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Responses of key understory plants in the boreal forests of western North America to natural versus anthropogenic nitrogen levels

R. Boonstra [a,*], C.J. Krebs [b], K. Cowcill [b]

[a] *Department of Biological Sciences, University of Toronto Scarborough, Toronto, Ontario M1C 1A4, Canada*
[b] *Department of Zoology, University of British Columbia, Vancouver, B.C. V6T 1Z4, Canada*

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ABSTRACT

The understory plants of the boreal forests have evolved divergent strategies to succeed under low nitrogen conditions, with their ability to respond to nitrogen addition varying greatly. We examined the response of 5 key understory North American boreal forest species in the Yukon (4 shrubs and a herb) to low levels of nitrogen that could occur from natural pulses and to high levels that could occur because of anthropogenic deposition from either atmospheric deposition or as a management strategy to increase tree growth. We fertilized 240 one m^2 plots for the three dwarf shrubs and one herb and 60 three m^2 plots for one tall shrub at 0, 0.5, 1.0, 2.0, 4.0, and 17.5 g nitrogen/m^2 in June 2004 and May 2005. We measured changes in cover, growth, leaf metrics, and berry production in three dwarf shrubs (*Arctostaphylos rubra* [deciduous] and *A. uva-ursi* and *Empetrum nigrum* [both evergreen]), one herb (*Geocaulon lividum*), and one tall shrub (*Shepherdia canadensis*). We predicted the first three would be strongly affected by variation in nitrogen levels but that neither *Geocaulon* (a hemi-parasite) nor *Shepherdia* (a nitrogen fixer) would be. To examine for long-term effects of nitrogen application, we also fertilized four 2.8 ha plots in 2004 and 2005 with 1.0 and 2.0 g/m^2 and then measured berry production in 2006 and 2007 on the two *Arctostaphylos* species. Nitrogen addition at all levels had no effect on either *Geocaulon* or *Shepherdia*. There were general positive effects at low nitrogen levels and negative ones at high levels on the other 3 dwarf shrub species in a species-specific manner. There were marked year effects in some plant growth metrics and in berry production, emphasizing the role of climate, but also clear evidence that individual species tradeoff somatic growth for reproduction. There was a pronounced long-term negative effect of low nitrogen addition on the large plots, causing marked reductions in berry production in both *Arctostaphylos* species. We conclude that these dwarf shrubs are constrained to function optimally within a narrow range of nitrogen levels normally encountered, but are unable to cope with higher levels. Both *Geocaulon* and *Shepherdia* function independently of nitrogen limitation. Thus the life history adaptations of these understory plants to variation in nitrogen levels are species-specific and understanding their individual responses is key in predicting their fate and the biodiversity and organization of boreal forest ecosystem when challenged with higher anthropogenic levels of nitrogen.

1. Introduction

The boreal forests of the northern hemisphere are one of the major forested regions of the world (Elliott-Fisk, 1988; McLaren and Turkington, 2013), constituting 25–30% of its forests (Bonan and Shugart, 1989; Burton et al., 2003). In North America they cover 5,120,000 km^2 (Kuusela, 1992). Though these forests in northwestern Europe and western Northern America are similar at the tree level, they differ fundamentally at the understory level (Boonstra et al., 2016). In the former, dwarf shrubs dominate whereas in the latter, tall shrubs dominate. The key driver of this difference is the much more severe winter climate in the North American than in the northwestern Eurasian boreal forests. This difference drives distinct food web organization and dynamics in each of these two continents (Henttonen et al., 1987; Krebs et al., 2014) and, as a consequence, the evolutionary adaptations of organisms in these two forests have diverged fundamentally.

In North America, the boreal forest is a matrix of closed- and open-canopy forests and bogs, with tree species diversity being low (5 major conifer species and 3 deciduous species, Jerabkova et al., 2006), but understory tall shrub, dwarf shrub, herb, and nonvascular species diversity being modestly rich (Turkington et al., 1998, 2002). In the white spruce forests of western North America

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* Corresponding author.
E-mail address: boonstra@utsc.utoronto.ca (R. Boonstra).

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there are ~64 species (13 woody plants including trees, 28 herbaceous plants and 23 bryophytes; La Roi, 1967; Qian et al., 1998). The understory is dominated by a tall shrub layer (*Salix* spp., *Betula* spp. and locally, *Shepherdia canadensis* (L.) Nutt.) up to 2 m high that is not found in the boreal forests of northwestern Europe (Boonstra et al., 2016). These tall shrubs play a central role in these forests as they are the only thing snowshoe hares (*Lepus americanus* Erxleben) eat in winter and hares are the keystone herbivore of these forests. These hares, their predators, and several other herbivores go through highly repeatable 10-year cycles that dominate much of the food web and the biomass changes of these boreal forests (Krebs et al., 2001a, 2014). However, many species are not directly tied to the 10-year cycle. The dwarf shrubs, herbs, grasses, and nonvascular species are critical to the vertebrate biodiversity of these forests, supplying part or all the needs (food and cover) for the large diversity of vertebrates. These include at least 22 bird species (17 songbirds [J. Weir, pers. comm.], 2 grouse and 3 ptarmigan [Martin et al., 2001]) and 18 mammal species (14 small mammals [Krebs and Wingate, 1976, 1985: Boonstra et al., 2001; Boonstra and Krebs, 2012; Sullivan et al., 2013; Dracup et al., 2016] and 4 large mammals [Renecker and Schwartz, 1998; Brown and Mallory, 2007; Obbard and Howe, 2008; McLellan, 2015). Thus understanding the factors that limit and regulate the understory layer of the boreal forest is critical both for conservation and forest management. We examine the sensitivity and productivity of five key understory plant species in northwestern North America to the potentially limiting nutrient – nitrogen. We added only nitrogen fertilizer and did not attempt to test co-limitation with phosphorus, which is limiting in some ecosystems (Olde Venterink et al., 2003; Wassen et al., 2013) but not others (i.e. the Fennoscandian boreal ecosystem – van Dobben et al., 1999; Nilsen, 2001).

Nitrogen (N) is a key limiting nutrient of primary productivity in many terrestrial and marine ecosystems (Vitousek et al., 1997; Bobbink et al., 2010), including the boreal forest (Tamm, 1991). Prior to the industrial revolution, the Earth's ecosystems received N deposition rates of ~0.5 kg/ha/year. Thereafter, human activities caused rates to increase dramatically, with many areas now receiving rates exceeding 10 kg/ha/year and these may double again by 2050 (Galloway et al., 2008). In the boreal forests, current atmospheric deposition rates vary markedly between the two continents. Nitrogen deposition rates in boreal western North America are ~0.25–0.5 kg/ha/year (Dentener et al., 2006) and thus these forests have been little affected by anthropogenic atmospheric deposition. In contrast, deposition rates in boreal NW Europe are about 5–10 times higher, ranging from ~1.3 kg/ha/year in northern Sweden to 6.8 kg/ha/year in southern Sweden (Binkley and Högbert, 2016).

The plants of the North American boreal forest have evolved under low nutrient conditions (Turkington et al., 1998, 2002; Nitschke et al., 2017). However, the response of these boreal forests to N addition has focused on high anthropogenic levels significantly above those to which the plants have evolved. Most of the N additions have targeted trees to increase their productivity (e.g. Lautenschlager, 2000; Brockley, 2007; Lindgren et al., 2007; Park and Wilson, 2007). However, to assess how the entire boreal forest ecosystem (both plants and animals) might respond to the removal of N limitation, Turkington et al. (1998) added N at levels comparable to other studies during a long-term study in the southern Yukon as part of the Kluane Boreal Forest Ecosystem Project (Krebs et al., 2001b). Over each of 8 years, 17.5 g nitrogen/m^2 (175 kg/ha/yr), 5 g phosphorus/m^2 and 2.5 g potassium/m^2 were added over two 1 km^2 areas and similar levels were continued on smaller plots thereafter for a total of 20 years (Turkington et al., 2014). The response to these levels was not uniform across all strata. The tree layer (Boonstra et al., 2008), the tall shrub layer (Nams et al., 1993; Turkington et al., 1998, 2002; Melnychuk and Krebs, 2005), the graminoids and some of the herb layer (Turkington et al., 1998, 2002, 2014) responded positively. However, 13 ground layer species disappeared, including the prostrate shrubs *Linnaea borealis* L., and *Arctostaphylos uva-ursi* (L.) Spreng., along with *Anemone parviflora* Michx., *Lupinus arcticus* S. Wats., mosses, and *Peltigera canina* (L.) Willd. (a N-fixing lichen) (Turkington et al., 2014). Thus, the response to these very high levels of N addition was dramatic, but variable and species dependent. The question that this research did not address was how plant species in these forests respond to variation in low N levels. Our main question was to determine how boreal forest understory plants respond to variation in low levels of nitrogen addition (0–4 g/m^2) that they are likely to encounter naturally.

In North America, there is one key factor that can cause a short-term pulse in N levels in the boreal forest soils that is not seen in northwestern Eurasia: the snowshoe hare cycle. In northwestern Europe, hare cycles are absent (Boonstra et al., 2016). The 10-year snowshoe hare cycle in North America has been occurring for at least 300 years (Krebs et al., 2001b). Nutrient pulses occur approximately every decade and are associated with the 10-year snowshoe hare cycle. This is a consequence of the intense browsing at the hare peak followed by the flush of nutrients produced by the decay of the resulting large numbers of feces.

We measured both plant growth and berry production. We applied levels within the range of what these plants could be expected to experience naturally and contrasted these responses with those at a higher level (17.5 g N/m^2) that could occur because of anthropogenic deposition. We sampled 5 common understory plants. Three were dwarf shrub species (*Arctostaphylos rubra* (Rehd. & Wils.) Fern. (deciduous), *A. uva-ursi* (evergreen), and *Empetrum nigrum* L. (evergreen). These were predicted to be highly vulnerable to N addition based on responses we had earlier observed from a large-scale fertilization experiment in the Yukon (Turkington et al., 1998) and on responses of similar ericaceous species in NW Europe (van Dobben et al., 1999; Strengbom et al., 2002; Nordin et al., 2005). We also sampled two control species, both deciduous, and not predicted to respond to N addition because of their strategies to avoid N limitation. False toadflax (*Geocaulon lividum* (Richards) Fern.) is a hemi-parasitic perennial plant that gets its nutrients from a host of trees, tall shrubs, dwarf shrubs, and herb species (Warrington, 1970). Soapberry (*S. canadensis*) is a tall shrub that has an association with nitrogen fixing fungi and thus can flourish independent of soil N conditions (Baker and Mullin, 1992).

2. Methods

2.1. Study area

We carried out the study in the boreal forest of the southwestern Yukon, approximately 2 km southeast of the Arctic Institute Base at Kluane Lake (61°01′N, 138°24′W). The study area is between 600 and 1000 m above sea level and lies within the Shakwak Trench system in the rain shadow of the St. Elias Mountains. The tree community is dominated by white spruce (*Picea glauca* (Moench) Voss) interspersed with less abundant trembling aspen (*Populus tremuloides* Michx.) and balsam poplar (*Populus balsamifera* L.). The tall shrub layer is composed of willows (dominated by *Salix glauca* (L.)), dwarf birches (*Betula glandulosa* Michx. and *B. nana* L.), and soapberry (*S. canadensis*). The ground layer is composed of ericaceous dwarf shrubs – bearberries (*A. rubra* and *A. uva-ursi*), and blueberry/cranberry species (*Vaccinium* spp.), of crowberry (*E. nigrum*), and herbs such as toadflax (*G. lividum*) arctic lupine (*L. arcticus*), and other forbs (Turkington et al., 2002). The