N addition suppresses the performance of grassland caterpillars (Gynaephora alpherakjj) by decreasing ground temperature

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Citation: Yang, Y., X. Xi, X. Zhong, N. Eisenhauer, and S. Sun. 2017. N addition suppresses the performance of grassland caterpillars (Gynaephora alpherakjj) by decreasing ground temperature. Ecosphere 8(3):e01755. 10.1002/ecs2.1755

Abstract. Nitrogen deposition may stimulate plant biomass production and improve the quality of plant tissue, with both effects potentially facilitating herbivore growth and development. We hypothesized that simulated N deposition (N addition) would facilitate the growth and development of the grassland caterpillar Gynaephora alpherakjj, a notorious pest species in the alpine Tibetan meadow. We tested this hypothesis in two complementary experiments. The first field experiment tested N (ambient N levels vs. N addition) and caterpillar effects (caterpillar absence vs. presence) on plant community and sedge (major food plant species for caterpillars) biomass, growth, and development rate of the caterpillars, and micro-habitat temperature. The second chamber experiment tested N addition effects through plant tissue quality on caterpillar performance. Results show that N addition increased the biomass and leaf N concentration of the sedge species, but decreased the feeding time, growth, and development rate of the caterpillars in the field experiment. The independent chamber experiment showed that increased leaf N facilitated the caterpillar growth and development. These results suggest that the reduced performance of caterpillars was not caused by an N addition-induced change in food quality. By contrast, N addition significantly reduced the ground surface temperature presumably because of canopy shading, as indicated by increased plant height and biomass in the N addition treatment. A significant quadratic relationship between ground surface temperature and the number of feeding caterpillars in the field experiment explained the difference in feeding time between the N addition and ambient N treatments. It can thus be concluded that N addition reduced caterpillar performance by stimulating plant growth leading to reduced ground surface temperatures, which decreased caterpillar feeding activity. Our results suggest that the effect of N deposition on abiotic factors could be critical to the growth, development, and survival of immobile herbivore species or the individuals at immobile stages that cannot quickly respond to changing microclimatic environments.

Key words: feeding activity; global change; grassland caterpillar; Gynaephora alpherakjj; N deposition; Tibetan Plateau.

Received 10 May 2016; revised 18 January 2017; accepted 14 February 2017. Corresponding Editor: Andrew C. McCall.

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INTRODUCTION

Anthropogenic nitrogen (N) deposition and its consequences is a global issue. The estimated amount of atmospheric reactive N deposition was ~112–116 Mton in the year 2012 and is predicted to increase in the foreseeable future (Peñuelas et al. 2012). Added N compounds in nature, mostly in the form of active compounds, may shift the dynamics of N cycling and biological communities
in both aquatic and terrestrial ecosystems (Bobbink et al. 2010). Studies have shown that in most terrestrial ecosystems short-term deposition of N increases soil N availability, leading to increased N uptake and growth in plants and primary production (Binkley and Högberg 1997, Matson et al. 2002, Magill et al. 2004). However, there is no consensus about whether N deposition facilitates herbivore growth and development or not (e.g., Franěk et al. 2000, Throop and Lerdau 2004, Tao and Hunter 2012, Tao et al. 2014).

N deposition may change herbivore performance via different mechanisms (Erwin et al. 2013, Han et al. 2014, 2015). Typically, N addition facilitates plant growth and biomass accumulation as widely demonstrated in many previous studies (Tate 1992, Binkley and Högberg 1997, Matson et al. 2002), likely increasing food availability to herbivores (Karowe and Martin 1989). Moreover, N addition may change plant quality to affect herbivore performance as plant N is vital to herbivore growth and reproduction (Franěk et al. 2000). Animals often require more N for growth than plants (Bautista-Teruel et al. 2003) such that herbivore performance might mostly be suppressed by a N deficit (Mattson 1980, White 1993), which is referred to as the “N limitation hypothesis.” Studies have shown that N addition often increases foliar N contents of plants (Liu et al. 2012), which may release herbivores from N limitation and possibly leads to outbreaks of herbivore populations, especially of insect species (Karowe and Martin 1989, Ball et al. 2000, Mace and Mills 2015). However, it is also possible that N addition may sometimes decrease plant tissue quality (Tao et al. 2014). For example, increased N availability may lead to decreased allocation to C-based secondary chemicals but increased levels of N-based defense compounds, such as alkaloids (Gerson and Kelsey 1999, Royer et al. 2013, Larbat et al. 2015). Because secondary defense chemicals are often detrimental to the growth and development of herbivores, N addition may decrease the performance of herbivore species (Biere et al. 2004). In addition, under chronic excessive N supply, some herbivorous insects decrease their feeding rates presumably to retain their N homeostasis (Franěk et al. 2000). Thus, N deposition may positively or negatively affect the performance of herbivores via bottom-up effects of plants.

Despite abundant literature about the effect of N deposition on herbivores via changing plant quality and quantity as noted above, the potential indirect effects of N addition on herbivores via changing abiotic environments have been rarely considered. Activities of invertebrate herbivores are largely dependent on physical environmental conditions, such as light, temperature, and humidity (Matthews and Matthews 2009). Temperature can regulate herbivore feeding behavior (Lemoine et al. 2013). For example, a modest increase in temperature often accelerates feeding rate, growth, and development of insect herbivores (Bale et al. 2002), but extreme temperatures may have an adverse effect on insect performance (Denlinger and Lee 2010). Light is critical to insect visual detection of plants (Prokop and Owens 1983), and change in light intensity dominates insect circadian rhythms (Brady 1969) and navigation (Shimoda and Honda 2013). Air humidity and soil moisture are also important to insect activity of feeding, searching, or communication (Kaspari and Weiser 2000, Matthews and Matthews 2009). All these physical conditions are associated with vegetation properties (e.g., species composition and seasonal phase) and plant traits (including plant height, leaf size, and number) (Gough et al. 2000, Renhua et al. 2001, Brown et al. 2010). Since N deposition can directly change plant (community) traits (Binkley and Högberg 1997, Matson et al. 2002, Clark and Tilman 2008) being related to abiotic environmental conditions, N deposition may indirectly alter herbivorous insect performance. Such an abiotic effect could be particularly prominent for small insect herbivores that are not mobile or during immobile states of life history. However, empirical evidence for such an indirect effect through alterations in microclimate is limited.

China is experiencing intense N deposition primarily caused by anthropogenic organic N emissions (Richter et al. 2005), and in the Tibetan Plateau, N deposition has increased over the previous (at least three) decades (Liu et al. 2013). Possibly because low soil N content is a major limiting factor of plant growth on the Tibetan Plateau (Wu et al. 2011), N addition has been shown to relax the limitation and increased primary production in alpine meadows (Bai et al. 2010) with potential cascading effects on insect herbivores.
The caterpillar species *Gynaephora alpherakjj* is widely distributed in the alpine and Arctic tundra of the Northern Hemisphere, as well as in meadows of the Tibetan Plateau (Zhang and Yuan 2013). This species is among the most notorious insect pests damaging livestock: It not only competes for food plant material with livestock, but it also causes cattle disease (e.g., oral membrane inflammation), which substantially limits the sustainable development of animal husbandry of Tibetan Plateau (Shang et al. 2014). Since 1960s, the Chinese government has been investing large amounts of human and financial resources in pest control, but the population density of this insect herbivore is still out of control (Zhang and Yuan 2013). Moreover, outbreak events have been frequently reported in recent years, which might be attributed to N deposition or climate change in this region (Wei 2004).

In order to determine the effect of N deposition on the performance of the grassland caterpillars, we conducted two complementary microcosm experiments (a field experiment with a two-level factorial design and a chamber experiment) in an alpine Tibetan meadow. We investigated the effects of N addition on aboveground biomass of the plants that serve as food resource for the grassland caterpillars, leaf N content, as well as microhabitat temperature, and we further examined the growth and development rate of the caterpillars. The specific questions we asked were whether N addition (simulated N deposition) (1) increases plant growth and leaf quality for the caterpillars, (2) affects microhabitat temperature, and (3) enhances the survival, growth, and development rates of the grassland caterpillars.

**Materials and Methods**

**Study sites and species**

This study was conducted in Hongyuan County (32°48' N, 102°33' E), Sichuan Province, China, eastern part of Tibetan Plateau. The altitude is about 3500 m a.s.l. The climate is characterized by short spring and autumn, a long winter, and a mild to cool summer. Mean annual temperature is 0.9°C, and the maximum and minimum monthly means are 10.9°C and −10.3°C in July and January, respectively. Mean annual precipitation is about 690 mm, 80% of which occurs during May to August.

The major vegetation type is alpine meadow, and vegetation coverage is over 90%. The plant community is dominated by sedges, such as *Carex muriensis*, *Carex atrofusca*, *Deschampsia caespitose*, *Kobresia humilis*, and *Kobresia setchwanensis*, and forbs including *Potentilla anserine*, *Chamaesium paradoxum*, *Cremanthodium brunneo-pilosum*, *Caltha scaposa*, *Pedicularis longiflora*, *Cremanthodium lineare*, *Saussurea nigrescens*, *Anaphalis flavescens*, *Taraxacum lugubre*, and *Saussurea stella*. The distribution of plant species was mostly homogenous throughout the study meadow, so that >80% of plant species can be found in any 20 × 20 cm patch. The alpine meadow is used as a pasture for yak (*Bos grunniens*), which is the most important livestock species reared by native Tibetans. According to the policy of the local government, this pasture is allowed for cattle grazing during winter only.

Herbivorous insects are abundant in the pasture during the growing season from June to September. One of the most important and abundant insect herbivores is the grassland caterpillar *G. alpherakjj*, whose larval density ranges from 10/m² to 200/m² in summer. The caterpillars are gluttonous, mostly feeding on sedges and occasionally on forbs. Moreover, the activity of caterpillars is sensitive to temperature change: They crawl onto the top of plant shoots feeding from top to lower parts of shoots at high temperatures (e.g., at noon), and they rest under large leaves of forb species or on ground surface at low temperatures (e.g., at night), as detailed in Xi et al. (2013).

**Field experiment**

We conducted a two-factorial experiment during the growing season in the meadow. The experiment consisted of four treatments: (1) N addition (N+C−), (2) N addition and caterpillars added (N+C+), (3) caterpillars added (N−C+), and (4) control (N−C−). Each treatment had five replicates, and each replicate consisted of cages that enclosed naturally occurring plants. Each cage was a cylindrical enclosure, with a diameter of 0.6 m and height of 0.6 m. The cage had a steel frame covered by steel screen with a mesh size of 0.2 × 0.2 mm, which was small enough to prevent the caterpillars and their predators and parasitoids from migration. All 20 cages were positioned randomly in the meadow, separated by at least two meters from each other.
In the N addition treatments (N+C− and N+C+), we applied 2.8 g NH₄NO₃ to each cage (calculated as total N addition 3.5 g/m², within the range [0.2–5.3 g/m²] of N deposition across natural terrestrial ecosystems of China; Liu et al. 2011, Lu et al. 2011) in June when plants started growing and before caterpillars were added. The NH₄NO₃ was dissolved in 2 L water and then sprayed on soil surface for the N+ cages, and 2 L water was sprayed to each N− cage. The N addition was also applied to an additional plot (~6 m², NH₄NO₃ 10 g/m²), which was designed to provide high-quality leaves for the chamber experiment (see Chamber experiment).

The experimental caterpillars were collected from neighboring areas, and only healthy, medium-sized individuals (~0.15 g in fresh body mass) were used. Ten caterpillars were placed into the cages of the treatments designed to stock caterpillars on July 18th (N+C+ and N−C+). The resulting density (39/m²) was within the range of observed densities in the field but much lower than that in outbreak years. The field experiment started on 18 July and ended on 10 September, lasting about seven weeks.

On five sunny days during the experiment, we recorded the number of feeding individuals each hour from 7 a.m. to 8 p.m., and at the same time, we measured the temperatures at the ground surface and at the top of the plant community using mercury thermometers that hung 2 and 30 cm above the ground surface in the center of all cages (with a steel line tied to the cage sides, for each cage of the N+C+ and N−C+ treatments, respectively).

Moreover, we measured the fresh body mass of the caterpillars once a week during the experiment. For each measurement, at least three caterpillars were moved out of each cage and were immediately weighed with a portable analytical balance (Sartorius, Germany; precision 0.001 g) and then returned back to the cages. In addition, we checked the cocoon number for each cage including caterpillars every day after the emergence of the first cocoon in the late period of the experiment.

We also followed changes in the plant community. We measured the height of the tallest leaf on five randomly selected plants in each cage in mid-August, when plants began to senescence. We averaged the leaf height within each cage as community plant height. When all the caterpillars had cocooned, we harvested aboveground plant parts for each cage. The harvested plants were divided into two groups: sedges and other plants. The plants were dried at 65°C for 48 h and then weighed.

**Chamber experiment**

To test whether the change in leaf quality due to N addition affected caterpillar growth, we conducted a complementary chamber experiment during the same period as the field experiment, in which only leaf quality was used as treatment factor, and the other factors, such as temperature, light, and humidity were controlled. The chamber was set at a day/night regime of 14/10 h and 20/8°C, respectively, and the humidity was set at 45%. Those chamber settings were close to the climate in August in the meadow. The chamber experiment included two treatments: (1) caterpillars feeding on sedge leaves collected from the additional, fertilized plot and (2) caterpillars feeding on sedge leaves collected from an unfertilized control plot. Each treatment had five replicates, and each replicate consisted of a glass box (20 × 21 × 17 cm), in which plant leaves (from 20 g per 24 h at an early experimental stage to 50 g per 24 h toward the end of the experiment) and 10 caterpillars were placed. The leaves were replaced by the fresh material every three days. These caterpillars were also weighed during the experiment as for the field experiment. Likewise, we recorded the number of cocoons every day during the late period of the experiment. In addition, total leaf N was determined for five samples using the Kjeldahl method (Bradstreet 1969) for the fertilized and unfertilized plots, respectively, as a gross proxy for leaf tissue quality.

**Data analysis**

Two-way ANOVAs were used to test the effects of caterpillars and N addition on plant height, leaf content, and aboveground plant biomass, followed by post hoc Tukey’s honestly significant difference (HSD) tests, whenever a significant difference was detected. Generalized linear mixed-effects models (GLMMs with Poisson errors) were used to test the effects of N addition on the number of feeding caterpillars (per observation hour), where N addition and observation day were included as fixed factors
and cage IDs were included as a random factor. And GLMMs with the same factors were used to test the effects of N addition on the temperature in the field experiment. GLMMs were also used to test the effects of N addition on fresh body mass and the number of cocoons of the focal caterpillar species for the both field and chamber experiments, where N addition and observation day were included in the model as fixed factors and cage/box IDs were included as a random factor. Again, once a significant effect was detected, post hoc Tukey’s HSD test was used to determine the difference among means for each observation time (time of the day for temperature and the number of feeding caterpillars, observation day for plant biomass, and the number of cocoons). In addition, a quadratic model and a linear fitting were used to determine the relationship between temperature and the number of feeding caterpillars for the whole dataset and the morning time (from 7:00 to 11:00, when the ground surface temperature was significantly different between N−C+ and N+C+ treatments; see Results – Field experiment), respectively. All the data analyses were conducted using JMP 10.0.0 (SAS Institute Inc., Cary, North Carolina, USA).

Results

Field experiment

Nitrogen addition significantly increased total N content of the sedge leaves (the food source of the caterpillars) by ~10% (Fig. 1; Appendix S1: Table S1) and (community) plant height by 25% (Fig. 1; Appendix S1: Table S1). The presence of caterpillars showed no significant effect on plant N content but significantly reduced plant height by ~20% (Fig. 1; Appendix S1: Table S1). Moreover, the interaction effect between N addition and caterpillar presence was not significant for both leaf N content and plant height.

Nitrogen addition showed no significant effect on the air temperature above the plant community (Fig. 2A; Appendix S1: Table S2), but significantly decreased the ground surface temperature particularly during morning time by ~5.5°C (Fig. 2B; Appendix S1: Table S2). Moreover, N addition significantly decreased the number of feeding caterpillars during morning time (Fig. 2C; Appendix S1: Table S3). Assuming that the observed feeding caterpillars were consuming plants during the whole observation interval, we estimated that the average daily feeding time of a caterpillar individual was ~27% shorter ($F_{1,8} = 36.49, P < 0.001$; two-way ANOVA) in the N+C+ treatment (3.2 h) than in the N−C+ treatment (4.4 h).

A linear relationship was found between the ground surface temperature and the number of feeding caterpillars in the morning time, where
the variation in the ground surface temperature accounted for >80% variation in the number of feeding caterpillars (Fig. 3).

Overall, N addition significantly reduced caterpillar growth. Fresh body mass of individual caterpillars was indistinguishable between the N+C+ treatment and N−C+ treatment for the first two weeks, but in the third week after it was significantly lower in the N+C+ treatment (Fig. 4A; Appendix S1: Table S3). The timing of caterpillar cocooning was significantly delayed in response to N addition (Appendix S1: Table S3). The number of cocoons was significantly higher from 19th August (the second day since first caterpillar cocooned) until 4th September (four days before all caterpillars cocooned) in the N+C+ than in N−C+ treatments (Fig. 4B; Appendix S1: Table S3). However, mortality rate was not affected by N addition. Mortality rate was <10%

Fig. 2. The diurnal variation in temperatures above the plant community (A) as well as on the ground surface (B), the number of feeding caterpillars, and (C) in the treatments with and without N addition (caterpillars always present). The error bars = 1 standard error. ‘P < 0.05; ‘‘P < 0.01; ‘‘‘P < 0.001.

Fig. 3. The relationship between ground surface temperature and the number of feeding caterpillars in the field experiment during the morning period.

Fig. 4. Fresh body mass (A) and the number of cocoons (B) for the treatments with and without N addition in the field experiment. The error bars = 1 standard error. ‘P < 0.05; ‘‘P < 0.01; ‘‘‘P < 0.001.
The negative effect of caterpillars on aboveground plant biomass was weakened by N addition, as indicated by the significant interaction effect of caterpillars and N addition (Fig. 5A; Appendix S1: Table S1). Similarly, caterpillars significantly reduced (−54.2%) but N addition significantly increased the biomass of sedges (+20.1%). Nevertheless, the interaction effect of caterpillars and N addition on sedge biomass was not significant (Fig. 5B; Appendix S1: Table S1).

**Chamber experiment**

N addition significantly increased leaf N content by +22% in the additional field plots. The effect of leaf quality on the growth of caterpillars was marginally significant; that is, growth of caterpillars was slightly increased in the treatment with fertilized leaves (Fig. 6A; Appendix S1: Table S3). Average fresh body mass of the caterpillars was consistently and slightly higher in the treatment with leaves from fertilized plots than in those with leaves from unfertilized plots (Fig. 6A; Appendix S1: Table S1). Likewise, leaf quality also significantly facilitated the development of the caterpillars (Appendix S1: Table S3). For example, the number of cocooning caterpillars was slightly but significantly larger in the treatment with fertilized leaves than in the treatment with unfertilized leaves on 24 August and 25 August (Fig. 6B; Appendix S1: Table S3).
DISCUSSION

Our study shows that N addition significantly increased aboveground plant biomass of both the whole plant community and the sedge species group. Further, N addition increased leaf N content, which could slightly improve the growth and development rate of caterpillars under controlled environmental conditions. However, increased resource quantity and quality suppressed but not facilitated caterpillar growth and development in the field experiment, which was in contrast to the N limitation hypothesis (LeBauer and Treseder 2008). Instead, this counterintuitive finding could be attributed to significantly reduced ground surface temperature caused by a N addition-induced increase in canopy shading by increased plant height and biomass accumulation. Although our study methodology of using mesocosms might have induced several artifacts and hence might not be directly transferrable to real world because of changing light intensity, wind speed, and animal migration, our results clearly suggest that the indirect effect of N deposition on abiotic factors can be crucial to herbivore behavior, performance, and therefore should be considered for predicting the growth and development of herbivores affected by N deposition.

The positive effect of N addition on aboveground plant biomass is consistent with results of numerous previous studies addressing the short-term ecosystem consequences of N deposition (Throop and Lerdau 2004, LeBauer and Treseder 2008). Although it is sometimes reported that excess N deposition may result in nutrient imbalance in plants, which can reduce photosynthesis and plant growth (Mo et al. 2008), the positive N addition effect on soil N availability, plant growth, and primary productivity is well known (Nadelhoffer 2000, LeBauer and Treseder 2008).

N shortage is a major limiting factor for plant growth in Tibetan grassland (Wu et al. 2011). Studies have shown that fertilization can largely increase primary production of alpine grassland (Liu et al. 2011, 2013) and that fast dung decomposition and nutrient release into soil can improve plant growth in the short growing season (Wu et al. 2015). In the present study, the aboveground biomass of sedge species, the food resource of the caterpillars, was also significantly increased by N addition. This indicates that N addition increased food provision for the caterpillars. Importantly, the remaining sedge biomass after caterpillar feeding was greater in the N+C+ treatment than in the N–C+ treatment of the field experiment, suggesting that the caterpillar performance was not likely to be restricted by food availability in the N addition treatment.

The positive effect of N addition on leaf N content is also consistent with results of previous studies. N addition has been reported to increase plant leaf N content by 10–37%, depending on plant species identity and location (Pilkington et al. 2005, Liu et al. 2012, Mani 2013). In our study, N addition significantly increased leaf N content (by 22%), and this increase could further facilitate caterpillar growth and development, as indicated by the results of the chamber experiment. Under the controlled experimental conditions, caterpillars performed consistently better (albeit non-significantly on some days) when they were fed with leaves with high N contents than individuals that were fed with control leaves. This clearly indicates that the change in leaf tissue quality due to N addition did not lead to the suppression of caterpillar growth and development in the field experiment, as it would be the case if high concentrations of plant defense compounds would be produced (Mithöfer and Boland 2012).

In contrast to common theory regarding the dominance of plant quantity and quality effects, our results suggest that reduced ground surface temperature may account for the decreased performance of the caterpillars. In the field experiment, N addition greatly increased plant height and probably plant shoot density in some vegetatively reproductive species, as suggested by the increased aboveground plant biomass; this could increase plant canopy shading and thus significantly reduced ground surface temperature but not temperature above plant canopy. Such a canopy shading effect on ground temperature has been observed in both forests and grasslands (Martens et al. 2000, Li and Ma 2002). For example, when a reed community increased from 1.5 to 3.8 m in plant height and from 88% to 93% in coverage, daily light radiation decreased by >50%, and daily average ground temperature dropped from 32.2°C to 24.9°C (Fu et al. 2006). Our study meadow is low in average ground temperature with a high
diurnal fluctuation (e.g., >20°C in middle August), which highly varies with sunshine intensity. The changes in plant height and density likely have reduced light incidence on the ground surface, which significantly reduced ground surface temperature, particularly in the morning hours, when the temperature is low and sun angle is small.

Extremely high or low temperature is one of the most important limiting factors for the activity of insect herbivores in the alpine meadow (Mani 2013, Xi et al. 2015). Specifically, the negative effect of high or low temperature on feeding has been observed in many caterpillar species, and the optimal temperature range is usually between 20° and 30°C (Klok and Chown 1997, Kingsolver and Woods 1998, Niesenbaum and Kluger 2006). We observed that the caterpillars are often not active when temperature is low at night, they stay resting on the ground surface or under large plant leaves, and when sunshine intensity and temperature increase in the morning, the caterpillars become active, crawling to the top of plant shoots to start feeding. Therefore, the reduced temperature due to increased plant growth delayed the timing of caterpillar feeding in the morning, as clearly indicated by the linear relationship between ground surface temperature and the number of feeding caterpillars. Moreover, the caterpillars were observed to move down to the ground resting during evening at the same time for the N addition and the ambient N treatments, despite a higher ground surface temperature in the N addition treatment, as shown by the quadratic relationship between ground surface temperature and the number of feeding caterpillars. This could be because the caterpillars were high up in the vegetation sensing the temperature above the plant community, which was indistinguishable between the treatments. It is worthwhile to note that the caterpillars did not change their feeding behavioral response to ground temperature during their ontogeny in the field experiment. We observed similar caterpillar responses on all the five sunny days that spanned across the experiment before cocooning. Thus, N addition shortened the daily feeding time for the caterpillars. These factors above might have collectively led to the suppression of caterpillar growth and development in response to N addition. Such associations between low temperature and suppressed performance have been widely recorded in insect herbivores (Zvereva and Kozlov 2006, Asch et al. 2007, Bale and Hayward 2010). One of our previous works has also confirmed that reduced feeding time leads to the suppression of growth and development in the same caterpillar species (Xi et al. 2013).

In summary, we demonstrate that N addition reduced the growth and development of grassland caterpillars, even though it increased plant growth, N tissue content, and primary productivity. This mismatch between plant growth and herbivore performance may cause further changes in herbivory, consumer community composition, and ecosystem function. Our results suggest that the changes in abiotic factors resulting from N deposition should be considered in plant–animal interactions, particularly when immobile herbivore insects or individuals at an immobile stage are involved. In addition, we suggest that N deposition might not totally account for the population increase of this caterpillar during the passing decades; research on the interactions among habitat type, global warming, and N deposition may help better understanding why this pest species has become more abundant in the Tibetan Plateau.

Acknowledgment

We thank Rui Cao, Kai He, and Xinwei Wu for field assistance and Qinghai-Tibetan Research Base of Southwest Normality University for providing research convenience. This study was supported by National Science Foundation of China (31530007, 31325004, and 31500395).

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