

Reindeer herbivory reduces willow growth and grouse forage in a forest-tundra ecotone

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Abstract

Browsing mammals strongly modify the structure of vegetation of forest-tundra ecotones. We investigated the impact of reindeer browsing on growth and morphology of an arctic willow, *Salix glauca*, by studying plants inside and outside fenced areas in a tundra habitat at the tree line. We also studied if reindeer feeding has an effect on the forage availability for willow grouse, a herbivore sharing the same food plant. Analyses of 6-year data show that reindeer strongly reduces the growth of tundra willow and changes plant morphology to a stunted growth form. Intense reindeer browsing on willow limited the forage availability for willow grouse and grouse fed less on reindeer-browsed willow than willows protected from reindeer browsing. The results of this study imply that herbivores can counteract the increase of shrubs in forest-tundra ecotones, as has been predicted in some studies discussing the effects of climatic warming on vegetation. Furthermore, trophic interactions should be incorporated in modelling vegetation changes as a response to increased temperatures.

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Zusammenfassung

Weidende Säugetiere beeinflussen die Struktur von Wald-Tundra-Ökotonen stark. Wir untersuchten den Einfluss der Beweidung durch Rentiere auf das Wachstum und die Morphologie einer arktischen Weide, *Salix glauca*, indem wir Pflanzen innerhalb und außerhalb von gezäunten Flächen in einem Tundra-Habitat an der Baumgrenze untersuchten. Wir untersuchten außerdem, ob der Fraß der Rentiere die Nahrungsverfügbarkeit für das Moorschneehuhn beeinflusste, einen Pflanzenfresser, der dieselbe Pflanze nutzt. Analysen von Daten aus sechs Jahren zeigen, dass die Rentiere das Wachstum der Tundra-Weiden stark beeinträchtigen und Krüppelwuchs verursachen. Intensives Befressen der Weiden durch Rentiere begrenzte die Nahrungsverfügbarkeit für das Moorschneehuhn, und die Schneehühner fraßen weniger an Weiden, die von Rentieren befressen worden waren, als an geschützten Weiden. Die Ergebnisse dieser Studie legen nahe, dass Pflanzenfresser der Zunahme von Sträuchern in Wald-Tundra-Ökotonen entgegenwirken können, die in einigen Untersuchungen, die die Effekte der Klimaerwärmung auf die

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Vegetation diskutieren, vorhergesagt wurde. Trophische Interaktionen sollten berücksichtigt werden, wenn Vegetationsveränderungen als Folge von Temperaturveränderungen modelliert werden.

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Introduction

Wild and semi-domestic reindeer have shaped vegetation patterns of northernmost Fennoscandia since the last glacial epoch and they can therefore be considered as a natural or semi-anthropogenic part of northern boreal and subarctic ecosystems. High densities of reindeer are in some cases held responsible for large-scale habitat degradation (van der Wal et al., 2003) and have shown the ability to cause vegetation state transitions (van der Wal, 2005). Furthermore, in northernmost Fennoscandia, herbivores can have a great impact on the structure and position of tree lines (Oksanen, Moen, & Helle, 1995).

In the near future, anthropogenic changes in our atmosphere may also start having a serious impact on arctic and subarctic ecosystems. Climatic modelling research predicts that the effects of global warming will be strongest in the arctic region (ACIA, 2004; McCarthy, Canziani, Leary, Dokken, & White, 2001; Moritz, Bitz, & Steig, 2002; Watson, Zinyowera, & Moss, 1998). During the past 150 years, the Arctic warmed to the highest temperatures since temperature started to be recorded systematically about four centuries ago (Overpeck & Hughen, 1997). Winter and spring warming was especially pronounced over the last three decades and is suggested to increase plant growth and vegetation productivity in tundra and cause a northward movement of the tree line (Epstein, Walker, Chapin III, & Starfield, 2000; Lloyd, 2005; Serreze et al., 2000). Indeed, the last two decades have seen increased shrub abundance in northern Alaska (Chapin III, Shaver, Giblin, Nadelhoffer, & Laundre, 1995; Stow et al., 2004; Tape, Sturm, & Racine, 2006). Recent papers mostly report accelerated growth of woody species at the transitional boreal–arctic zone (Kullman, 2002, 2003; Lloyd, 2005; Moore, 2004; Sturm, Racine, & Tape, 2001) and link this to climatic trends. However, there is recent evidence that herbivores can have an impact on vegetation in forest-tundra ecotonal areas (Cairns & Moen, 2004; Husheer, Robertson, Coomes, & Frampton, 2006). Much of the interest has been directed to the changes in timberline in Fennoscandia (Oksanen et al., 1995) while there is less evidence concerning the extensive shrublands formed by willow.

Despite much effort over the past decades on the ecological consequences of global warming, ecologists

still do not have a good understanding of the role of species interactions in response to environmental change. Only few studies examined the effects of interspecific competition and predation on species responses to temperature change (Jiang & Kulczycki, 2004). For instance, one study found that climatic variation changed the hunting behaviour of wolves, thereby limiting the abundance of moose, which in turn had effects on the abundance of fir trees and primary productivity (Post, Peterson, Stenseth, & McLaren, 1999).

Some generalist insect herbivores, e.g. the autumnal moth *Epirrita autumnata* and the spruce budworm *Choristoneura fumiferana*, can also have a large impact on circum-boreal and arctic vegetation and outbreaks of these insects are predicted to become more frequent, mainly due to milder winter conditions (Ayles & Lombardero, 2000; Logan, Regniere, & Powell, 2003; Neuvonen, Niemelä, & Virtanen, 1999; Virtanen & Neuvonen, 1999; Virtanen, Neuvonen, & Nikula, 1998; Volney & Fleming, 2000). Poor regeneration from seedlings in mountain birch forests (*Betula pubescens* ssp. *czerepanovii*), which are destroyed by the autumnal moth, could be due to grazing by reindeer (Lehtonen & Heikkinen, 1995) and browsing by reindeer also strongly modifies tree lines (Oksanen et al., 1995). In this context, it would be important to gain further experimental evidence of the role of herbivory on the growth and survival of woody plants. In this study, we investigated the effects of reindeer browsing on regeneration ability, growth and morphology of the bluish willow, *Salix glauca*. Using fenced enclosures, we also studied if reindeer feeding has an effect on the forage availability for willow grouse, *Lagopus lagopus lagopus*, an herbivore sharing the same forage plant.

Materials and methods

Study area and experimental design

Our experimental area was situated in north-western Finnish Lapland, 5 km southwest of Mt. Muotkatakkavaara on a west-facing slope of a low hill at the tree line (68°55'N, 20°57'E). The area is characterised by gently sloping low mountains where continental mountain birch forest is the predominant vegetation, which

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