i>Kobresia pygmaea</i> , <i>Kobresia kansuensis</i>
UG5	33°21'30.24 "	97°18'10.08 "	4198.1	No grazing	Fencdd and ungrazing in 2009	<i>Elymus natans</i> , <i>Poa crymophila</i> , <i>Kobresia pygmaea</i>

## Plots sampling

Three plots were prepared for each type (i.e., three replicates), and six *Poa alpigena* adult plants per replicate were sampled, for a total of 18 plants. Samples were collected in early August in 2013–2015. Stems and leaves were cut into 1–2 cm pieces, and then placed in brown bottles containing formalin–acetic acid–alcohol. The bottle openings were filled with a rubber plug, after which the air was extracted until the plant tissues settled at the bottom. The bottles were then preserved at 4 °C until analyzed.

## Sample preparation for microscopic analyses

Paraffin sections of plant tissues were prepared to study the root, stem, and leaf cross sections. The treated materials were washed with water, dehydrated, cleared, dipped in wax, embedded, and manually sliced (10 µm thick). The slices were dried and sealed with neutral gum to prepare permanent sections for microscopic analyses.

## Microscopy

The Shineso-MIC microscopic image analysis system was used to obtain images of the prepared plant tissues (40×, 100×, and 400× magnifications). The system software (Shineso-MIC) was used to analyze the stem and leaf epidermal cell size and area, vascular bundles, mechanical tissues, and other related plant parts.

## Data analysis

Data were collected for several leaf structural characteristics, including leaf thickness, upper epidermis thickness, upper epidermal cell area, mesophyll cell size, mesophyll cell density, phloem and xylem, catheter caliber, and catheter wall thickness. Additionally, data were obtained for stem structural features, such as epidermal cuticle thickness, epidermal cell area, phloem and xylem thickness, stem and tube wall thickness, catheter diameter, mechanical cell area, and mechanical cell wall thickness. Differences in the stem and leaf structures among the YG, UG3, and UG5 samples were analyzed by a single factor analysis of variance. so that revealed the extent of the influence of overgrazing on anatomical characteristics. The plasticity indices of the leaf and stem structures were calculated with the following formula(Yuxiangzhi et al,2007):  $PI = 1 - x / X$ , where x and X refer to the lowest and highest averages for a certain trait. Statistical analysis used for SPSS 17.0 software to variance analysis, correlation analysis, and 0.05 and 0.01 level significance test. The data was mapped by SigmaPlot 12.0.

## Results

### *Poa alpigena* stem and leaf structures

The epidermal cells were round and tightly packed at the epidermal surface. The mesophyll cells were nearly circular and densely distributed close to the cell wall. Each circular vascular bundle consisted of xylem and phloem (Fig. 1a and 1b).

The stem epidermal cuticle consisted of one layer of nearly round uniform epidermal cells that were tightly packed. The individual circular vascular bundles consisted of xylem and phloem. The basic plant tissue consisted of two or three layers of parenchyma cells just below the epidermis. These parenchyma cells were responsible for the mechanical organization. A medullary cavity was observed in the middle of the stems (Figure 1c and 1d).

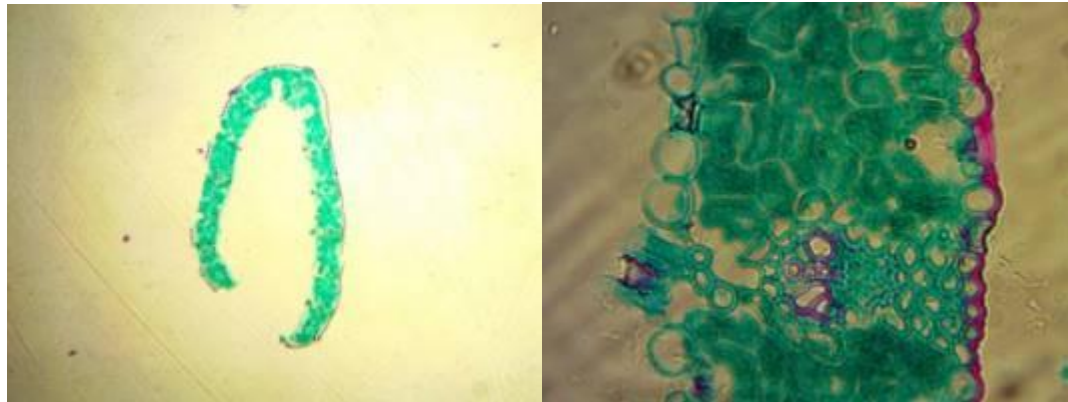


Figure 1a  $\times 40$

Figure 1b  $\times 100$

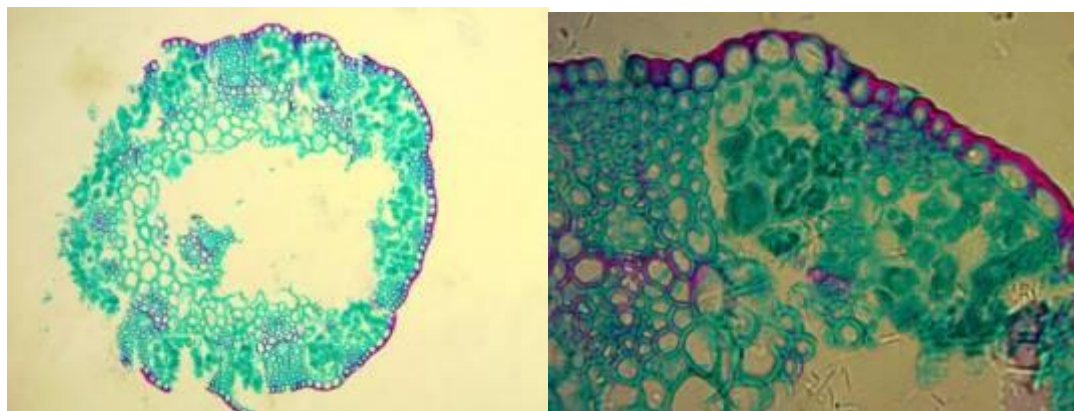


Figure 1c  $\times 100$

Figure 1d  $\times 400$

Fig. 1 *Poa alpigena* leaf (fig 1a,fig1b) and stem structures(fig 1c,fig 1d)

### Effects of overgrazing and enclosed on leaf structures

Leaves are the main plant organs for important functions (e.g., photosynthesis, respiration, transpiration, and protection), and are very sensitive to environmental conditions (Gao et al.2008). Thus, analyzing *Poa alpigena* structural characteristics in response to open and enclosed grazing is necessary.

### Effects of overgrazing and enclosures on leaf thickness

Leaf thickness is somewhat susceptible to the external environment. There were significant differences ( $p < 0.05$ ) in leaf thickness due to open or enclosed grazing, with the YG leaves considerably thicker than the UG5 or UG3 leaves ( $YG > UG5 > UG3$ ) (Fig. 2).

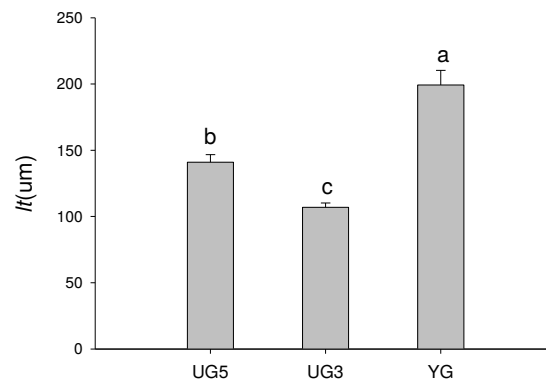


Fig. 2 Effects of overgrazing and enclosed on leaf thickness. Significant differences are indicated by lowercase letters ( $P < 0.05$ ). Data are presented as the mean  $\pm$  standard error. *lt*, leaf thickness.

### Effects of overgrazing and enclosed on the epidermal cuticle

We observed significant differences in the thickness of the epidermal cuticle ( $P < 0.05$ ), with the samples collected from the overgrazing site being thicker than those collected from the enclosed locations ( $YG > UG3 > UG5$ ) (Fig. 3). The cell area was significantly larger for the upper epidermal cells than for the lower epidermal cells ( $P < 0.05$ ). Additionally, the area of the upper and lower epidermal cells was larger in the samples collected from overgrazing site than in the samples collected from the enclosed site ( $YG > UG5 > UG3$ ) (Fig. 3).

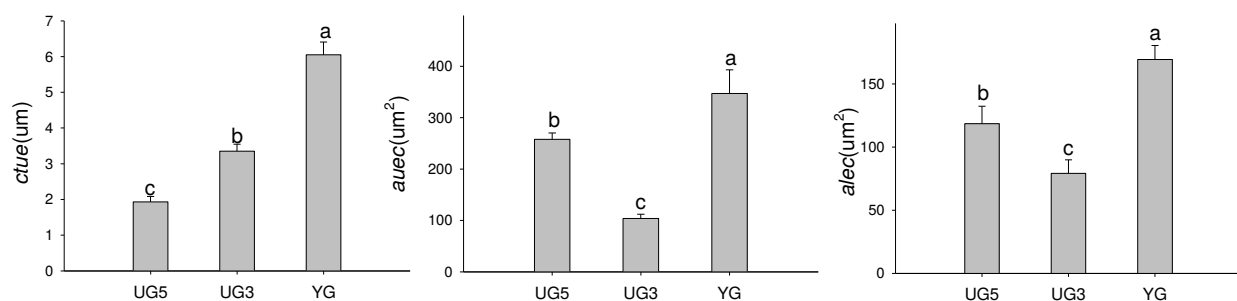


Fig. 3 Effects of overgrazing and enclosed on the epidermal cuticle. Significant differences are indicated by lowercase letters ( $P < 0.05$ ). Data are presented as the mean  $\pm$  standard error. *uctue*, upper epidermal cuticle thickness; *auec*, area of the upper epidermal cells; *alec*, area of the lower epidermal cells.

### Effects of overgrazing and enclosed on mesophyll cells

There were significant differences in *Poa alpigena* mesophyll cell size among the samples harvested from overgrazing and enclosed study locations ( $P < 0.05$ ), with mesophyll cell size increasing as the enclosure duration increased ( $UG5 > UG3 > YG$ ) (Fig. 4). However, grazing

type did not significantly affect mesophyll density ( $P > 0.05$ ).

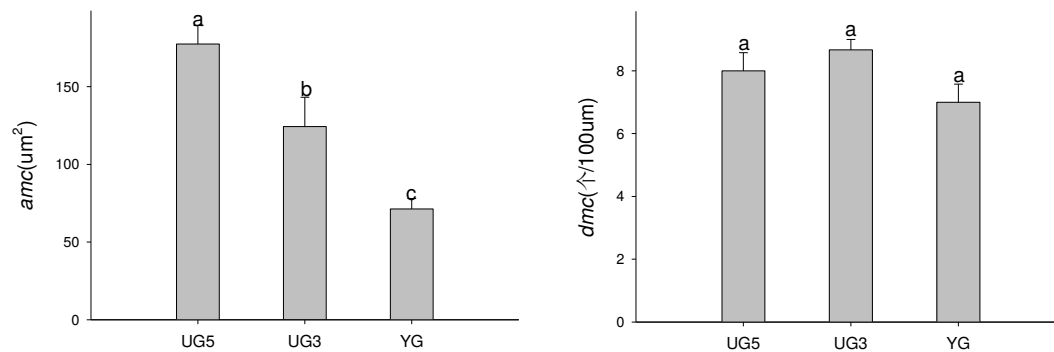


Fig. 4 Effects of overgrazing and enclosed on mesophyll cells. Significant differences are indicated by lowercase letters ( $P < 0.05$ ). Data are presented as the mean  $\pm$  standard error. *amc*, area of mesophyll cells; *dmc*, density of mesophyll cells.

#### Effects of overgrazing and enclosed on phloem and xylem thickness

The phloem of YG samples was significantly thicker than that of UG3 samples ( $P < 0.05$ ), while there was no difference between YG and UG5 samples ( $P > 0.05$ ) (Fig. 5). Additionally, xylem was significantly thicker in UG5 samples than in the other collected samples ( $UG5 > YG > UG3$ ) ( $P < 0.05$ ).

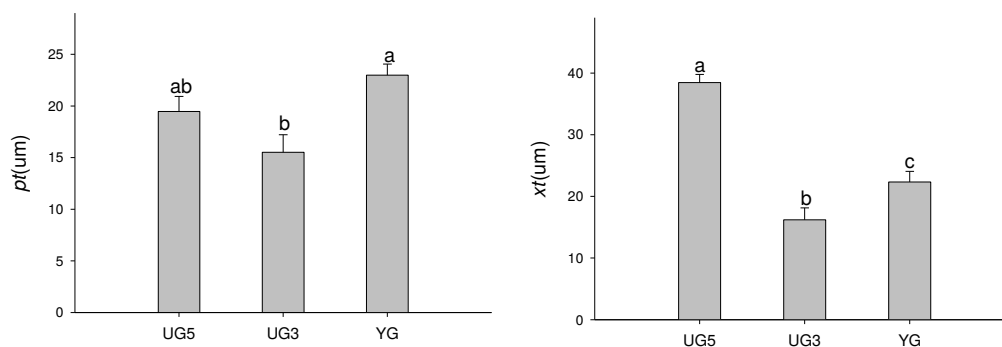


Fig. 5 Effects of overgrazing and enclosed on phloem and xylem thickness. Significant differences are indicated by lowercase letters ( $P < 0.05$ ). Data are presented as the mean  $\pm$  standard error. *pt*, phloem thickness; *xt*, xylem thickness.

#### Effects of overgrazing and enclosed on vessels

There was no significant difference among study sites regarding vessel diameters ( $P > 0.05$ ) (Fig. 6). In contrast, there were significant differences in the catheter wall thickness between



the UG5, UG3, and YG samples ( $UG3 > YG > UG5$ ) ( $P < 0.05$ ).

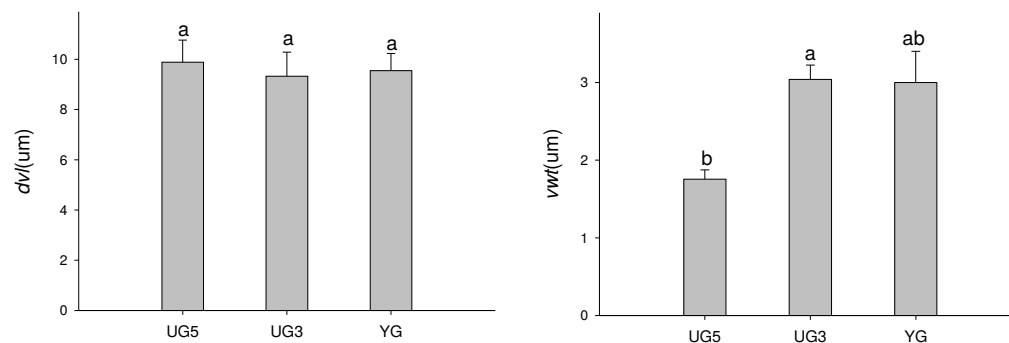


Fig. 6 Effects of overgrazing and enclosed on vessels. Significant differences are indicated by lowercase letters ( $P < 0.05$ ). Data are presented as the mean  $\pm$  standard error. *dvl*, diameter of vessels; *vwt*, vessel wall thickness

### Effect of overgrazing and enclosed on *Poa alpigena* stem structures

The stem is vital for transporting water and nutrients throughout the plant [20], and changes to environmental conditions can influence stem structures [21]. Therefore, analyzing *Poa alpigena* stem structures under overgrazing and enclosed conditions is warranted.

#### Effects of overgrazing on the stem epidermis

The stem epidermal cell area of YG and UG3 plants was significantly smaller than that of UG5 plants ( $P < 0.05$ ) (Fig. 7). Additionally, the stem epidermal cuticle was significantly thicker in YG and UG5 plants than in UG3 plants ( $P < 0.05$ ).

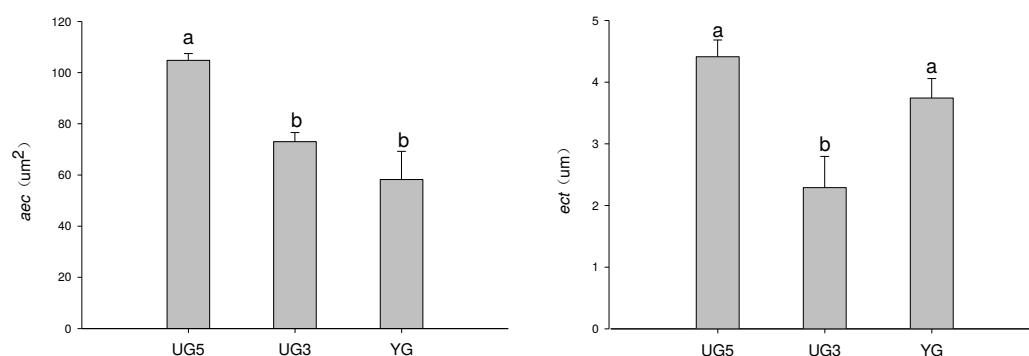


Fig. 7 Effects of overgrazing and enclosed on stem epidermal features. Significant differences are indicated by lowercase letters ( $P < 0.05$ ). Data are presented as the mean  $\pm$  standard error. *aec*, area of epidermal cells; *ect*, epidermal cuticle thickness.

### Effect of overgrazing on stem vascular bundle features



There were significant differences ( $P < 0.05$ ) in stem phloem thickness ( $UG5 > YG > UG3$ ) and xylem thickness ( $UG5 > UG3 > YG$ ) (Fig. 8).

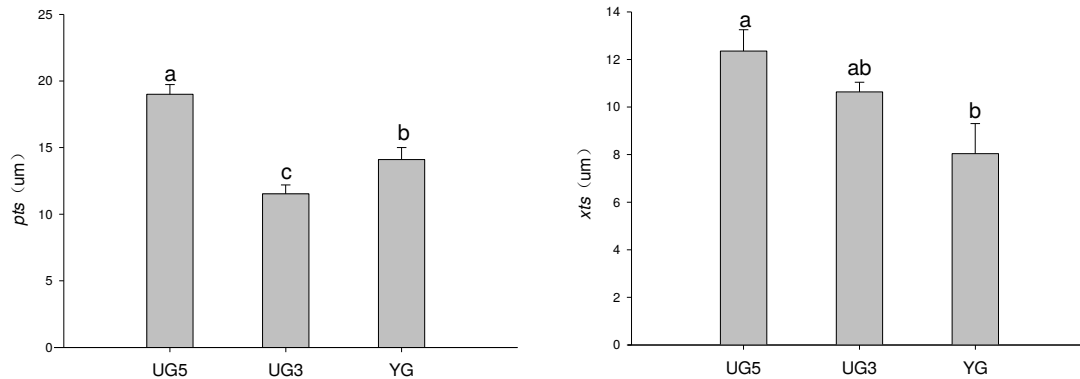


Fig. 8 Effects of overgrazing and enclosed on stem vascular bundle features. Significant differences are indicated by lowercase letters ( $P < 0.05$ ). Data are presented as the mean  $\pm$  standard error. *pts*, phloem thickness; *xts*, xylem thickness.

### Effects of open grazing on stem vessel features

As indicated in Fig. 9, the largest stem vessel diameters were observed for UG5 samples ( $P < 0.05$ ), while there were no significant differences between the UG3 and YG samples. In contrast, the YG samples had the thickest vessel walls ( $P < 0.05$ ), while there were no significant differences between the UG5 and UG3 samples.

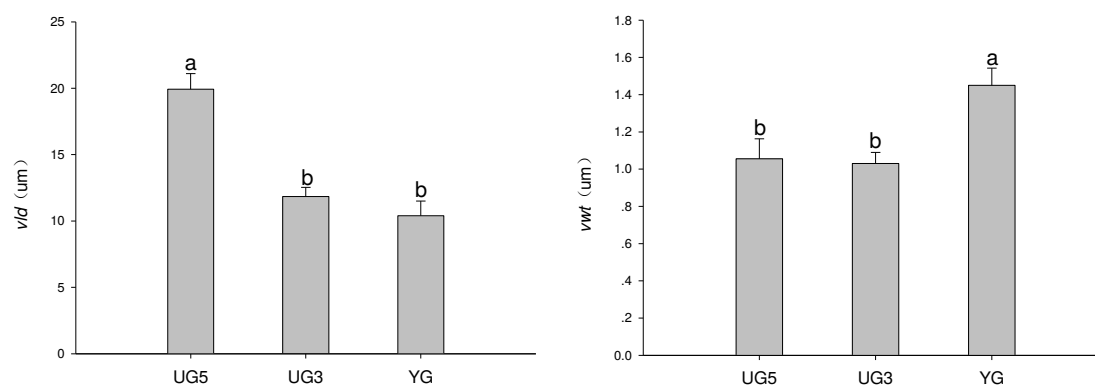


Fig. 9 Effects of overgrazing and enclosed on stem vessel features. Significant differences are indicated by lowercase letters ( $P < 0.05$ ). Data are presented as the mean  $\pm$  standard error. *vld*, vessel diameter; *vwt*, vessel wall thickness.

### Effects of overgrazing on stem mechanical tissue features

Our data revealed that the area of mechanical tissue cells was smaller in UG3 samples than in UG5 or YG samples ( $P < 0.05$ ), while there were no significant differences in the mechanical tissue cell thickness ( $P > 0.05$ ) (Fig. 10).

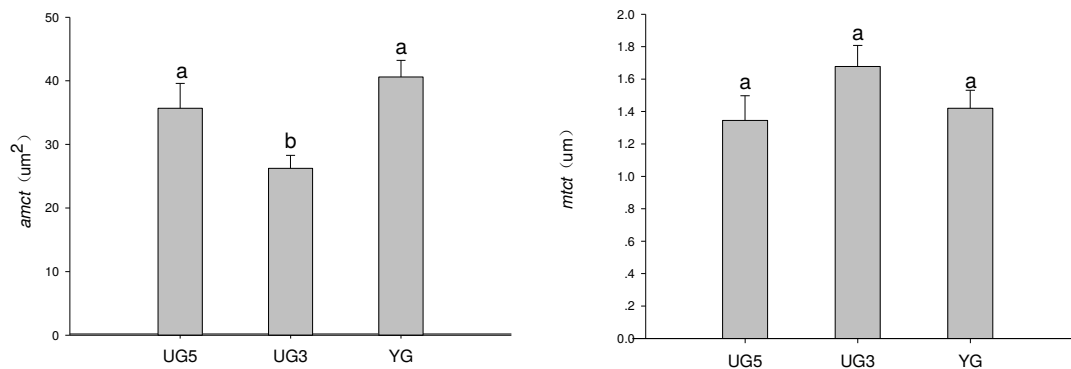


Fig. 10 Effects of overgrazing and enclosed on stem mechanical tissue features. Significant differences are indicated by lowercase letters ( $P < 0.05$ ). Data are presented as the mean  $\pm$  standard error. *amct*, area of mechanical tissue cells; *mtct*, mechanical tissue cell thickness.

### Plasticity of leaf and stem structures

Relatively high plasticity indices were observed for all leaf measurements (Table 2). The plasticity indices were greater than 0.5 for leaf area, upper epidermal cutin layer thickness, and xylem thickness. The plasticity indices were 0.4–0.5 for leaf thickness and leaf vessel thickness. The lowest plasticity indices (less than 0.4) were observed for leaf phloem thickness and mesophyll cell and leaf vessel diameters.

Table 2 Plasticity indices of leaf structural characteristics

<i>lt</i>	<i>uct</i>	<i>auc</i>	<i>ale</i>	<i>amc</i>	<i>dmc</i>	<i>pt</i>	<i>xt</i>	<i>dvl</i>	<i>vwt</i>
0.46	0.68	0.53	0.70	0.60	0.19	0.33	0.58	0.06	0.42

Note: *lt*, leaf thickness; *uct*, upper epidermal cuticle thickness; *auc*, area of the upper epidermal cells; *alec*, area of the lower epidermal cells; *amc*, area of mesophyll cells; *dmc*, density of mesophyll cells. *pt*, phloem thickness; *xt*, xylem thickness; *dvl*, diameter of vessels; *vwt*, vessel wall thickness.

In contrast to the plasticity indices of the leaf measurements, those for the stem characteristics were relatively low (Table.3). The highest plasticity indices (greater than 0.4) were recorded for stem vessel diameter, epidermal cell size, and epidermal cutin layer thickness. The plasticity

indices were 0.3–0.4 for xylem thickness, phloem thickness, and mechanical tissue cell area. Meanwhile, the plasticity indices of vessel thickness, parenchymal cell size, and mechanical tissue cell thickness were all less than 0.3.

Table 3 Plasticity indices of stem structural characteristics

<i>vld</i>	<i>vwt</i>	<i>aec</i>	<i>ect</i>	<i>xts</i>	<i>pts</i>	<i>mtct</i>	<i>amtc</i>
0.41	0.29	0.44	0.48	0.35	0.39	0.20	0.35

Note:*vld*, vessel diameter; *vwt*, vessel wall thickness; *aec*, area of epidermal cells; *ect*, epidermal cuticle thickness; *xts*, xylem thickness; *pts*, phloem thickness; *mtct*, mechanical tissue cell thickness; *amtc*, area of mechanical tissue cells.

## Discussion

### Effects of overgrazing and enclosed on leaf structures

The leaf is one of the main plant organs involved in photosynthesis and transpiration (Gao,2008). It is also the most sensitive plant organ to external stimuli (Wang, 1989). Thus, leaf morphological features can reflect plant adaptations to environmental conditions (Li et al,2015). Leaf thickness and internal structures are altered in response to various external stresses (Wylic,1946). A previous study revealed that leaf thickness may be useful as a morphological indicator of environmental effects on plants (Zhang et al,2005). We observed that the leaves were thicker in the samples collected from the open grazing site than the samples from the enclosed grazing locations ( $P < 0.05$ ). Livestock grazing and trampling induce plants to increase leaf thickness.

Cutin layer thickness is an important indicator of plant drought resistance. We observed that YG samples had thicker leaves and cutin layers than the UG3 or UG5 samples ( $P < 0.05$ ), suggesting that plants adapt to the effects of open grazing by increasing the cutin layer thickness. Doing so can prevent water loss due to excessive transpiration. Therefore, plants adapted to drought conditions usually have a well-developed cutin layer (Zhao, 2009). One of the consequences of grazing is increased soil density, which results in decreased soil permeability (Fan et al,2006). Increasing the thickness of the cutin layer may improve water use efficiency and decrease the palatability of the plants to grazing animals. Therefore, under overgrazing conditions, *Poa alpigena* plants thicken their corneous layer to defend against the stress imposed by grazing livestock (Yin et al,1993). The leaf epidermis usually consists of the corneum and one layer of epidermal cells. The epidermal cell traits may reflect the overall plant traits to some extent (Yu et al,1993).

Mesophyll cells represent one of the main sites of photosynthesis and respiration activities,

and their structural traits directly influence plant growth. Our data suggest that in response to increasing grazing, mesophyll cell area tends to decrease ( $P < 0.05$ ), while mesophyll cell density is unaffected ( $P > 0.05$ ). *Poa alpigena* leaves are relatively short under overgrazing conditions. Decreases in mesophyll cell size can minimize transpiration and improve water use efficiency to ensure normal photosynthetic activities (Wang, 1999). Thus, decreases in mesophyll cell area may be the main factor influencing the dwarfing of *Poa alpigena* plants.

Vascular bundles (i.e., xylem and phloem) are essential for plant growth because of their role in transporting nutrients and water throughout the plant. Phloem thickness increased under overgrazing conditions, while xylem thickness exhibited the opposite trend. The thickening of phloem likely increases the mechanical strength of leaves, and may help to protect leaves from grazing livestock under overgrazing conditions. In contrast, decreases in xylem thickness affects leaf transpiration and water use efficiency. Thus, the observed changes to the thickness of *Poa alpigena* leaf phloem and xylem thickness under overgrazing conditions are related to plant adaptations to grazing stress.

The vessels of the water transport system have important functions throughout the plant development period. These vessels are made from the lignified walls of dead cells, and are prevalent in the xylem of angiosperms. The vessel diameter affects the efficiency of water conductance, with wider vessels correlated with more efficient water transport (Yu et al, 2007). Additionally, the vessel characteristics influence xylem mechanical strength, and vessel thickness is the main structural feature used as an indicator of the mechanical properties of plants (Yu et al, 2007). We did not observe any significant differences in vessel diameter among the collected samples ( $P > 0.05$ ). However, our data indicated that vessel walls were thicker in the YG samples compared with the UG3 or UG5 samples ( $P < 0.05$ ). These results suggest that plants protect themselves from mechanical damages caused by the trampling and grazing of livestock under overgrazing conditions by increasing the catheter wall thickness.

#### Effects of grazing on stem structures

The stem epidermal cells are in direct contact with the external environment. These cells have a considerable role in regulating the internal conditions of plant tissues, and they also help plants adapt to external stresses. The extent of any changes to the external environment influences the changes to the stem epidermal cutin layer thickness (Yu *et al.* 2007). In our study, the epidermal cutin layer thickened with increasing grazing intensity ( $P < 0.05$ ). This thickening of the cutin layer represents a defense strategy adopted by plants in response to overgrazing. Additionally, the *Poa alpigena* epidermal cell area decreased because of grazing, implying that one of the plant adaptive responses involves shortening of the stem.

Xylem and phloem regulate the water and nutrient use efficiency of plants. Structural

changes to the vascular bundles mediate whether plant activities are directed toward survival or growth (Yu *et al.* 2007). The thickness of the stem phloem and xylem increased with longer enclosure periods. This suggests that if plants are not required to respond to grazing stress, more resources may be used for growth and development (e.g., increased plant height).

Overgrazing conditions resulted in a significant decrease in stem diameter ( $P < 0.05$ ). Under these conditions, plants regulate their use of the limited water resources by inducing changes to the catheter diameter, leading to significant increases in the catheter wall thickness ( $P < 0.05$ ). Thickening of the vessel wall can ensure the long-distance transport of water. The size and thickness of stem mechanical cells tended to increase under overgrazing conditions, which may enhance the mechanical strength of the stem.

### Adaptability of stem and leaf structures to overgrazing

Environmental conditions influence plant morphology and anatomy. Plants adapt to environmental factors *via* morphological changes (Zhen *et al.* 2007; Li *et al.* 2007). We compared the plasticity of *Poa alpigena* stem and leaf structural features. The plasticity indices were higher for the leaves than for the stems, suggesting the leaves are more susceptible to grazing stress. Regarding the plasticity indices of specific traits, the epidermal cell area, thickness of the upper epidermis, and leaf xylem thickness were relatively high (i.e., greater than 0.5). Additionally, the plasticity indices were greater than 0.4 for stem vessel diameter, epidermal cell size, and epidermal cutin layer thickness. Our results imply these traits are sensitive indicators of *Poa alpigena* responses to grazing stress.

### Anatomical changes associated with dwarfing *Poa alpigena* plants

Under overgrazing conditions, the selective feeding behavior of livestock leads to the shortening of tall grasses. Because of the resulting weakening of the shading effect, plants are exposed to increasing light intensity. Additionally, livestock trampling increases the grassland soil surface density. This decreases the soil water infiltration rate, which affects plant water absorption. The trampling and grazing of livestock under overgrazing conditions affect the nutrient content and nutrient use efficiency of the plant community. The resulting small changes to plant growth conditions alter plant structures, leading to the dwarfing of individual plants (Wang *et al.* 2000). The observations described herein reveal that plants undergo structural changes to adapt to open grazing conditions. This is consistent with the findings of an earlier study (Shi *et al.* 20067). Decreases in mesophyll and stem epidermal cell area result in the production of short leaves and stems. This suggests that decreases in mesophyll and stem epidermal cell area are critical for the dwarfing of *Poa alpigena* plants.

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