



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



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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 m² plots for the three dwarf shrubs and one herb and 60 three m² plots for one tall shrub at 0, 0.5, 1.0, 2.0, 4.0, and 17.5 g nitrogen/m² 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/m² 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.

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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 km² (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 non-vascular species diversity being modestly rich (Turkington et al., 1998, 2002). In the white spruce forests of western North America

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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/m² (175 kg/ha/yr), 5 g phosphorus/m² and 2.5 g potassium/m² were added over two 1 km² 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/m²) 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/m²) 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 Shawk 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

study site was moderately open to closed spruce forest (55–80% canopy cover) with a well-developed (>80% cover) dwarf shrub and herbaceous understory. The site was last burned in ~1872 (Dale et al., 2001).

2.2. Natural history and distributional range of understory species

We studied 5 widespread, understory North American boreal forest shrubs: three are prostrate, dwarf shrubs (*A. rubra*, *A. uva-ursi*, and *E. nigrum*), one is a perennial herb (*G. lividum*), and one is a tall shrub (*S. canadensis*). Both *A. rubra* and *A. uva-ursi* are in the family Ericaceae. *A. rubra* has a distributional range across the tundra and boreal forests of North America to Greenland and extends west into eastern Siberia. It is a low, spreading deciduous shrub growing up to 15 cm tall. *A. uva-ursi* has a circumpolar and circumboreal distributional range and in both North America and Eurasia also occurs in cordilleran areas in the Rocky Mountains and Appalachian mountains and in Spain, Italy, and Greece, respectively. It is an evergreen shrub 5–30 cm tall. *E. nigrum* is in the family Empetraceae, is a low mat-forming, evergreen shrub that has a circumpolar and circumboreal distributional range, is 5–10 cm tall (taller on warmer sites), and usually has prostrate stems. *G. lividum* is in the family Santalaceae and is found only in the boreal forests of North America as well as into northern states of the USA. It is a common hemi-parasitic herb, parasitizing a wide diversity of boreal forest trees, shrubs, and herbs including many of those found our study area (Warrington, 1970). It is 10–30 cm tall, deciduous, and flowers in late May (see <http://www.alaskawildflowers.us>). *S. canadensis* is in the family Elaeagnaceae and is found throughout boreal North America, into the northern states of the USA, and down the Rocky Mountains to northern Mexico. It is a deciduous, nitrogen-fixing shrub from 1 to 3 m high (Baker and Mullin, 1992). For detailed summaries of the natural history and distribution of these plants, see the Fire Effects Information System, U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Missoula Fire Sciences Laboratory (<http://www.feis-crs.org/feis/>).

2.3. Weather data

Rainfall and temperature in years $t - 1$ and $t - 2$ are key determinants of understory shrub productivity in year t (Krebs et al., 2009) and thus we document both the long-term averages and the year-by-year differences that occurred over the study. Weather data were obtained from the Burwash Airport weather station (Environment Canada) ~65 km northwest of the Arctic Institute Base. Both the weather station and the Base are on Klauene Lake and thus in the same valley system. Mean annual precipitation (1981–2010) was 274.7 mm, including an average annual snowfall of approximately 105.5 cm. Mean annual temperature was -3.2 °C, with the mean temperatures during the growing season months of May, June, July, and August being 5.7, 11.1, 13.1, and 10.9 °C, respectively. The frost-free period over the period from 1966 to 1996 averaged 30 days and that from 1981 to 2010 averaged 42 days; thus the growing season is getting longer.

In 2004, May–August conditions were the driest of the 4 years (total rainfall 2004 – 146 mm; 2005 – 237 mm; 2006 – 171 mm; 2007 – 165 mm) and the warmest (mean temperature 2004 – 12.2 °C; 2005 – 11.4 °C, 2006 – 10.8 °C; 2007 – 10.7 °C). The dates of the last two overnight frosts varied among years, being earlier in 2004 than in the other years (2004: 3 June -4.5 °C and 4 June -2.5 °C; 2005: 8 June -2.0 °C and 22 June -0.5 °C; 2006: 8 June -1.0 °C and 24 June -2.5 °C; 2007: 9 June -3.5 °C and 10 June -1.0 °C). There is likely some variation between the weather experienced at our study sites and that at the Burwash weather station. Nevertheless no summer snow was recorded at either site in 2004

or 2007. In 2005, 2 cm fell at Burwash on 1 June and ~8 cm at our field site on 5 June and buried the flowering shrubs, killing many of the open flowers. In 2006, 2.6 cm fell on 4 June at Burwash, but none fell at our field site.

2.4. Small scale plot manipulations

2.4.1. Nitrogen treatments

Two fertilization experimental treatments were carried out: an intense, small scale, short-term species-based treatment in 2004 and 2005; and a large-scale, grid-based treatment in 2004 and 2005 that was monitored post fertilization in 2006 and 2007. In the small-scale treatment, a total of 240 dwarf shrub/herb plots were established, 60 for each of the four species. Each of the sixty 1 m² circular plots were set out in a non-random manner. These 5 species have a patchy distribution in the forest, and therefore we targeted our treatments to be on plots that consisted largely of the species of interest. Each plot was a minimum of 3 m distant from any other plot and both control and experimental plots were trenched in both years to a depth of 20–25 cm to sever roots that extended beyond the plot to prevent any exchange of nitrogen along root systems with plants outside the treatment plots. Within each species the 60 plots were randomly assigned to 6 treatment groups of 10 plots each. The tall shrub, *S. canadensis*, was treated in the same manner as above except the 60 circular plots were 3 m² since 1 m² was too small to enclose an entire plant. The diameters of two of the main stems per plot were measured at ground level and then tagged for berry counts later in the season.

All plots were randomly assigned to one of six nitrogen addition treatments (g/m²): 0 (the control), 0.5, 1.0, 2.0, 4.0 and 17.5 (equivalent to 0, 5, 10, 20, 40 and 175 kg/ha), giving 10 replicates per treatment. All plots were fertilized in early June in 2004, and again in mid-May in 2005 with commercial ammonium nitrate (NH₄-NO₃) fertilizer. The four low N treatments (0.5 g to 4.0 g/m²) simulated the range of nitrogen released from decaying snowshoe hare pellets during years of high snowshoe hare density (D. Hik pers. comm.), and the treatment 17.5 g/m² mimicked the level of N addition carried out during the previous 10-yr study (the Klauene Boreal Forest Ecosystem Project) (Turkington et al., 1998; Krebs et al., 2001b). From a study designed to predict snowshoe hare densities based on annual hare pellet counts (Krebs et al., 2001c), we estimated that at the peak of the 10-year snowshoe hare cycles in autumn 1979 (3.61 hares/ha), autumn 1990 (2.64 hares/ha), and autumn 1998 (2.73 hares/ha), hares deposited 61, 45, and 46 pellets, respectively, on every m² of forest floor (see Krebs et al., 2014 for hare densities). Obviously numerous pellets were also being deposited onto the forest floor on either side of the hare peak. In contrast, at the low of cycle following these peaks, hares in autumn 1986 (0.20 hares/ha), autumn 1992 (0.14 hares/ha), and autumn 2001 (0.07 hares/ha) deposited ~2.6, 1.6, and 0.8 pellets, respectively, on every m² of forest floor. Low levels of nutrients likely to come from the large numbers of decaying pellets at or slightly before and after the peak may be sufficient to stimulate plant growth and berry and seed production.

To assess the response of the plants to the fertilizer treatments, we made 4 measurements on each plot. For each, except percent cover, 10 plants were selected every 10 cm along a north-south transect within each plot. This avoided possible observer bias from unconsciously selecting larger individuals. If fewer than 10 plants occurred along a north-south transect, then an east-west transect was also used until 10 plants had been sampled. Measurements were taken at the end of the growing season in late July – early August in 2004 and 2005. This was the low to the early increase phase of the next hare cycle (Krebs et al., 2014).

2.4.2. Measurements

1. Berry number: The number of berries of the 3 dwarf shrubs and the herb were counted on a total area of 975 cm² on each plot. Berry counts were then extrapolated to the number of berries/m² by measuring the shrubs' percent cover within the two transects. All berry counts were conducted in mid to late July before they ripened and could be eaten by birds and mammals. Berries on *Shepherdia* were counted as follows: two branches of the shrub were randomly selected, the basal diameters measured, marked with permanent aluminum tags, green berries counted on each of the two branches, and counts standardized to a 10 mm diameter branch size.
2. Berry dry mass: Where possible, 10–30 berries per plot were collected (no two berries coming from the same plant), sealed in labeled empty film canisters, and weighed immediately upon return from the field. The berries were then placed in envelopes and dried for 5 days in the oven at 60° C and reweighed. Mass was calculated on a per berry basis. Not all plots produced berries in all years and hence the sample size varied slightly.
3. Cover: In late summer 2004 and 2005 percent cover of the 3 dwarf shrubs and the herb was measured within the 1 m² plots by the use of a ¼ circle (pie-shaped) piece of transparent vinyl divided into sections to assist in visually estimating cover in each quarter of the plot to the nearest 5%. We were not able to measure cover accurately in *Shepherdia*.
4. Leaf size and mass: Leaf samples of *A. rubra*, *A. uva-ursi*, *G. lividum*, and *S. canadensis* were collected from separate plants (i.e. no individual plant had more than one leaf sampled). Leaf samples were placed between the pages of a loose-leaf notebook and the top page was rubbed with graphite to produce leaf tracings. The tracings were sprayed with hair spray to prevent the graphite from smearing. Length and breadth of the leaves were measured using the graphite leaf tracings. Leaves were placed in small labeled envelopes and dried in an oven at 60° C for 5 days and weighed to the nearest 0.001 g to give dry mass per leaf. *E. nigrum* leaves were not measured as they were too small.
5. Growth: New terminal stem growth on *A. uva-ursi*, *E. nigrum*, *G. lividum*, and *S. canadensis*, was measured (mm) at the end of growing season in late July to early August. New growth on *A. rubra* was not measured due to the difficulty of differentiating between new stem growth and new leaf growth. For *G. lividum* the new growth consisted of the entire plant from the soil surface to the tip of the upwardly folded top leaves. New leaf growth (numbers) was counted on ten samples/plot each of *A. rubra*, *A. uva-ursi*, *G. lividum*, and *S. canadensis*. *E. nigrum* leaves were not counted as they were small, numerous, and readily shed from the stem when handled.

2.5. Large scale plot manipulations

To assess the longer-term consequences of nitrogen treatment that may mimic the effect of nitrogen deposition from the decay of hare feces at the peak of the cycle, we carried out a parallel, but less intensive, larger scale assessment of nitrogen addition. In June 2004 and again in May 2005, we fertilized four areas, each of 2.8 ha. Two were fertilized each year with 1 g N/m² (10 kg/ha), and two with 2 g N/m² (20 kg/ha). In late summer 2006 and 2007 we counted the number of berries of both *Arctostaphylos* species on each of these larger fertilized areas with forty 40 cm square plots set out at permanent positions and compared these to 40 control plots. The Control plots had plentiful *A. rubra* and *A. uva-ursi*, but few *Empetrum*, *Geocaulon*, and *Shepherdia*, and thus the latter were not included in our assessment of long-term effects.

2.6. Statistical analysis

Data are expressed throughout as means ± 1 SE. To test for the effect of year on all plant measures on control plots, we used a paired *t*-test. To test for the effect of fertilization treatment and year on all plant measures, we used a 2-way ANOVA. Probabilities will be given only if they are significant or nearly so. If there was a time lag in the response of a plant species to the treatments, we expected to pick this up as an interaction between year and nitrogen treatment. All analyses were done with NCSS 8 (<http://www.ncss.com/>) and with StatView (SAS Institute Inc. 1998). We used the Tukey-Kramer multiple comparison post hoc test to examine for significance difference among fertilization levels. All the ANOVA results are given in Table 1. None of the interactions between nitrogen treatment and years were significant.

3. Results

3.1. *Arctostaphylos rubra*

A. rubra had 2.5 times more berries on control plots in 2004 than in 2005, but there was high variation among plots (Fig. 1). This variation became minor relative to the year differences when all plots were used: the 2-way ANOVA indicated no fertilizer effect, but a very strong year effect (Table 1; all plots combined in 2004 had 2.1 times more berries than in 2005). In addition, the berries in 2004 weighed 18% more than those in 2005 (0.052 g ± 0.0017 versus 0.044 g ± 0.002, respectively, mean over all plots with no fertilizer effect, Table 1). Plant cover was 26% greater in 2004 than in 2005 (Fig. 1). However, though there was no effect of fertilizer treatment level on cover at levels ≤ 4 g/m² in 2004 or in 2005, cover was ~20% less in 2005 on all plots (including that on the control plots, Fig. 2, Table 1). The exception was those plots receiving 17.5 g/m²; they had a 50% cover reduction in 2005 (from 65.2% to 31.8%, respectively; treatments 0, 1, and 2 were significantly different from that at 17.5 g/m²). Hence, the decline in cover from 2004 to 2005 for the control and treatments 0.5–2 g/m² was simply a year effect but in 2005 cover started to decline at 4 g/m² and became pronounced at 17.5 g/m² and thus was a nitrogen effect.

Leaves weighed ~10% less in 2004 than in 2005 on control plots (Fig. 1). Only plants at the highest N level (17.5 g/m², both years combined) showed an increase in leaf mass, with their leaves being significantly heavier than those on controls and the low level nitrogen treatments (Fig. 3). There was no treatment effect on leaf length, and no clear pattern. Finally, there was no treatment effect on leaf width, but there was a year effect with leaves (all plots pooled) being about 5% narrower in 2004 than in 2005 (18.35 mm ± 0.27 vs. 19.37 ± 0.28, respectively, Table 1). Thus, leaves weighed less and were smaller in 2004 than 2005, and high N increased leaf mass.

In summary, there were marked differences between years, with more, heavier berries and greater cover in 2004 than 2005, but plants produced lighter, smaller leaves in 2004 than 2005, suggesting a tradeoff between berry production and photosynthetic tissue. N addition had a negative effect on cover for the deciduous herb *A. rubra*, but only in the second year and only at the highest level, and a positive effect on leaf mass at the highest level.

3.2. *Arctostaphylos uva-ursi*

A. uva-ursi had 2 times more berries on control plots in 2004 than in 2005 (Fig. 1) and 3 times more on all plots combined (Table 1) and they weighed 9% more in 2004 than in 2005 (0.076 g ± 0.0036 versus 0.070 g ± 0.0024, respectively, all plots combined Table 1). There were significantly more berries at

Table 1

Summary of the 2-way ANOVA results for the mean responses of five boreal forest understory plant species on the control and to 5 levels of nitrogen fertilization (0.5–17.5 g/m²) on 60 plots in each of 2 years. Sample sizes are given after the plant measure. For some measures sample sizes are less than 120, either because problems developed in the field or lab with the plot or samples or the plants in a plot produced no berries. P values are * < 0.05). Significant multiple comparison groups indicated by superscript letters. No letters indicate no treatment effect. There were no significant interactions between nitrogen treatment and year in any of these data.

	Nitrogen treatment (g N per m ²)						Year	
	0	0.5	1.0	2.0	4.0	17.5	2004	2005
<i>Arctostaphylos rubra</i>								
Berry number (119)	15.6	18.3	17.4	13.3	11.8	7.6	18.9 [*]	9.0 [*]
Berry mass (99)	0.047	0.048	0.052	0.044	0.047	0.050	0.052 [*]	0.044 [*]
Cover (119)	68.4 ^A	62.5 ^A	62.9 ^A	65.2 ^A	54.8 ^B	48.5 ^C	67.4 [*]	53.4 ^{**}
Leaf mass (118)	0.36 ^A	0.34 ^A	0.37 ^A	0.38 ^A	0.33 ^A	0.43 ^B	0.35 [*]	0.39 [*]
Leaf length (118)	40.8	39.0	40.1	41.3	38.3	41.5	0.48	0.49
Leaf width (118)	19.0	18.5	19.1	18.8	18.1	19.8	18.4 [*]	19.4 [*]
<i>Arctostaphylos uva-ursi</i>								
Berry number (120)	4.6 ^A	2.7 ^A	9.1 ^B	2.8 ^A	2.0 ^A	3.4 ^A	6.2 [*]	2.1 [*]
Berry mass (77)	0.075	0.068	0.071	0.073	0.073	0.079	0.076	0.070
Cover (120)	60.2	56.4	56.9	63.0	59.6	57.1	58.9	58.7
Leaf mass (120)	1.22	1.17	1.01	1.12	1.00	1.19	0.96 [*]	1.27 [*]
Leaf length (120)	16.4	15.6	15.0	15.7	15.2	15.3	15.3 [*]	15.8 [*]
Leaf width (120)	7.58	7.53	7.68	7.63	7.18	7.46	7.09 [*]	7.92 [*]
Growth (101)	4.0	4.5	3.8	4.8	4.8	3.8	3.84 [*]	4.53 [*]
<i>Empetrum nigrum</i>								
Berry number (120)	54.5	80.8	58.2	76.7	59.7	62.2	107.9 [*]	22.8 [*]
Berry mass (118)	0.027 ^A	0.025 ^A	0.031 ^B	0.030 ^B	0.026 ^A	0.023 ^A	0.025 [*]	0.029 [*]
Cover (120)	44.4	45.3	49.2	43.9	50.8	45.6	53.9 [*]	39.2 [*]
Growth (119)	10.4 ^A	13.5 ^A	16.2 ^{AB}	13.7 ^A	14.5 ^A	18.3 ^B	14.8	15.5
<i>Geocaulon lividum</i>								
Berry number (120)	34.2	31.6	30.3	25.4	30.4	28.6	22.6 [*]	37.5 [*]
Berry mass (98)	0.059	0.051	0.063	0.054	0.051	0.059	0.070 [*]	0.043 [*]
Cover (120)	44.2	42.6	37.1	45.2	43.0	41.7	42.8	41.9
Leaf mass (120)	0.17	0.17	0.17	0.17	0.18	0.18	0.20 [*]	0.14 [*]
Leaf length (120)	25.7	25.8	26.7	27.2	26.8	27.3	25.9	27.2
Leaf width (120)	12.9	12.8	13.6	13.2	13.2	13.7	13.1	13.4
Growth (112)	13.8	13.7	13.6	13.9	13.9	13.9	13.4 [*]	14.2 [*]
<i>Shepherdia canadensis</i>								
Berry number (120)	20.8	37.3	26.6	35.6	26.4	17.2	38.9 [*]	15.8 [*]
Berry mass (101)	0.038	0.034	0.041	0.038	0.040	0.038	0.044 [*]	0.032 [*]
Leaf mass (120)	0.75	0.72	0.66	0.67	0.70	0.72	0.67 [*]	0.74 [*]
Leaf length (120)	46.1	45.3	44.5	41.9	45.5	45.3	45.11	44.4
Leaf width (120)	24.4	23.3	23.9	22.8	24.7	24.6	23.7	24.3
Growth (120)	4.57	5.26	5.79	5.21	5.53	5.29	5.17	5.37

1.0 g/m² than at 0.5, 2 and 4 g/m² (Fig. 4, Table 1). We think that this was likely a sampling artifact and thus not a reliable indication of a true effect or at least it should be repeated to determine that degree of sensitivity of this plant to this N level. Cover was not affected by N (Fig. 1, Table 1). However, leaves weighed significantly more (~38% control plots – Fig. 1; and 31% more on all plots combined – Table 1) in 2005 than in 2004. Leaves were both significantly shorter (3%) in 2004 than in 2005 (15.27 mm ± 0.133 versus 15.79 ± 0.22, respectively – all plots combined) and narrower (12%) in 2004 than in 2005 (7.09 mm ± 0.085 versus 7.92 ± 0.098, respectively – all plots combined). Plant growth was not affected by N (Table 1), but was significantly (18%) less in 2004 than in 2005 (3.84 mm ± 0.13 versus 4.53 ± 0.12, respectively – all plots combined).

In summary, *A. uva-ursi* produced more, heavier berries in 2004 than 2005, but the plants grew less in 2004 and their leaves were lighter and smaller. Again these results indicate a tradeoff between photosynthetic tissue and reproduction. N addition had a negative effect on leaf mass at low N levels.

3.3. *Empetrum nigrum*

E. nigrum had 2.8 times more berries on control plots in 2004 than in 2005 (Fig. 1) and 4.8 times over all plots combined (Table 1), but berry number was not affected by the N treatment. Though the berry mass was not different on control plots in the two years (Fig. 5), when all plots were combined, they were 16% lighter in

2004 than in 2005 (mean 0.025 g ± 0.0007 versus 0.029 g ± 0.0013, respectively, Fig. 5 and Table 1). There was a significant N effect, with berry mass being heavier at 1.0 than at 2.0 and 4.0 g/m² (Fig. 5). Thus there were more berries in 2004 than 2005, but they weighed less, and N had a positive effect on mass at low levels. Cover was not affected by treatment, but was 42% greater in 2004 than in 2005 on control plots (Fig. 1; 37% greater when all plots were pooled – Table 1). Growth did not differ between years, but was affected by treatment, with control plants growing significantly less than those receiving 1, 2 and 17.5 g N/m² (Fig. 6, Table 1).

In summary, N had no effect on berry number, but did result in heavier berries at low N levels, and in increased plant growth at the highest N levels. There were marked differences between years, with more, but smaller berries, in 2004 than in 2005, and *E. nigrum* covered more of the plots in 2004 than in 2005.

3.4. *Geocaulon lividum*

G. lividum showed no response to the N treatments nor were there any interaction effects between year and treatment (Table 1). It exhibited the opposite year effect in berry number to that of the above 3 species, producing 83% fewer berries in 2004 than in 2005 on control plots (Fig. 1; 40% fewer when all plots were combined Table 1), but they were 63% heavier in 2004 than in 2005 (0.070 g ± 0.001 versus 0.043 g ± 0.003 respectively, all plots combined). Cover did not change between years. However, dry leaf mass

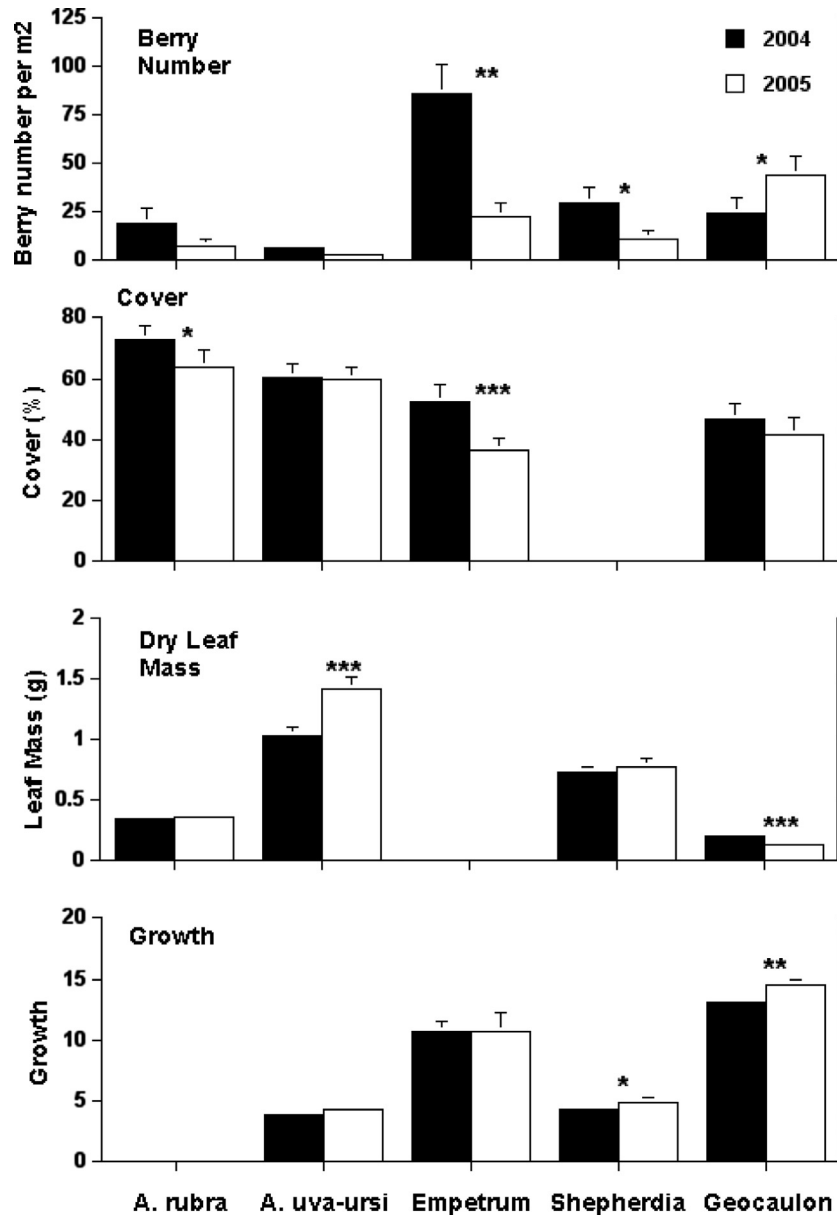


Fig. 1. The performance of five species of dwarf plants from the boreal of the Yukon on control plots in 2004 and 2005. The four primary measures – berry number/m², cover (%), dry leaf mass (g), and growth (mm) are presented (means \pm 1 SE). Where columns are absent for a species, measures could not be obtained reliably. For details on the measurement methods, see the text. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

was 72% heavier in 2004 than in 2005 (Fig. 1; 43% heavier when all plots were combined Table 1), but leaves were ~5% shorter in 2004 than in 2005 ($25.90 \text{ mm} \pm 0.26$ versus 27.22 ± 0.41 , respectively, all plots combined). However, leaf width was unaffected and the plants grew ~6% less in 2004 than in 2005.

In summary, there was no effect of variation in N levels on berry number, berry mass, plant cover, leaf mass, or growth for this hemiparasitic herb. There were marked differences between years, with fewer berries being produced in 2004 than in 2005, and growth was greater in 2005, but their leaves were smaller. Thus *Geocaulon*'s response was either the opposite to that of the above species (berry number, dry leaf mass) or it was unresponsive (cover).

3.5. *Shepherdia canadensis*

S. canadensis showed no response to the N treatments nor were there any interaction effects between year and treatment (Table 1).

Plants had 1.6 times more berries in 2004 than in 2005 on control plots (Fig. 1, ~2.5 times more on all plots combined Table 1) and their berries were 46% heavier in 2004 than 2005 (mean $0.186 \text{ g} \pm 0.0056$ versus $0.127 \text{ g} \pm 0.005$, respectively, wet weight all plots combined). However their leaves on the control plots were not different between years (Fig. 1), but a larger sample size (all plots combined, Table 1) indicated they were 10% lighter in 2004 than in 2005. Neither leaf length nor width changed over time. Plant growth was ~13% greater on control plots in 2005 than 2004, but this difference disappeared when all plots were combined (Table 1).

In summary, there was no effect of variation in N levels on berry number, berry mass, leaf mass, or growth in this nitrogen-fixing tall shrub. There were marked differences between years, with more, heavier berries being produced in 2004 than 2005, and, though leaves weighed less in 2004, neither leaf shape (length or width) nor plant growth differed between years.

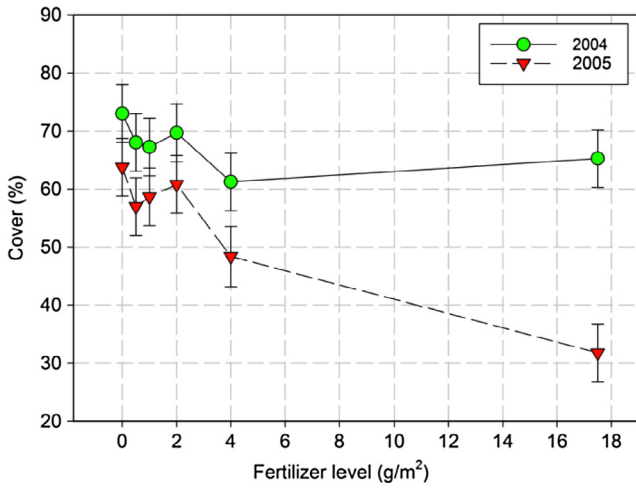


Fig. 2. Changes in the percentage cover of *Arctostaphylos rubra* in response to 5 levels of N fertilization applied in both 2004 and 2005; 0 was the control response. See Table 1 for significance of the differences among the means. Data are presented as means ± 1 SE.

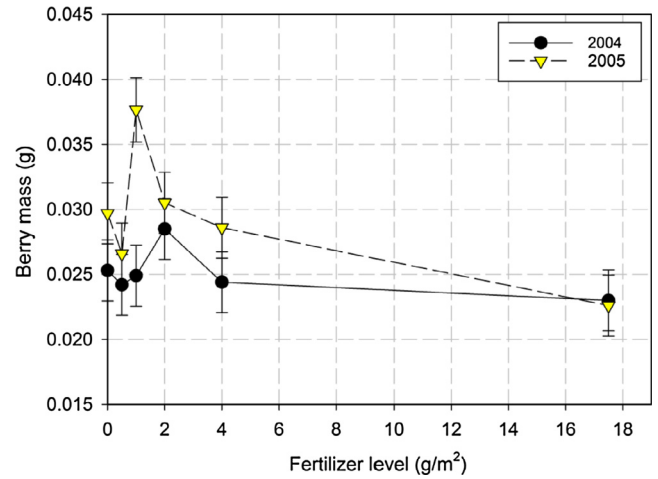


Fig. 5. Changes in the dry berry mass (g) of *Empetrum nigrum* in response to 5 levels of fertilization applied in both 2004 and 2005; 0 was the control response. See Table 1 for significance of the differences among the means. Data are presented as means ± 1 SE.

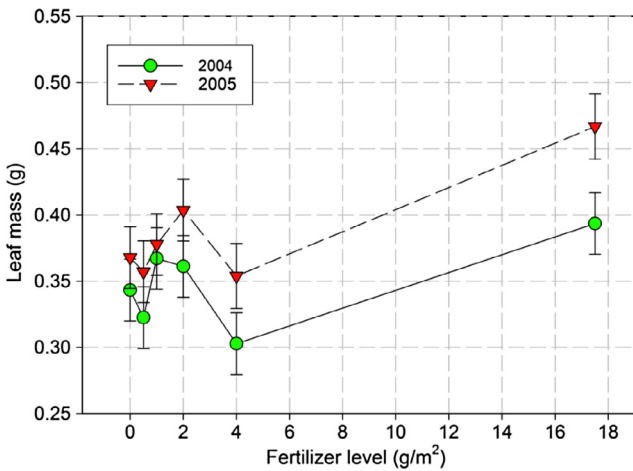


Fig. 3. Changes in the dry single leaf mass (g) of *Arctostaphylos rubra* in response to 5 levels of fertilization applied in both 2004 and 2005; 0 was the control response. See Table 1 for significance of the differences among the means. Data are presented as means ± 1 SE.

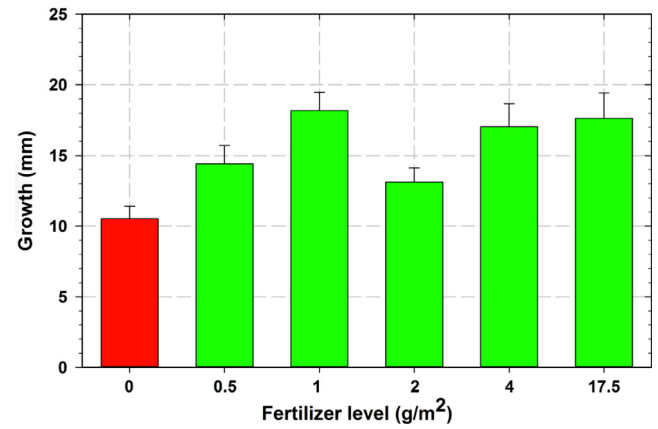


Fig. 6. Changes in the stem growth of *E. nigrum* in response to 5 levels of fertilization (2004 and 2005 pooled); 0 was the control response. See Table 1 for significance of the differences among the means. Data are presented as means ± 1 SE.

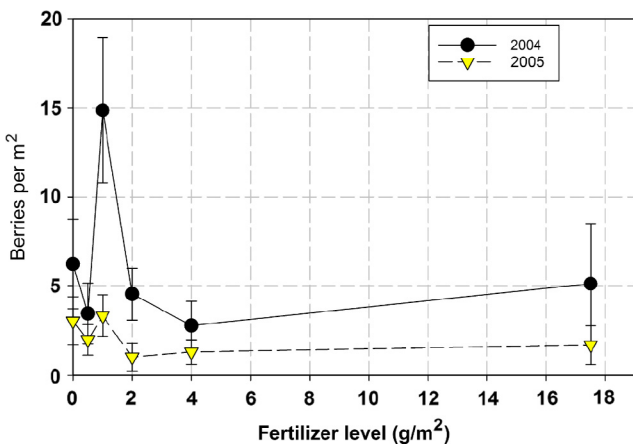


Fig. 4. Changes in the number of berries/m² of *Arctostaphylos uva-ursi* in response to 5 levels of fertilization applied in both 2004 and 2005; 0 was the control response. See text for significance of the differences among the means. Data are presented as means ± 1 SE.

3.6. Long-term large scale N addition effects

Both ericaceous species showed strong evidence of long-term, carry-over effects to fertilization in 2004 and 2005: they responded negatively to low levels of N addition relative to the control plot (Table 2). In *A. rubra* there was no effect in 2006, but by 2007 there was reduction of 75% and 63% in berry production at 1 and 2 g N/m², respectively ($p < 0.01$). In *A. uva-ursi* there was a marked reduction in both years (reductions in 2006, by 95% and 78%, and in 2007, by 68% and 76% at 1 and 2 g N/m², respectively; $p < 0.01$). Thus even at these low N application rates, there were very pronounced, long-term negative effects on berry production that lasted at least 2 years after N application.

4. Discussion

We tested the hypothesis that nitrogen within the range that normally occurs in the North American boreal forest stimulates plant growth and berry production of the five common berry-producing shrubs. We examined this in 3 species predicted to be sensitive to variation in N levels (*A. rubra*, *A. uva-ursi*, *E. nigrum*)

Table 2

Response of berry counts of *Arctostaphylos rubra* and *A. uva-ursi* to low level nitrogen fertilization. Two sites of 2.8 ha each were fertilized in June 2004 and again in May 2005 at each of two levels of nitrogen addition, and berries were counted in August 2006 and August 2007. Data are the number of berries per m² for 100% plant cover of that particular species. N = 40 for all counts. P values compare control versus N treatment and are * < 0.01.

Species and year	Control		1 g/m ² of N		2 g/m ² of N	
	Mean	95% confidence limits	Mean	95% confidence limits	Mean	95% confidence limits
<i>Arctostaphylos rubra</i>						
2006	106.7	90–124	93.5	74.5–114.6	124.6	93.1–158.7
2007	118.5	98–141	29.5 [*]	23.4–36.4	43.1 [*]	23.7–66.6
<i>Arctostaphylos uva-ursi</i>						
2006	276.2	238–316	12.5 [*]	3.6–21.4	61.1 [*]	37.5–88.2
2007	203.4	169–240	66.1 [*]	40.6–92.2	47.6 [*]	33.3–65.9

and 2 species (*G. lividum*, *S. canadensis*) predicted to be insensitive because of their unique life history strategies. Our findings lead to 4 major conclusions. First, the 3 sensitive species do indeed respond to variation in N levels (Figs. 2–6, Table 1), but their responses are species specific and there is no general pattern. In contrast, neither of the 2 insensitive species respond at all to variation in N levels (Table 1). Second, year effects are pronounced, causing pronounced differences between years (Fig. 1). For some measures, most of the species respond the same way (i.e. berry number and dry leaf mass [but *Geocaulon* does the opposite in both cases]), but for other measures there is species specificity in response (i.e. cover, growth). Third, we found evidence for tradeoffs between reproduction and somatic growth in some, but not all species, so that when plants invest in berry production, they invest less in leaf mass and growth (Fig. 1). Fourth, we reject the fecal nutrient enrichment hypothesis (Boonstra et al., 2001; Boonstra and Krebs, 2006): in only one species (*A. uva-ursi*) were berry numbers initially stimulated by the low levels of N likely to result from snowshoe hare fecal decay (Fig. 4), and the large scale N fertilization at these levels led to marked reductions in berry numbers within 2 years of application (Table 2).

Before we discuss our results, we raise one caveat. There are difficulties in testing the role of N limitation in these shrubs as these forests are subject to the vagaries of the weather and it can act as an overriding filter for nutrient effects. Thus, we might observe a strong nitrogen effect only in years of good weather. Severe spring frosts, such as we had in 2005, can destroy berry crops even when nutrients are superabundant. However the weight of evidence using the other plant metrics (cover, leaf mass and size, growth) measured simultaneously (Figs. 2–6, Table 1) and our use of 3 nitrogen-limited species to examine for generality and 2 species that are not nitrogen-limited to act as control species (*Geocaulon* and *Shepherdia*) strengthen our conclusions.

Nitrogen did affect aspects of the growth and productivity of the 3 nitrogen-limited species (*A. rubra*, *A. uva-ursi*, and *E. nigrum*), but these effects were species specific, even within the same genus. Similar results have been obtained in European studies (Wassen et al., 2013; Wilkins et al., 2016). Thus, only the deciduous *A. rubra* showed a major reduction in cover at 17.5 g/m² of N and then only in the second year (Fig. 2). Oddly this was associated with a significant increase in leaf mass (Fig. 3) (not seen in the other two species). *A. uva-ursi* produced more berries at 1.0 g/m² of N (10 kg/ha) than at other levels (Fig. 4), indicating possibly a threshold effect (though it may also be a sampling artifact), but this was not seen in the other two species. Berry mass increased only in *E. nigrum* and only at 1.0 g/m² of N (particularly obvious in 2005 and again possibly a threshold effect) (Fig. 5). Growth in *E. nigrum* was enhanced above controls at virtually all levels above 1.0 g/m² of N (Fig. 6), but *A. uva-ursi* did not respond in this way (*A. rubra* was not measured). No response to any level of nitrogen was seen in either *Geocaulon* or *Shepherdia*. In terms of potential vulnerability to N deposition, only *A. rubra* shows a marked reduction in

cover within 2 years of application of 17.5 g/m² of N and similar reductions were seen in *A. uva-ursi* within 3–4 years at such levels (Turkington et al., 2014). However it is not clear how these species would respond over the long term with deposition levels <2 g/m² of N. High levels of N will cause a shift in community structure, favoring grasses and some herbs (Turkington et al., 2014), but it is not certain that chronic low levels would do the same. Our findings do suggest that these three plant species have the capacity to respond positively and modestly to increases in N, but only within the narrow window normally found and hence they can persist within this range. Thereafter they may lack the adaptations to respond to higher levels (Chapin et al., 1986) and their persistence is jeopardized (Turkington et al., 2002).

Climatic effects are major determinants of berry production. Krebs et al. (2009) examined variation only in berry counts for all the species we studied over a 12 year period and concluded that weather could explain 80–96% of this variation. They concluded that there was no common set of weather variables that could explain berry count variation in all species. We arrived at an identical conclusion with respect to N. Our experiment targeted N as a limiting factor, and we do indeed find that for the three susceptible dwarf shrubs (Figs. 2–6, Table 1) there were both positive and negative significant responses to increased N deposition, but there was no consistent pattern among them in the variables that they responded to: each species responded differently. Thus it does suggest that there are different evolutionary solutions to the same ecological problem.

The late frost and snow in June in 2005 killed the flowers in 4 of 5 species, causing in a major reduction in berries in 2005 (Fig. 1). However, *Geocaulon* showed the opposite pattern – an increase in berry production in 2005. This difference was not due to later flowering of *Geocaulon* that would have permitted them to escape the frost. In nearby Alaska, flowers are already out by late May (see <http://www.alaskawildflowers.us>). Thus it is likely that their flowers are much more tolerant of freezing and snowfall than those of *Arctostaphylos* or *Empetrum*.

Our results provide evidence of tradeoffs between reproduction and somatic growth in some of these berry-producing understory plants but again the patterns are not consistent among all species, with each often allocating resources differently to these two processes. Ideally to examine this robustly we should have marked each plant and followed its individual performance over time. However our findings are still indicative. Both *A. rubra* and *A. uva-ursi* produced more, bigger berries in 2004 and bigger, heavier leaves in 2005. In contrast, *E. nigrum* produced more, but smaller berries in 2004 (leaf size not measured). *Geocaulon* produced more, but smaller berries in 2005 than 2004, and heavier and slightly smaller leaves in 2004. Finally, *Shepherdia* produced more, bigger berries in 2004 and they had heavier but similar sized leaves in 2005. Our findings build on a long history of similar work, initially compiled by Harper (1977) (see a more recent review by Obeso (2002)) indicating the complexity of these plant tradeoffs. Obeso

found that the literature indicates there was an inverse correlation between vegetative growth and production of fruit and seed, showing that there is an internal allocation shift in resources. The occurrence of the costs of reproduction and hence differential allocation should be more apparent in habitats with low resource availability (Reznick, 1985). The pronounced tradeoffs we observed argues that our boreal forest site indeed has low resource availability and hence that these shrubs cannot simultaneously maximize both reproduction and growth.

Direct fertilization to increase tree growth in the temperate zone of North America does affect understory herbs and shrubs, but the effects appear transient, particularly for 1–2 applications, even in the boreal forest (Lindgren and Sullivan, 2013). For much longer fertilization applications (12–16 years) Thomas et al. (1999) found dramatic declines in understory vegetation, with species affinity for high soil moisture being the best predictor of the fertilization impact. In NW Europe, researchers also report that the impact of fertilization varied as a function of site and endogenous nutrient levels. In Norway, earlier N-fertilization studies reported positive effects on *Vaccinium myrtillus* and *V. vitis-idaea* for both vegetative growth and berry production (Brantseg 1966, as cited in Nilsen, 2001). In Finland, there was no consistent effect on biomass of herbs from nitrogen fertilization, but the two *Vaccinium* spp. declined on fertile sites, but not necessarily on poor sites (Mäkipää, 1994). Nitrogen fertilization had variable and contradictory effects on *Vaccinium* berry crops (reviewed by Saarsalmi and Malkonen, 2001). The decline in berry crops after fertilization on fertile sites may be related to the enhanced growth of grasses and forbs on those specific sites (see Turkington et al., 1998, 2002, 2014 for similar findings in our study sites in the Yukon). However, fertilization apparently had no harmful effects on the nutrient concentrations of the berries, as indicated by several authors in Saarsalmi and Malkonen (2001). However, relative to the NW North American boreal forest, the key thing is that the environmental conditions (mild cold in winter, deep snow depth, etc.) in NW Europe are so much less severe (Boonstra et al., 2016) that the research findings on the impact of fertilization on dwarf shrubs and how they have adapted to their particular environment are unlikely to apply to the boreal forest North American situation (MacColl, 2011).

We think that the effect of anthropogenic nitrogen additions to these North American boreal forests will likely change the community structure of the dominant plants in the understory (Turkington et al., 1998, 2002, 2014) rather than increasing the productivity of the existing the *Arctostaphylos* and *Empetrum* shrubs (Gilliam, 2006). These dwarf shrubs can respond an increase in nitrogen but their adaptive responses appear narrow; in contrast the graminoids and other herbs can respond rapidly and we predict that these shrubs would be rapidly outcompeted. Both *Geocaulon* and *Shepherdia* are likely to fare better, but it will depend on competition for light and space with the graminoids and other herbs. Current anthropogenic atmospheric depositions in boreal western North America are very low ($\sim 0.025\text{--}0.05\text{ g/m}^2$, Dentener et al., 2006) and hence this is unlikely to be the source of change. Direct fertilization to increase tree growth will affect the understory plants, and because of the importance of these to the vertebrate diversity, the negative effects can be expected to cascade upwards.

Author contributions

Kevan Cowcill, Charles Krebs, and Rudy Boonstra conceived the study and designed it; Kevan Cowcill performed all the field work and compilation of the data. Rudy Boonstra and Charles Krebs analyzed the data and generated the graphs and tables. Rudy Boonstra

wrote the manuscript with contributions from Charles Krebs and Kevan Cowcill.

Conflict of interest

The authors declare no conflict of interest. The funding sponsors had no role in the design of the study, the collection, analyses, and interpretation, of the data, or in the decision to publish the results and writing the manuscript.

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