Excessive plant compensatory growth: a potential endogenous driver of meadow degradation on the Qinghai-Tibetan Plateau

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ABSTRACT

Degradation of meadow ecosystems in the largest alpine region of the world, i.e., the Qinghai-Tibetan Plateau (QTP), is a crucial ecological issue that has ardently discussed in recent years. Many factors, such as livestock overgrazing, climate change and overpopulation of small mammals are treated as important factors that cause the degradation of meadow ecosystems in the QTP. However, there are few hypotheses focus on the potential role of plant compensatory growth on meadow degradation. We proposed a compensatory growth-related hypothesis to understand the potential degradation process of meadow ecosystems in the QTP. We discussed that there are two stages of meadow degradation, i.e. the beginning stage of meadow degradation that is triggered by high-strength overcompensation; and the intensification stage of meadow degradation, which are driven by external factors such as climate warming, small mammals and thawing of permafrost. The mechanism of meadow degradation driven by plant compensatory growth is the asynchronism of plant consumption and the availability of soil nutrients. Our hypothesis that plant compensatory growth drives meadow degradation under the overgrazing condition requires re-examination and modification by testing the balance between soil nutrient cycling rates and the strength of plant compensatory growth in alpine regions.

The QTP, also called the third pole, with an area of nearly \(2.5 \times 10^6\) km\(^2\), is the largest alpine region on the Earth. It has generally been reported that the alpine meadow ecosystems are suffering serious degradation in the QTP (Qiu 2016; Yao et al. 2012). There are numerous studies describing the performances of meadow degradation, such as the reduction of plant cover (Feng et al. 2009), decrease in plant reproductive success (Dong et al. 2015), shift in plant community structure (Tang et al. 2015), and altered ecosystem functions (Wang et al. 2015). The degradation of meadow ecosystems is primarily theorized to be the consequence of climate change and long-term livestock overgrazing (Dong et al. 2013; Harris 2010; Lehner et al. 2016; Wang et al. 2016; Zhou et al. 2005). It has been shown that repeated heavy grazing can inhibit plant recovery from damage and cause the degradation of the meadow ecosystem (Loeser, Crews, and Sisk 2004). However, an important issue remains unanswered: how does plant–soil interaction trigger meadow degradation under the overgrazing condition? The clarification of this issue is helpful to examine the strategies of plants in response to herbivory. The compensatory growth, defined as positive responses of plants to damage (Belsky 1986), is an important strategy of plants in response to herbivory (Agrawal 2000; Paige and Whitham 1987). There are three types of compensatory growth, i.e., under-compensation, no-compensation, and over-compensation (Belsky 1986). We mean compensatory growth as over-compensation in this essay. It suggests that plants tend to overcompensate more frequently under unfavorable growth conditions to survive (Hawkes and Sullivan 2001). An appropriate compensatory growth is of benefit to maintain or even improve the efficiency of a livestock grazing system (Grime 1973; Hilbert et al. 1981; McNaughton 1983). The interaction between plant compensatory growth and herbivory could be stable if grazing intensity is suitable (Agrawal 2000; Sun et al. 2019); however, this balance would be disrupted under overgrazing conditions. Overgrazing is easier to happen in the present than the historical period as the increase of livestock number and the shift of grazing regimes, which changed from a nomadic one to an immobilization one, in the QTP (Cao et al. 2013; Sun et al. 2014). Therefore, we hypothesized a possible process of meadow degradation in the QTP: high-strength compensatory growth under overgrazing in the alpine meadow drives the degradation of the entire ecosystem. To illustrate this hypothesis, several questions have to be considered and addressed:
• Does the plant compensatory growth occur in alpine meadow ecosystems under grazing conditions?
• How plant compensatory growth drives the degradation of meadow ecosystems in alpine regions? What does the role of other external factors (especially climate warming) play during the process of meadow degradation?
• What is the mechanism of the degradation process driven by plant compensatory growth in alpine regions?

Does the plant compensatory growth occur in alpine meadow ecosystems?

Compensatory growth phenomena

Plant compensatory growth usually happens after tissue reduction caused by herbivory (McNaughton 1983). Plant functional types (e.g., growth form) and the resources level of the habitat (e.g., light, nutrients, and water) strongly determine the compensatory growth of plant community (Li et al. 2011a; Wang and Wesche 2016; Wise and Abrahamson 2005). The compensatory growth of the same plant functional type varies among different resource levels (Hawkes and Sullivan 2001). More details about the mechanism of the compensatory growth could be found in previous reviews by McNaughton (1983), Tiffin (2000), etc. We, here, focus on the general conditions on the appearance of compensatory growth and discuss whether the compensatory growth is detected by experimental studies in alpine regions. Generally, the compensatory growth occurs under special conditions, e.g., resource-rich environment (high light, nutrients, and water levels), and low levels of competition (Agrawal 2000; Kinsinger and Hopkins 1961). Experimental studies suggested that in tropical or temperate grassland ecosystems that are dominated by C₄ grasses, there is little evidence for plant compensatory growth (Knapp et al. 2012). However, plant compensatory growth under livestock grazing was observed in the Eurasian steppe ecosystems that are dominated by C₃ grasses when the growing season was wet (Schönbach et al. 2011). In alpine and subalpine regions where are cold and wet, such as the QTP where alpine meadow ecosystems occupy over 4.5 × 10⁴ km² of the area (Miehe 2008), both clipping (Klein, Harte, and Zhao 2007) and livestock grazing (Zhu et al. 2010; Li et al. 2020a) caused plant compensatory growth. A meta-analysis suggests that plant compensatory growth, which is a primary mechanism that causes the enhancement of belowground biomass, is generally detected under moderate grazing intensity on the QTP (Sun et al. 2019). In addition, plant compensatory growth has been observed after both clipping and livestock grazing in grassland ecosystems in subalpine regions outside the QTP (Loeser, Crews, and Sisk 2004). These results give evidence for the phenomena of plant compensatory growth in alpine and subalpine regions.

Compensatory growth foundation

In alpine regions, livestock grazing could promote the root turnover rate under moderate stocking rates (Pucheta et al. 2004). Moreover, fine roots are the primary structure through which plants take up water and nutrients (Bardgett, Denton, and Cook 1999). Therefore, the increase in root turnover rate and fine root growth is an enhancement strategy for plant structure, which complies with the definition of compensatory growth. In addition, removal of plant aboveground biomass to some extent, e.g., clipping, could stimulate soil microbial biomass in upland grasslands (Mawdsley and Bardgett 1997). The increase in soil microbial biomass could accelerate soil nutrient cycling (Bardgett 2005), producing sufficient available nutrients for enhanced plant growth. Moreover, the growing season is about four months (i.e., from May to August) in alpine regions of the QTP because the precipitation is concentrated from May to September (Kato et al. 2004), while there is a considerably long time for the mineralization of soil nutrients underground, which could support the compensatory growth of plants. Therefore, it is clear that plant compensatory growth generally happens in alpine meadow ecosystems in alpine regions such as the QTP.

How does plant compensatory growth drive degradation of meadow ecosystems?

The process of meadow degradation under heavy grazing condition could divide into two stages. The first stage is the beginning of meadow degradation when high-strength compensatory growth undermines the health of meadow ecosystems by causing the loss of nutrients, the reduction of root biomass, and the shortage of available nutrients. The second stage is the intensification of meadow degradation when the health of meadow ecosystems are strongly deteriorated by external factors, such as rainfall, thawing of permafrost, climate warming, and small mammals.

The beginning of meadow degradation

The degradation of a meadow ecosystem will occur when plants could not survive. The survival and growth of plants is largely based on a good ability of root in nutrients absorbing and an adequate supply of soil nutrients. Livestock browses a mass of aboveground biomass and promotes plant compensatory growth, which would undermine the health of meadow ecosystems if grazing intensity was strong (or compensatory growth intensity was strong) (Figure 1). There are at least three primary
Compensatory growth

Livestock’s browse

Aboveground biomass

Belowground biomass + litters

Soil available nutrients

Matter decomposing

Soil water content

Soil animals
Soil microbes

External factors (e.g., wind, climate change, break out of small mammals et al.)

Figure 1. The process of meadow degradation driven by compensatory growth. Two primary processes cause the nonviability of plants and the entire degradation of alpine meadow ecosystems: (1) Livestock grazing stimulates excessive plant compensatory growth and undermines the health of meadow ecosystems. Under an excessive compensatory growth, livestock would take a lot of plant biomass, and fewer photosynthesis products accumulate into the plant root. The reducing of root not only weaken the ability of plant in nutrients absorbing but makes soil erodible and affects the process of matter decomposition in soil, decreasing the supply of soil available nutrients. Consequently, the alpine plants could not survive. (2) External factors (such as climate change and break out of small mammals) accelerate the degradation of meadow ecosystems after the reduction of root biomass and the appearance of bare ground.

processes contribute to the beginning of meadow degradation:

Firstly, a mass of nutrients lose from meadow ecosystems. Livestock could ingest more biomass if there is an attendance of compensatory growth when compared with an absence one. Correspondingly, a lot of soil nutrients and photosynthesis products accumulate into livestock products (e.g., meat and milk) via livestock grazing under the condition of compensatory growth. Most of these livestock products do not return to meadow ecosystems. They are consumed by anthropic economic activities. The return of livestock dung could enhance soil nitrogen supply for the growth of meadow plants in the QTP (Cheng, Cai, and Wang 2016). However, as the main living fuel in the pastoral area in the QTP, most of the dung of livestock is collected and burned by local pastoralists, which is beneficial to the regeneration of plants by reducing the amount of dung patches but reduces the return of nutrients to soil at the same time. The processes mentioned above would cause a drastic loss of nutrients from soil, which will negatively affect the sustainability of meadow ecosystems in the long term.

Secondly, the ability of plants in nutrient absorbing would decrease and soil becomes erodible because of the reduction of root biomass. Compensatory growth could lead to the reallocation of products of photosynthesis, resulting in fewer photosynthetic products into the roots. There is a prominent hypothesis that the compensatory growth of aboveground biomass may come at the expense of belowground biomass (Kinsinger and Hopkins 1961; Overbeek 1966). In fact, evidence from both simulated grazing (i.e., clipping) and mammalian grazing studies suggest that long-term livestock grazing could reduce root biomass (Biondini, Patton, and Nvren 1998; Dawson, Grayston, and Paterson 2000; Jameson 1963). We get some direct evidence to illustrate the process of photosynthetic relocation between shoot biomass and root biomass in a rotational grazing experiment conducted in the QTP, which grazed by yaks with a high stocking rate. In our experiment, the aboveground biomass showed an over compensatory growth (Figure 2(a)). Moreover, the aboveground biomass showed an increasing trend but the belowground biomass showed a decreasing trend from 2014 to 2016 (Figure 2(a,b)). A mowing...
Figure 2. Aboveground net primary productivity (ANPP) (a), belowground net primary productivity (BNPP) (b) and the contents of available nitrogen (c, d) and available phosphorous (AP) (e) of an alpine meadow ecosystem under a heavy rotational grazing management in the QTP. 2014BG: before grazing in 2014, 2014AG: after grazing in 2014. CK: no-grazing treatment. Cited from Zhang (2016a). The detailed methodology of this field experiment could find in Zhang (2016a). Here, we briefly introduce the methodology of cited results. The grazing intensity was high, i.e. four adult yaks per ha², in this rotational grazing experiment. The ANPP is estimated by the aboveground weight of air-drying plant tissues that clipped from 1 m × 1 m quadrats. The BNPP is estimated by the belowground weight of air-drying plant tissues that collected from soil cores with a scale of 3.14 × 6.25 cm² × 15 cm. The contents of soil available nutrients are measured by a flow injection auto-analyzer (AACE, Germany). One-way ANOVA is used to test the variance of parameters between CK and Rotational grazing (the significant level is α = 0.05).

experiment conducted in Canada obtained the same results, i.e., the aboveground biomass under mowing treatment trends to be higher than that under control treatment while the belowground biomass showed an opposite pattern (Zhang et al. 2018). In a healthy alpine meadow of the QTP, over 95% of plant roots concentrate in 0 – 30 cm belowground (Yang et al. 2009). The surface 30 cm range is generally called “sod layer,” which plays crucial roles in the conservation of water and soil in QTP (Shang et al. 2008). The reduction of root biomass (especially the reduction of living roots) weakens the primary pathway through which plants uptake water and nutrients. Meanwhile, this reduction provides preconditions for eventual soil erosion and the exposure of bare ground.

Thirdly, plant growth could be restricted because of the shortage of available nutrients caused by long-term compensatory growth. Soil fauna and microbes, which have mutualistic relationships with plant roots, play irreplaceable roles in soil nutrient transfer and root growth in grassland ecosystems (Bardgett, Denton, and Cook 1999). Under an excessive compensatory growth, the decrease of plant roots would change the species richness and community structure of these mutualisms. Moreover, fewer plant litters introduce into soil because of the ingestion of livestock, which could make these soil dwellers hard to survive (Bardgett, Denton, and Cook 1999). In addition, low-temperature can restrict the decomposition rate of matter in alpine meadow ecosystems (Xu et al. 2013; Li et al. 2020b). Consequently, the supply of soil available nutrients would become unsustainable.

The intensification of meadow degradation

Fewer photosynthetic products allocate into belowground (i.e., the reduction of plant roots) under an excessive compensatory growth would make the soil become easier to be eroded by external forces in alpine regions. High root: shoot ratio is typical for a healthy alpine meadow ecosystem (Yang et al. 2009). The fixation of vast plant roots is benefits to soil physical structure to resist livestock’s trampling. Soil physical structure will be easily destroyed by livestock’s trampling as the loss of plant roots. Permafrost generally exists in the
QTP, but it is melting due to the climate change (Yang et al. 2010). It reported that the loss of permafrost could change alpine meadows into steppes (Jin et al. 2009). This suggests that erosion caused by external factors (e.g., rainfall and thawing of permafrost) will speed up the degradation process. Moreover, if the plant cover is removed (i.e., barren patches are formed) the variation of radiation among patches would enlarge the scale of bare ground in the QTP (Wei, Lin, and Wang 2015).

Climate change could promote the process of plant compensatory growth. The climatic condition tends to be warm and wet in the central of QTP (Ganjurjav et al. 2018). Field experiments with open top chambers (OTCs) in the QTP found that warming could change soil physical (especially surface temperature and moisture) and chemical conditions, shift the composition of soil microbial communities (Ganjurjav et al. 2018; Zhang et al. 2016b) and accelerate the turnover rate of nitrogen (Wang et al. 2014). These warming-induced changes could increase the access of soil available nutrients, which improved plant biomass in a short-term period (Ganjurjav et al. 2016). The enhancement of plant compensatory growth may speed up the process of meadow degradation if soil available nutrients could not maintain under a warmer and wetter climate condition.

Some small mammals, mainly plateau pika (Ochotona curzoniae), are keystone species in the QTP (Smith and Foggin 1999). Activities of these mammals could promote plant growth and maintain hydrological functioning in this region (Wilson and Smith 2015; Zhang et al. 2016c). However, these mammals can overpopulate in degraded meadow ecosystems and aggravate grassland degradation. In fact, it might be the change in soil surface temperature and soil physical structure caused an increase in pika populations (Li et al. 2011b). There are more cracks in degraded areas because of the reduction in plant roots and soil moisture. These cracks make it easier for pikas to burrow and create a drier dwelling (Wang, Zhang, and Wang 2006).

The mechanism of meadow degradation driven by plant over compensatory growth

Each biological process has a specific reaction time in an ecosystem. The entire efficiency of an ecosystem is determined by the slowest process, which means that any external factor that forces part of the ecosystem to operate faster than the overall rate will lead to an imbalance (Commoner 1971). The maintenance of nutrient’s cycling is the most mentioned issue when the grazing optimization is discussed (De Mazancourt, Loreau, and Abbadie 1998). We proposed that the mechanism of meadow degradation driven by plant compensatory growth was the asynchronism of the rate of plant consumption and the availability of soil nutrients. In other words, the nutritional requirement of plant growth is greater than the supply of soil available nutrients in a meadow ecosystem. This asynchronism between plant consumption and soil available nutrient is an endogenous driver that causes the degradation of meadow ecosystems. There is a rebalancing process between plant consumption and the availability of soil nutrients during meadow degradation. This rebalancing process can be separated into three stages.

The first stage is the beginning of compensatory growth. Plant consumption increases with the appearance of compensatory growth. At the beginning of plant compensatory growth, which is similar to the condition of moderate grazing, available nutrients in soil may be promoted by an increased mineralization rate (Qiao et al. 2012). Our grazing experiment obtained some evidence as well (Figure 2(c,e)). Therefore, both plant consumption and the ability of soil nutrients supply are higher than the normal condition (Figure 3(a)).

The second stage is the peak of compensatory growth. Plant compensatory growth peaks through the increased supply of soil available nutrients. The peak of plant compensatory growth appears after the peak of the availability of soil nutrients (Figure 3(a)). The consumption and supply relationship of the meadow ecosystem might return to its normal condition if livestock grazing is excluded before or near the peak of compensatory growth (Figure 3(b)). The process that showed in Figure 3(b) might be the reason why traditional grazing management in the QTP, i.e. the nomadism, was sustainable, while if livestock grazing continues at the peak of compensatory growth, meadow degradation is triggered because the support of soil available nutrients is lower than a normal situation.

The third stage is the degradation of the meadow ecosystem. In this stage, the availability of soil nutrients is lower than it is in a normal condition. Plant consumption continuously decreases until it is less than in the normal condition (Figure 3(a)). Then, the grassland ecosystem shifts from a high-level plant–soil balance to a low-level one.

Conclusion and significance

In brief, we discussed a possible hypothesis of meadow degradation in the QTP by demonstrating: 1) high-strength overcompensation is a potential endogenous driver that triggers the degradation of alpine meadow ecosystems under an overgrazing condition in the QTP. 2) Well-known factors, including climate warming, small mammals, and thawing of permafrost are external forces that intensify meadow degradation. And 3) the asynchronism of the rate of plant consumption and the availability of soil nutrients are the fundamental issue of the hypothesis that high-strength compensatory growth drives the degradation of alpine meadow ecosystems. Our hypothesis sheds light on the degradation processes of alpine meadow and
would contribute to formulate grassland protection policy for local government.

To test this meadow degradation hypothesis, some issues should be considered in future studies: 1) the reallocation of photosynthetic products between aboveground and belowground and its consequences (including soil fauna, soil microbes and soil nutrient’s cycling, etc.) under the condition of long-term overgrazing. 2) The point at which plant compensatory growth peaks in alpine meadow ecosystems. 3) The ability of the soil system (especially the availability of nutrients) to support the growth of plants at different spatial and temporal scales. 4) The balance between the rate of soil nutrient cycling and the strength of plant compensatory growth under livestock grazing in the QTP. Moreover, the effects of external factors (e.g., climate change) on this balance should be considered.

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