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Effects of insect herbivory on the performance of *Larix sibirica* in a forest-steppe ecotone

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Abstract

The potential of insects to cause temporary spatial shifts of the forest-steppe borderline was investigated in a case study in the northern Mongolian mountain taiga, where *Larix sibirica* forests border on montane meadow steppe. Insect herbivores of *L. sibirica* in northern Mongolia include gypsy moth (*Lymantria dispar*) and grasshoppers, which defoliate trees. Grasshoppers have (like mice) an additional detrimental effect by decorticating stems of tree seedlings. The hypothesis was tested that insect herbivores cause spatial shifts of the forest-steppe borderline by, first, increasing the mortality of mature trees and, secondly, inhibiting rejuvenation.

The first hypothesis was tested by investigating a *L. sibirica*-meadow steppe ecotone, which was heavily defoliated by gypsy moth in early summer 2005. Defoliation was more severe at the forest edge than in the forest interior. Though only 10% of the larch needles at the forest edge endured the gypsy moth invasion without feeding damage, trees were not sustainably affected, as trees were fully foliated in the subsequent year. This suggests that single gypsy moth invasions, which are frequent in Mongolia’s forest-steppe ecotone, do not necessarily result in permanent damage of *L. sibirica* and, with it, not necessarily lead to local shifts of the treeline, though entire forest edges are often completely defoliated.

The second hypothesis was tested by planting 2-year-old seedlings of *L. sibirica* along the treeline towards the meadow steppe and in the interior of the adjacent light taiga forest. Seedling mortality within 3 months was significantly higher at the forest edge (87%) than in the forest interior (40%). Seedlings at the forest edge died either due to insect and small mammal herbivory (65%) or due to drought (25%). Herbivore damage in the seedlings included defoliation by gypsy moth and grasshoppers as well as decortication by grasshoppers and mice. The high feeding pressure for seedlings at the forest edge suggests that insects and mice inhibit or at least retard forest regeneration at the treeline and can thereby lead to temporary spatial shifts of the treeline towards the steppe, after trees have died, e.g., due to fire or logging.

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1. Introduction

Steppes in northern Mongolia and southern central Siberia primarily border on taiga forests of *L. sibirica* (Hilbig, 1995; Dulamsuren et al., 2005a). In Mongolia, *L. sibirica* covers 80% of the forested area (Gunin et al., 1999). Though modified by human activities (Hilbig et al., 2004; Rösch et al., 2005), the southern distribution limit of *L. sibirica* is generally controlled by drought (Gunin et al., 1999; Dulamsuren et al., in press). As water supply and evapotranspiration vary with the physiognomy of the landscape, the ecotone between forest and steppe is an aspect-dependent vegetation mosaic with forests on northern slopes and in dry valley and grasslands on southern slopes and in moist valley bottoms (Dulamsuren et al., 2005a,b).

Treelines towards the steppe are generally not static, but underlie spatial variation with temporarily varying influences of climate, fire activity, herbivore densities, and human utilization intensity (Jeffrey, 1961; Schwarz and Wein, 1999). Studies of temporal shifts of forest-steppe treelines include *L. sibirica* stands of northern Mongolia (Korotkov and Dorjsuren, 1988; Treter, 2000; Sankey et al., 2006).

Insect invasions are one possible cause that can lead to an expansion of grasslands into the forest. The highest potential to damage *L. sibirica* in northern Mongolia and southern Siberia among the insects has gypsy moth (*Lymantria dispar L*). Gypsy moth in north-eastern Asia, where the species has evolved, is genetically distinct from western populations in Europe (Reineke and Zebitz, 1999). Asian populations have...
volant females and males and infest a wide range of tree species. European populations have a strong preference for oak and their females are incapable of flight. Gypsy moth was introduced to North America in the 19th or 20th century, respectively, from Europe and the Russian Far East (Liebhold et al., 1992; Régnière and Sharov, 1998). Outbreaks of gypsy moth in northern Mongolia and southern Siberia (Gninenko and Orlinskii, 2003) are more frequent and more persistent than in Europe. One reason for this is the dispersibility of the females. Furthermore, resistance to low winter temperatures and promotion by forest susceptibility to herbivore attacks (Williams et al., 1990; Sharov et al., 1999) probably contribute to the frequency of gypsy moth invasions in Mongolia and southern Siberia. High forest susceptibility can be assumed because trees occur in this area at their drought limit (Dulamsuren et al., in press; Li et al., 2007).

In Mongolia, gypsy moth often more or less completely defoliates entire forest edges towards the steppe (Fig. 1A). Forest edges are subject to more intense gypsy moth damage than trees in the forest interior, as gypsy moth females preferentially deposit their eggs on rock outcrops within the steppe (Fig. 1D) and gypsy moth larvae are wind-dispersed after hatching in springtime (Dulamsuren et al., in press). Though trees at forest edges infested by gypsy moth larvae are often so severely defoliated that they look dead, no information is available in the literature whether such damage in L. sibirica is reversible or not. Effects of feeding damage on tree vitality might be particularly severe in Mongolia, as L. sibirica regularly suffers from drought stress in addition (Dulamsuren et al., in press). In the present study, we therefore studied the effect of a severe gypsy moth outbreak in two consecutive years. The aim was to test the hypothesis that a massive gypsy moth invasion would result in the dieback of larch trees and, thus, in a local retreat of the treeline.

In addition to the impact of gypsy moth on mature trees, the potential of small herbivores at inhibiting the rejuvenation of L. sibirica was studied. Dulamsuren et al. (in press) showed with planting experiments that seedlings of L. sibirica in a northern Mongolian meadow steppe suffered from feeding by gypsy moth, grasshoppers and small mammals. In that study, feeding was more severe in the open meadow steppe than in the meadow steppe along the forest edge. This was attributed to the proximity to gypsy moth colonies and to the prevalence of polyphagous grasshoppers of the Oedipodinae, Calliptaminae, Decticinae and Bradyporinae in the open meadow steppe, whereas grass-eating grasshoppers of the Gomphocerinae were dominant at the forest edge (Dulamsuren et al., in press). In the present study, we

![Fig. 1. (A) Edge of Larix sibirica forest bordering on montane meadow steppe in the forest-steppe belt of the Khangay, central Mongolia. Most trees are completely defoliated. (B–D) Study site in the Khentey, located in the northern Mongolian mountain taiga. (B) Defoliated larch after gypsy moth invasion in 2005. (C) Completely recovered trees at the same site in the year subsequent to the gypsy moth invasion (2006). (D) Colony of gypsy moth larvae in rock outcrop on the steppe slope bordering to the studied forest.](image-url)
tested the hypothesis that \textit{L. sibirica} seedlings suffer more from feeding damage by small herbivores at the forest edge than in the forest interior.

2. Materials and methods

2.1. Study area

The study was carried out in the western Khentey Mountains, northern Mongolia, 130 km north of the Mongolian capital Ulan Bator. The study site was located near Khonin Nuga Research Station (49°4′48″N, 107°17′15″E) in the valley of the river Eroo, a tributary to the river Orkhon. Sampling was conducted on Mt. Bayantogol (49°5′N, 107°17′E) at 1100 m. Mt. Bayantogol rises on the northern shore of the Eroo river and is covered with a steep, 2 km wide steppe on its southern slope and a gently inclined Betula platyphylla–\textit{L. sibirica} light taiga (=subtaiga) forest on its northern slope.

The study area and its vascular plant vegetation have recently been characterized by Dulamsuren (2004) and Dulamsuren et al. (2005a,b,c). Zonal vegetation of the surroundings of Khonin Nuga Research Station primarily consists of dark taiga forests with \textit{Pinus sibirica}, \textit{Abies sibirica}, and \textit{Picea obovata} in the upper montane belt, light taiga (or also called subtaiga) forests with \textit{L. sibirica} and \textit{B. platyphylla} or \textit{Pinus sylvestris} on northern and eastern slopes of the lower montane belt as well as steppe grasslands on southern and western slopes of the lower montane belt (Dulamsuren, 2004; Dulamsuren et al., 2005a,b). In the surroundings of Khonin Nuga Research Station, a regular pattern of forests on northern slopes and steppes on southern slopes is found. Grasslands are composed of different types of meadow and mountain steppe depending on soil conditions, microclimate, inclination and aspect (Dulamsuren, 2004; Dulamsuren et al., 2005a,b). The study area has been traditionally avoided by pastoral nomads because of high wolf and bear populations and bad accessibility (Dulamsuren et al., in press).

Climate of the Khentey Mountains is characterized by the Asian anticyclone in winter, which typically has its center southwest of Lake Baikal and causes dry and cold winters with mean January temperatures as low as −23 to −28 °C (Tsegmid, 1989; Tsedendash, 1995). Mean July temperatures published from the Khentey range from 12 to 18 °C. Frost occurs from the end of August to early June on 280–300 days per year (Tsedendash, 1995). Annual precipitation at the closest weather stations (Bugant, Eroo) 42 or 87 km NW Khonin Nuga Research Station amounts to 250–260 mm (Dulamsuren et al., 2005a). At Khonin Nuga Research Station, annual precipitation June 2005–May 2006 amounted to 300 mm (Dulamsuren & Hauck unpubl.). Most precipitation is received during summer.

2.2. Survey of feeding damage in mature trees

Three parallel plots of 7000 m$^2$ (175 m × 40 m) were installed (1) directly at the forest edge towards the steppe, and (2) 50 m or (3) 100 m behind the treeline in the forest interior. Many trees on the plots suffered from feeding damage due to a gypsy moth invasion in early summer 2005. Feeding activity of gypsy moth larvae was highest in June. For estimation of feeding damage, all trees of Siberian larch (\textit{L. sibirica} Ledeb.) with branches in the lower 4 m above soil level were marked. This included 106 trees on the plot at the forest edge, 67 trees at 50 m ad 59 trees at a distance of 100 m from the forest edge. Feeding damage was estimated in percent of total needles on ten randomly chosen twig sections of 20 cm length within the lower 4 m of each sample tree. Estimation of feeding damage was conducted in the diapause of gypsy moth larvae in July 2005 and was repeated in early summer June 2006.

2.3. Planting experiment

Two-year old seedlings of \textit{L. sibirica} brought up from seeds collected in the southern Khentey Mountains were obtained from a nursery in Ulan Bator. They were planted in a row along the forest edge, 20 m in front of the outermost tree, and in a row in the forest interior, 100 m behind the treeline. In each row, 30 larch seedlings were planted in a distance of 30 m from one another in May 2006. All trees were watered with 1.5 l on the day of planting. Feeding and drought damage as well as growth were estimated after 3 months in August 2006. Percentage of needles fed by herbivores or withered due to insufficient water supply were separately recorded and related to the original total needle area of each sample tree. Areas of stem bark removed by feeding were estimated as percentage of the total bark area. Furthermore, total shoot height and shoot increment from May to August 2006 were measured.

2.4. Statistics

Arithmetic means ± standard error are given throughout the paper. All data were not normally distributed, as tested with the Shapiro-Wilk test. Therefore, data of feeding damage in mature \textit{L. sibirica} trees were log-transformed before statistical analysis. Log-transformed data were positively tested for normal distribution. The significance of differences between more than two means calculated from these data was tested with Duncan’s multiple range test. We refrained from calculating a repeated measures ANOVA, because only one between-subject factor (viz. plot) had to be considered. Rather, we used the differences of parameters recorded in 2006 minus parameters recorded in 2005 to test for significant differences between sample plots with Duncan’s multiple range test. Mann–Whitney’s \textit{U}-test was employed for pairwise tests of the significance of differences between trees transplanted to the edge and the interior of the forest. Differences of frequencies were tested for statistical significance with the \textit{$\chi^2$}-test. Statistical analyses were computed with SAS 6.04 software (SAS Institute Inc., Cary, NC, U.S.A.).

3. Results

3.1. Feeding damage in mature larch trees

Feeding damage by gypsy moth was significantly more severe at the forest edge than in the plots located 50 or 100 m behind the treeline within the forest (Fig. 2). In the year of the gypsy...
moth invasion (2005), only 10% of the needles remained intact, whereas 59–67% of needles survived the invasion without damage inside the forest (Fig. 2A). At the forest edge, 17% of the needles were damaged by gypsy moth feeding (Fig. 2B) and 73% were completely fed (Fig. 2C). The percentage of damaged needles (11%) was similar in the forest interior (Fig. 2B), but the proportion of needles completely fed was much lower in the forest interior (23–30%) than at the forest edge (Fig. 2C).

Regeneration of larch needles already started immediately after the gypsy moth invasion in summer 2005. At the heavily affected forest edge, 14% of the needles fed in May and early June grew again within a few weeks subsequent to the invasion until late July (Fig. 2A). In the year after the gypsy moth invasion, the percentage of intact needles was independent of the intensity of feeding damage in the previous year varying between 83 and 85% in the three sample plots (Fig. 2A). The proportion of needles partly (9–10%) or totally consumed (6–8%) by herbivores did not differ either between the three plots in 2006 (Fig. 2B and C).

3.2. Feeding damage in planted larch seedlings

Within 3 months after planting in May 2006, significantly more trees died at the forest edge (87%) than in the forest interior (40%; $P \leq 0.001, \chi^2 = 10.3, n = 30$). In trees planted in the meadow steppe along the forest edge, nearly all needles were either consumed by herbivores (65%) or desiccated (25%; Fig. 3). In the forest interior, the percentage of fed needles was not significantly different from that fed in trees at the forest edge, whereas the proportion of desiccated needles was significantly lower (5%) than at the forest edge (Fig. 3). Decortication of the stem was of subordinate significance in the forest interior, but averaged to 15% of the bark area of the seedlings at the forest edge (Fig. 3). Mean shoot increment within the first 3 months after planting was significantly higher in seedlings planted in the interior than at the edge of the forest (Fig. 3). However, the study period was too short that this could have resulted in differences in total above-ground height of the seedlings (Fig. 3).

4. Discussion

Though larvae of gypsy moth were generally active in both study years, they only occurred in a sufficient number to exert severe damage on *L. sibirica* in the first year. Severe damage was clearly limited to the forest edge, where 90% of the needles were partly or completely consumed by gypsy moth. This suggests that the main factor determining the risk of feeding damage by gypsy moth is the distance of trees from the gypsy moth colonies located on the steppe slopes. The high feeding risk of forest edge trees implies that northern Mongolia’s frequent gypsy moth invasions are a factor that potentially could contribute to a shift of the treeline towards the steppe. However, our results also show that a single, though intense gypsy moth invasion has no long-term effect on the viability of *L. sibirica*. Removal of 90% of the needles at the forest edge by gypsy moth certainly resulted in reduced biomass production (Naidoo, 2001), but was not sufficient to cause a local retreat of the tree-
line. Our results do not rule out that *L. sibirica* might be lethally damaged by two or several gypsy moth invasions in consecutive years, but suggests that *L. sibirica* is well adapted to single invasions despite its latent suffering from drought stress at its southern distribution limit in Mongolia. The high regeneration capacity of mature *L. sibirica* trees is properly a prerequisite for their ability to inhabit forest-steppe ecotones with particularly high grazing pressure by small herbivores in addition to drought and high light resistance.

Seedling mortality was significantly higher in the meadow steppe along the forest edge than inside the forest. Survival at the forest edge was extremely low with 13% in the first three months after planting, whereas 60% of the seedlings survived this period in the forest interior. Mortality was caused by three factors, viz. by defoliation and defoliation by herbivores and by drought. The high seedling mortality at the forest edge can primarily be attributed to defoliation and drought, as the extent of defoliation was independent of the site. Defoliation of larch stems, which is caused by both grasshoppers and mice (Dulamsuren et al., in press), was limited to the forest edge. Defoliation of *L. sibirica* in the study area is primarily due to gypsy moth larvae (in late May and June) and grasshoppers (during mid and late summer; Dulamsuren et al., in press). Drought was more detrimental to seedling performance at the forest edge than in the forest interior. The lower herbivore and drought-related damage at the forest edge resulted in significantly higher biomass production in *L. sibirica* seedlings inside the forest than at the forest edge. The high susceptibility of *L. sibirica* seedlings appears to be inconsistent with the high regeneration capacity after defoliation known from other tree species occurring at forest-steppe borderlines elsewhere, such as Betula pendula or Populus tremuloides (Osier and Lindroth, 2004; Huttenen et al., 2007), or with other conifer seedlings (Chen et al., 2002). This apparent contradiction suggests that the combination of defoliation, defoliation and drought makes the larch seedlings in the Mongolian forest-steppe ecotone particularly sensitive to herbivore attacks, as the seedlings in the mentioned experiments were well water-supplied and their bark was intact.

Herbivores can affect stand and age structure of woodlands by influencing two parameters. First, they can increase mortality of mature trees (Fraser and Latifovic, 2005), and secondly, they can inhibit rejuvenation (Hanley, 1998). Our study suggests that the latter is more relevant for the spatial and temporal dynamics of the studied larch forest-meadow steppe ecotone in the northern Mongolian mountain taiga. Though defoliation of trees growing at the forest edge was severe in the first year of the study, the gypsy moth invasion responsible for this defoliation did not cause lethal damage in the trees. The potential of small herbivores (i.e., gypsy moth, grasshoppers and small mammals) to inhibit the rejuvenation of *L. sibirica* at the forest-steppe borderline is apparently much higher. Lethal damage in seedlings can cause a spatial shift in the treeline, as thereby herbivores hamper the replacement of trees, e.g., destroyed by fire or removed by logging. Forest regeneration is anyway difficult in the forest-steppe transitions because of limited water supply and high soil temperatures (Dulamsuren et al., in press). Though our results give a clear picture of the relations at the studied site during two years, the feasibility to generalize them is limited by the lack of temporal and spatial replication.

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