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N_2 fixing alder (*Alnus viridis* spp. *fruticosa*) effects on soil properties across a secondary successional chronosequence in interior Alaska

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Abstract Green alder (*Alnus viridis* ssp. *fruticosa*) is a dominant understory shrub during secondary successional development of upland forests throughout interior Alaska, where it contributes substantially to the nitrogen (N) economy through atmospheric N_2 fixation. Across a replicated 200+ year old vegetation chronosequence, we tested the hypotheses that green alder has strong effects on soil chemical properties, and that ecosystem-level N inputs via N_2 fixation decrease with secondary successional stand development. Across early-, mid-, and late-successional stands, alder created islands of elevated soil N and carbon (C), depleted soil phosphorus (P), and more acidic soils. These effects translated to the stand-level in response to alder stem density. Although neither N_2 fixation nor nodule biomass differed among stand types, increases in alder densities with successional time translated to increasing N inputs. Estimates of annual N inputs by *A. viridis* averaged across the upland chronosequence (6.6 ± 1.2 kg N ha^{-1} $year^{-1}$) are substantially less than inputs during early succession by *Alnus tenuifolia* growing along Alaskan floodplains. However, late-succession upland forests, where densities of *A. viridis* are highest, may persist for centuries, depending on fire return interval. This pattern of prolonged N inputs to late successional forests contradicts established theory predicting declines in N_2-fixation rates and N_2-fixer abundance as stands age.

Keywords Alder · Boreal · Nitrogen cycling · Nitrogen fixation · Secondary succession

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Introduction

The supply of fixed nitrogen (N) to forest ecosystems regulates species composition (Post and Pastor 1996), net primary production (Vitousek and Howarth 1991), rates of succession (Chapin et al. 1994), and landscape evolution (Hu et al. 2001). In addition to direct effects on ecosystem N budgets (Binkley et al. 1992; Helfield and Naiman 2002; Uliassi and Ruess 2002) and productivity (Bormann et al. 1994; Binkley 2003), plants with the capacity to support symbiotic N_2-fixation have strong indirect effects on soil physiochemical characteristics (Rhoades et al. 2001), including soil carbon (C) stocks (Rhoades et al. 1998; Resh et al. 2002) and pathways of N fluxes within ecosystems (Hart et al. 1997; Rhoades et al. 2001). For example, high rates of symbiotic N_2 fixation are often associated with increased rates of nitrification, denitrification (Pastor and Binkley 1998; Kielland et al. 2006), and soil acidification (van

Miegroet and Cole 1984; Binkley and Sollins 1990; Rhoades et al. 2001). N_2-fixing species are also responsible for strong interactions between N and phosphorus (P) cycling, because of the high P requirements of nodule development and growth as well as nitrogenase activity (Wall et al. 2000; Huss-Danell et al. 2002; Vitousek et al. 2002), and the capacity of these species to increase P cycling through elevated soil phosphatase activity (Giardina et al. 1995; Zou et al. 1995). Moreover, rates of N_2 fixation in tropical (Crews et al. 1995; Vitousek and Hobbie 2000; Binkley et al. 2003), temperate (Binkley et al. 1994), and boreal (Uliassi and Ruess 2002) forests are often limited by plant-available soil P.

Rastetter et al. (2001) developed an ecosystem model for temperate forests based on plant resource optimization explaining the general restriction of N_2-fixing vascular plants to early succession. Factors contributing to sustained activity of N_2 fixers in early succession included an open canopy and low soil N levels, while interspecific competition under a closed canopy and the costs of N fixation versus uptake were important factors explaining the loss of N_2-fixing plants from late succession (Vitousek and Howarth 1991; Chapin et al. 1994; Vitousek and Field 1999; Vitousek et al. 2002).

Although *Alnus viridis* ssp. *fruticosa* (hereafter *A. viridis*) is known to influence the N economy of Alaskan boreal forests (Van Cleve et al. 1986; Wurtz 1995; Rhoades et al. 2001; Anderson et al. 2004), no study has quantified N_2-fixation inputs by the species across a complete successional sequence or assessed the magnitude of N inputs to upland white spruce forests where the species is so abundant. Our primary objective was to assess the effects of *A. viridis* on subcanopy and stand-level N, P and C soil parameters across an upland vegetation chronosequence. We sought to test the hypotheses that (1) alder has strong direct and indirect effects on soil chemical properties, and (2) ecosystem-level N inputs by N_2-fixing alder decrease with secondary successional stand development of upland forests within interior Alaska.

Study area

Study stands representing seral stages of upland secondary successional forests were selected within the Bonanza Creek Experimental Forest (BCEF) located ~35 km southwest of Fairbanks, Alaska (64.8°N, 148.0°W). Replicate stands ($n = 3$/stage) of a seral sequence of successional stages are maintained within the BCEF by the Bonanza Creek Long-Term Ecological Research program (BNZ LTER); more detailed information regarding the stages described below can be found on the BNZ LTER webpage (http://www.lter.uaf.edu). We began our investigation in 1997, 14 years after the 1983 Rosie Creek fire burned extensive portions of the BCEF. We believe that alder individuals in this study regenerated from alder rootstocks that survived the fire (Wurtz 2000). At the time of our study, early succession (post-fire) stands were open, rapidly developing deciduous canopies with a dense herbaceous (*Epilobium angustifolium*) and graminoid (*Calamagrostis canadensis*) ground cover surrounding numerous but scattered *A. viridis* and willow (*Salix* spp.) shrubs, with isolated recruitment pockets of white spruce, paper birch (*Betula neoalaskana*) and trembling aspen (*Populus tremuloides*) saplings. Prior to the 1983 fire, these stands were dominated by mature white spruce (basal area ~35 m^2 ha^{-1}) and paper birch (http://www.lter.uaf.edu). In open-canopy post-fire environments, *A. viridis* grows as isolated shrubs with upright densely-clustered stems up to 5 m in height. Mid-succession stands (~60 years old) are dominated by paper birch, white spruce, and trembling aspen with basal areas of 18.5, 7.1, and 0.6 m^2 ha^{-1}, respectively (http://www.lter.uaf.edu). The understory tall shrub community consists of *A. viridis* and willow. Late succession conifer stands (~220 years old) are dominated by white spruce (basal area ~30 m^2 ha^{-1}) (http://www.lter.uaf.edu), with a discontinuous understory of *A. viridis*, and a ground cover of feather mosses (*Hylocomium splendens* and *Pleurozium schreberi*). In mid-and late-succession stands, *A. viridis* is a prominent understory shrub (up to 5 m in height) with a somewhat disorderly arrangement of fewer thicker stems. This growth morphology appears to be a function of the species' ability to both exploit overstory gaps and propagate vegetatively from prostrate stems. Across the successional sequence, soils consist of deep loess deposits with shallow, poorly developed surface horizons and no permafrost, and are classified as Lamellic Haplocryepts according to the US soil classification system (Mulligan 2006). Our replicate stands within each of these seral successional stages

correspond to BNZ LTER designated successional stages UP1, UP2 and UP3, which we will henceforth refer to as *post-fire*, *mid-succession*, and *white spruce* stages, respectively.

Climate in interior Alaska is strongly continental with extremely cold winters and dry warm summers. Air temperature ranges from −50 to +33°C with an annual average of −2.9°C and the frost free growing season averaging ∼145 days. Summer daylight hours are long (up to 21 h per day), and the region receives an average of 289 mm of precipitation annually, 60% of which falls as rain (Viereck et al. 1993).

Methods

Experimental design

We selected three replicate stands within each of the three successional stages described above. All stands were located within 10 km of one another and had slopes ranging from 10° to 30° with a predominantly southerly aspect. Where possible we used previously established and monitored BNZ LTER stands. *A. viridis* and *P. glauca* were largely absent in one steep, south-facing aspen-dominated replicate from the post-fire (UP1C) and mid-succession (UP2C) LTER stand series, where their germination and growth are thought to be limited by wind exposure and soil moisture (Johnstone 2005). These stands most likely represent an alternate successional trajectory, whereby aspen matures, burns and is self replaced without ever the development of a mature white spruce canopy (Cumming et al. 2000; Johnstone 2005; Kurkowski et al. 2008). We therefore substituted these stands with two additional stands where *A. viridis* was present and that closely resembled and were near to the established BNZ LTER stands.

We established three parallel 10 m × 100 m plots with a north-south orientation at each replicate stand. These plots were located close to but not overlapping the areas used for measurement of acetylene reduction activity (ARA) in 1997 and 1998 (Mitchell 2006; Mitchell and Ruess 2009). These plots were visited in September 1999 to collect soil cores for determination of nodule biomass (Mitchell and Ruess 2009) and soil chemical characteristics, and again in autumn of 2000 to record alder density and canopy cover.

Soil physical and chemical parameters

In September of 1999 we collected soil cores to identify stage, replicate stand, canopy, and soil horizon patterns of soil physical and chemical parameters. A pair of cores (5 cm in diameter by 20 cm in length) was collected for each of five haphazardly selected *A. viridis* individuals within each study plot. Soil core pairs included one core taken beneath the alder canopy within 2 m of the alder base, and a second core taken from interspace soils ∼2 m beyond the alder canopy perimeter. Soil cores were transported to the laboratory and frozen intact. Once thawed, the thickness of each horizon was measured, and the core was separated by horizon. The forest floor organic (O) horizon was comprised of Oi, Oe, and Oa horizons. Mineral A and C horizons were defined by the color of field moist soils (Munsell Color Company 1992). Where a distinct C horizon was absent the entire mineral soil was referred to as the A horizon. Mineral soil samples were sieved through a 2 mm mesh to remove coarse fragments. Each soil sample (soil core horizon) was oven-dried at 60°C for 96 h, weighed for calculation of bulk density and analyzed for chemical characterization. Samples were analyzed for total N and C concentrations using a LECO CNS 2000 autoanalyzer (LECO, St Joseph, MI, USA), and total soil P was determined colorometrically following perchloric acid digests using a modified Technicon autoanalyzer (Whitledge et al. 1981). Soil pH was determined on a 1:2 (v/v) soil:water suspension (Table 1).

Nodule biomass and N inputs

At each of the nine stands we selected a total of 70 *A. viridis* shrubs over an area of ∼2.5 ha. During each of seven sampling periods over the 1997 and 1998 growing seasons, we randomly selected 10 of the 70 *A. viridis* shrubs from each replicate stand for measurement of N_2 fixation (acetylene reductase activity), foliar morphology and chemistry, as well as concurrent soil temperature. Seasonal patterns and climate controls over N_2 fixation rates are presented Mitchell and Ruess (2009).

Nodule biomass was sampled in September 1999. At each stand, one soil core (15 cm diameter × 20 cm deep) was removed from beneath the canopy (within 1.5 m of the central ramet) of two

Table 1 Soil physical characteristics (to a depth of 20 cm) for upland forest stages within the Bonanza Creek Experimental Forest

Parameter	Post-fire	Mid-succession	White spruce
Organic BD (g cm^{-3})	0.16 ± 0.02	0.12 ± 0.02	0.16 ± 0.01
Mineral BD (g cm^{-3})	0.90 ± 0.02	0.79 ± 0.02	0.84 ± 0.02
Organic (kg m^{-2})	9.97 ± 0.99	7.94 ± 0.66	11.03 ± 0.66
Mineral (kg m^{-2})	122.2 ± 4.8	101.2 ± 4.0	106.8 ± 4.0

Organic soils are combined Oi, Oe, and Oa horizons. Mineral soils are combined A and C mineral horizons. *BD* bulk density. Values are means ± 1 SE ($N = 34$)

alder individuals, transported to the laboratory, and frozen. Thawed cores were washed clean of soil to isolate roots and nodules, and then sorted to separate nodules from roots. Nodule samples were oven-dried at 60°C for 48 h and then weighed to the nearest 0.1 mg. In the autumn of 2000 we revisited the study plots to record alder plant density, the number of stems per plant, and the diameter of each alder stem ≥1 cm diameter at a height 1 m above the soil surface. To estimate annual N inputs from N_2 fixation, we first fit a spline interpolation function to seasonal patterns of ARA for each stand, taken from Mitchell and Ruess (2009), in order to estimate daily input values, setting ARA values at zero for 21 May and 1 October. We then used the C_2H_2 to N_2 reduction ratio of 2:1 determined by Anderson et al. (2004) for *A. viridis*, and assumed that our measurements of ARA were representative of rates throughout each 24-h period. Total annual N inputs for each replicate stand (kg N ha^{-1} $year^{-1}$) were then obtained by multiplying N inputs per unit nodule biomass times nodule biomass per unit area.

Statistical analyses

SAS 9.1 (SAS Institute 2001) was used for all statistical analyses. Treatment effects (successional stage and canopy location) on soil parameters were analyzed using ANOVA (PROC GLM) with soil cores nested within stands, and stands as the level of replication. Any significant effects from general linear models were subsequently examined with a Tukey's HSD test.

Data were tested for normality using PROC UNIVARIATE, and transformed where necessary to meet statistical assumptions (Zar 1998). Significance for all tests was set at $P < 0.05$; however, we noted "marginally significant" values ($P < 0.10$) which we believed to be of ecological significance. Unless otherwise stated, values throughout the text are untransformed data and represent means ± 1 SE.

Results

Soil properties

Soil N of the top 20 cm was lowest in the mid-succession, and did not differ significantly between post-fire and late-succession white spruce stages ($P < 0.05$) (Fig. 1; Table 2). Soil C content did not differ between post-fire and mid-succession stands but was higher in white spruce stands ($P < 0.001$) (Fig. 1). Soil C:N ratio was lowest in the post-fire stage compared to mid-succession and white spruce stages, which did not differ. Total soil P content of the top 20 cm declined significantly with transition from post-fire to mid-succession and white spruce stages ($P < 0.0001$) (Fig. 2; Table 2). Soil pH ranged from 5.0 to 5.8 across successional stages and soil horizons (Table 2).

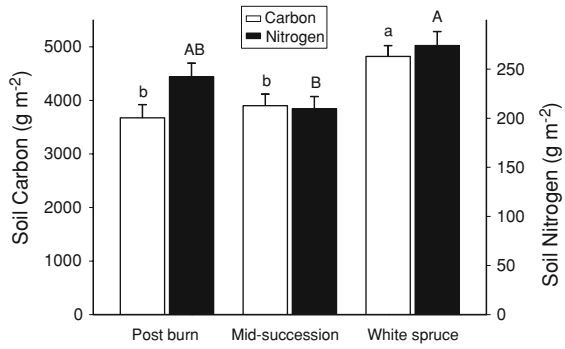

Fig. 1 Total soil nitrogen and carbon content (to 20 cm soil depth) in upland forest stages within the Bonanza Creek Experimental Forest. *Letters* indicate differences between stages at $P < 0.05$. Values are means ± 1 SE ($N = 34$)

Table 2 Soil chemical characteristics for upland forest stages within the Bonanza Creek Experimental Forest

Parameter	Post-fire	Mid-succession	White spruce	ANOVA
Carbon				
Total (g m^{-2})	**3674 ± 246**^{b}	**3901 ± 217**^{b}	**4820 ± 203**^{a}	$F_{2,90} = 7.88$, $P < 0.005$
O (g m^{-2})	**1842 ± 189**^{b}	**1938 ± 156**^{b}	**2563 ± 154**^{a}	$F_{2,90} = 5.92$, $P < 0.005$
A (g m^{-2})	1114 ± 90^{a}	911 ± 94^{a}	1153 ± 119^{a}	$F_{2,90} = 1.61$, $P = 0.21$
C (g m^{-2})	974 ± 82^{a}	1052 ± 82^{a}	1185 ± 120^{a}	$F_{2,79} = 2.07$, $P = 0.13$
O (%)	**19.56 ± 1.49**^{b}	**24.69 ± 0.97**^{a}	**25.17 ± 1.33**^{a}	$F_{2,90} = 7.21$ $P < 0.005$
A (%)	**2.55 ± 0.32**^{b}	**3.81 ± 0.37**^{ab}	**3.90 ± 0.37**^{a}	$F_{2,90} = 5.38$, $P < 0.05$
C (%)	**1.25 ± 0.09**^{a}	**1.42 ± 0.10**^{a}	**1.57 ± 0.18**^{a}	$F_{2,79} = 3.40$, $P < 0.05$
Nitrogen				
Total (g m^{-2})	**242 ± 13**^{ab}	**209 ± 12**^{b}	**274 ± 14**^{a}	$F_{2,90} = 4.54$, $P < 0.05$
O (g m^{-2})	94.0 ± 10.0^{a}	90 ± 7^{a}	117 ± 7^{a}	$F_{2,90} = 2.90$, $P < 0.10$
A (g m^{-2})	**89 ± 10**^{a}	**51 ± 4**^{b}	**83 ± 13**^{ab}	$F_{2,90} = 3.76$, $P < 0.05$
C (g m^{-2})	79 ± 8^{a}	68 ± 5^{a}	79 ± 7^{a}	$F_{2,79} = 1.10$, $P = 0.34$
O (%)	1.00 ± 0.07^{a}	1.14 ± 0.05^{a}	1.14 ± 0.06^{a}	$F_{2,90} = 2.18$, $P = 0.12$
A (%)	**0.17 ± 0.01**^{b}	**0.22 ± 0.02**^{ab}	**0.27 ± 0.03**^{a}	$F_{2,90} = 5.08$, $P < 0.05$
C (%)	0.10 ± 0.01^{a}	0.09 ± 0.01^{a}	0.11 ± 0.01^{a}	$F_{2,79} = 0.96$, $P = 0.40$
Phosphorus				
Total (g m^{-2})	**79 ± 2**^{a}	**54 ± 3**^{b}	**44 ± 3**^{c}	$F_{2,90} = 46.54$, $P < 0.0001$
O (g m^{-2})	9 ± 0^{a}	7 ± 0^{a}	8 ± 0^{a}	$F_{2,90} = 1.58$, $P = 0.21$
A (g m^{-2})	**34 ± 3**^{a}	**14 ± 1**^{b}	**14 ± 2**^{b}	$F_{2,90} = 23.38$, $P < 0.0001$
C (g m^{-2})	**47 ± 3**^{a}	**32 ± 2**^{b}	**23 ± 2**^{c}	$F_{2,79} = 27.28$, $P < 0.0001$
O (%)	**0.10 ± 0.00**^{a}	**0.09 ± 0.00**^{ab}	**0.08 ± 0.01**^{b}	$F_{2,90} = 5.78$, $P < 0.005$
A (%)	**0.06 ± 0.00**^{a}	**0.06 ± 0.00**^{a}	**0.04 ± 0.00**^{b}	$F_{2,90} = 10.63$, $P < 0.0001$
C (%)	**0.06 ± 0.00**^{a}	**0.04 ± 0.00**^{b}	**0.03 ± 0.00**^{c}	$F_{2,79} = 30.17$, $P < 0.0001$
Soil CN				
Total	**15.23 ± 0.55**^{b}	**19.06 ± 0.79**^{a}	**18.29 ± 0.73**^{a}	$F_{2,9} = 11.23$, $P < 0.0001$
O	**19.63 ± 0.68**^{b}	**22.10 ± 0.83**^{a}	**22.22 ± 0.64**^{a}	$F_{2,90} = 5.65$, $P < 0.005$
A	**14.10 ± 0.83**^{b}	**18.56 ± 1.50**^{a}	**16.28 ± 1.01**^{ab}	$F_{2,90} = 3.92$, $P < 0.05$
C	**12.77 ± 0.59**^{b}	**16.84 ± 1.32**^{a}	**15.35 ± 1.02**^{ab}	$F_{2,90} = 3.38$, $P < 0.05$
pH				
O	5.75 ± 0.09^{a}	5.68 ± 0.05^{a}	5.59 ± 0.10^{a}	$F_{2,90} = 1.70$, $P = 0.19$
A	5.12 ± 0.08^{a}	4.98 ± 0.07^{a}	5.12 ± 0.09^{a}	$F_{2,90} = 1.10$, $P = 0.34$
C	**5.08 ± 0.05**^{b}	**5.33 ± 0.08**^{a}	**5.15 ± 0.06**^{b}	$F_{2,90} = 4.34$, $P < 0.05$

Organic soils are combined Oi, Oe, and Oa horizons. Mineral soils are combined A and C mineral horizons to a depth of 20 cm. *BD* bulk density. Numbers within rows followed by different superscript letters are significantly different at $P < 0.05$. Significant ANOVAs are in bold font. Values are means ± 1 SE ($N = 34$)

Alder stem density and canopy effects on soil properties

Alnus viridis shrub density increased over successional time, averaging 90.0 ± 9.9, 178.9 ± 30.1 and 290.0 ± 62.3 shrubs ha^{-1} for post-fire, mid-succession and white spruce stages, respectively ($P < 0.0001$) (Table 3). However, because of variation in alder stem numbers per plant among stages, stem density was highest in white spruce stands (3630 ± 720 stems ha^{-1}), intermediate in post-fire (1806 ± 176 stems ha^{-1}) and least in mid-succession stands (898 ± 163 stems ha^{-1}) ($P < 0.0001$).

O horizon mass under alder canopies did not differ from non-canopy soils (Table 4). Only in white spruce stands did subcanopy soils have lower O

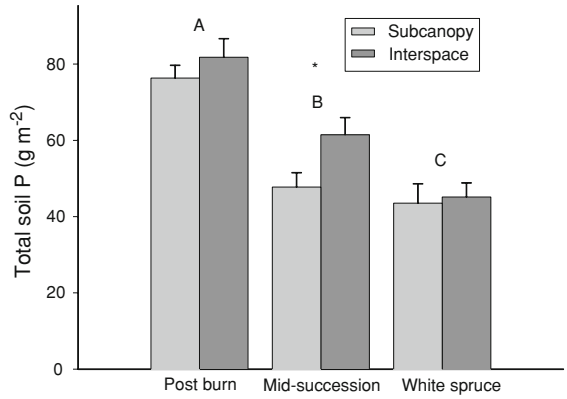

Fig. 2 Total phosphorus content (to 20 cm soil depth) of alder subcanopy and interspace soils in upland forest stages within the Bonanza Creek Experimental Forest. The *letters* indicate differences between stages and * indicate differences between soils under alder canopies compared to interspace soils at $P < 0.05$. Values are means ± 1 SE (N = 17)

horizon mass ($P < 0.05$) (Table 5) with lower bulk density ($P < 0.05$). Alder stem density was positively correlated with O horizon mass (g m^{-2}) across stages ($r^2 = 0.49$, $P < 0.0001$), within white spruce stands ($r^2 = 0.77$, $P < 0.05$), and marginally within post-fire stands ($r^2 = 0.35$, $P < 0.10$).

Carbon concentration of subcanopy O horizon soils was elevated relative to non-canopy soils when averaged across all stages ($P < 0.05$) (Table 4) and marginally in post-fire stands ($P < 0.10$) (Table 5). However, these values did not necessarily translate to higher subcanopy O horizon C content. Alder stem density related positively to O horizon ($r^2 = 0.37$, $P < 0.005$) (Fig. 3a) and total soil C content (g m^{-2}) ($r^2 = 0.22$, $P < 0.05$) (Fig. 3b) across all stages. These relationships between stem density and organic and total soil C content were also evident across post-fire stands ($r^2 = 0.69$, $P < 0.05$, and $r^2 = 0.39$, $P < 0.10$, respectively). Alder stem density in mid-succession stands was positively correlated only with mineral soil %C ($r^2 = 0.54$, $P < 0.05$). In white spruce stands, alder stem density was inversely correlated with organic soil %C ($r = -0.73$, $P < 0.05$).

When averaged across all stands and successional stages, %N of organic soil under alder canopies was significantly greater than in interspace soils ($P < 0.05$) (Table 4), but this difference was driven principally by a strong effect in white spruce stands ($P < 0.005$) (Table 5). Subcanopy depletion of soil N content was detected in mid-succession stands, where A horizon N content (g m^{-2}) was 28% lower under alder canopies compared with interspace soils ($P < 0.10$) (Table 5). Alder canopies did not affect soil C:N ratios across successional stages nor among post-fire or mid-succession stands; only in white spruce stands was an alder canopy associated with islands of reduced O horizon C:N ratio ($P < 0.05$) (Table 5).

Alder stem density related positively to O horizon ($r^2 = 0.35$, $P < 0.005$) (Fig. 3c) and total soil ($r^2 = 0.20$, $P < 0.05$) N content (g m^{-2}) across all stands. Within successional stages, these relationships were most evident in post-fire stands ($r^2 = 0.72$, $P < 0.005$ and $r^2 = 0.35$, $P < 0.10$, respectively). In mid-succession stands, alder stem density correlated positively with stand-level O horizon ($r^2 = 0.37$, $P < 0.10$) and A horizon ($r^2 = 0.45$, $P < 0.05$) %N. In contrast, alder stem density in white spruce stands was inversely correlated with %N of O horizon ($r = -0.89$, $P < 0.005$) and A horizon ($r = -0.86$, $P < 0.05$) soils, as well as with C horizon N content ($r = -0.66$, $P < 0.10$) but related positively to organic soil N content ($r^2 = 0.49$, $P = 0.05$).

Across successional stages, alder created islands of acidified C horizon soils ($P < 0.05$); the same effect was marginally evident in A horizon soils ($P < 0.10$) (Table 4). Patterns were most apparent in post-fire

Table 3 Selected vegetation parameters of *A. viridis* in upland forest stages within the Bonanza Creek Experimental Forest

Parameter	Post-fire	Mid-succession	White spruce	ANOVA
Stems $shrub^{-1}$	**21.1 ± 2.2**^{a}	**5.1 ± 0.4**^{c}	**13.1 ± 1.3**^{b}	$\boldsymbol{F_{2,26} = 29.29, P < 0.0001}$
Shrubs ha^{-1}	**90.00 ± 9.86**^{c}	**178.89 ± 30.07**^{b}	**290.00 ± 62.32**^{a}	$\boldsymbol{F_{2,26} = 20.08, P < 0.0001}$
Stems ha^{-1}	**1806 ± 175**^{b}	**898 ± 163**^{c}	**3630 ± 720**^{a}	$\boldsymbol{F_{2,26} = 31.34, P < 0.0001}$
Alder canopy cover (m^2 ha^{-1})	1725 ± 322^{a}	3001 ± 723^{a}	5058 ± 1981^{a}	$F_{2,8} = 1.86$, $P = 0.23$

Numbers within rows followed by different superscript letters are significantly different at $P < 0.05$. Significant ANOVAs are in bold font. Values for alder density measures are means ± 1 SE ($N = 9$). Values for alder canopy area are means ± 1 SE ($N = 3$)

Table 4 Soil chemical characteristics under *A. viridis* canopies compared to interspace averaged across three upland forest successional stages within the Bonanza Creek Experimental Forest

Parameter	Sub-canopy	Interspace	ANOVA
Organic soil			
Mass (g m^{-2})	9250 ± 639[a]	10014 ± 698[a]	$F_{1,96} = 1.51$, $P = 0.22$
Thickness (cm)	7.09 ± 0.34[a]	6.58 ± 0.30[a]	$F_{1,94} = 0.74$, $P = 0.39$
Carbon			
Total (g m^{-2})	4220 ± 195[a]	3992 ± 198[a]	$F_{1,90} = 1.07$, $P = 0.30$
O (g m^{-2})	2191 ± 155[a]	2007 ± 135[a]	$F_{1,90} = 1.04$, $P = 0.31$
A (g m^{-2})	1117 ± 91[a]	1005 ± 74[a]	$F_{1,90} = 0.66$, $P = 0.42$
C (g m^{-2})	1022 ± 66[a]	1122 ± 89[a]	$F_{1,79} = 0.36$, $P = 0.55$
O (%)	**24.40 ± 1.03**[a]	**21.56 ± 1.18**[b]	$\boldsymbol{F_{1,90} = 5.04}$, $\boldsymbol{P < 0.05}$
A (%)	3.40 ± 0.28[a]	3.35 ± 0.32[a]	$F_{1,90} = 0.11$, $P = 0.74$
C (%)	1.41 ± 0.08[a]	1.42 ± 0.13[a]	$F_{1,73} = 0.04$, $P = 0.85$
Nitrogen			
Total (g m^{-2})	246 ± 11[a]	237 ± 11[a]	$F_{1,90} = 0.24$, $P = 0.62$
O (g m^{-2})	105 ± 8[a]	95 ± 6[a]	$F_{1,90} = 1.15$, $P = 0.29$
A (g m^{-2})	75 ± 7[a]	74 ± 9[a]	$F_{1,90} = 0.01$, $P = 0.92$
C (g m^{-2})	73 ± 4[a]	77 ± 6[a]	$F_{1,79} = 0.31$, $P = 0.58$
O (%)	**1.16 ± 0.05**[a]	**1.02 ± 0.05**[b]	$\boldsymbol{F_{1,90} = 6.56}$, $\boldsymbol{P < 0.05}$
A (%)	0.22 ± 0.02[a]	0.21 ± 0.02[a]	$F_{1,90} = 0.15$, $P = 0.70$
C (%)	0.10 ± 0.01[a]	0.10 ± 0.01[a]	$F_{1,79} = 0.24$, $P = 0.62$
Phosphorus			
Total (g m^{-2})	**57 ± 3**[a]	**63 ± 3**[b]	$\boldsymbol{F_{1,90} = 4.96}$, $\boldsymbol{P < 0.05}$
O (g m^{-2})	7 ± 0[a]	8 ± 0[a]	$F_{1,90} = 1.70$, $P = 0.20$
A (g m^{-2})	22 ± 2[a]	21 ± 2[a]	$F_{1,90} = 0.00$, $P = 0.95$
C (g m^{-2})	**30 ± 2**[a]	**37 ± 2**[b]	$\boldsymbol{F_{1,79} = 5.79}$, $\boldsymbol{P < 0.05}$
O (%)	0.09 ± 0.00[a]	0.09 ± 0.00[a]	$F_{1,90} = 0.95$, $P = 0.33$
A (%)	0.05 ± 0.00[a]	0.06 ± 0.00[a]	$F_{1,90} = 0.36$, $P = 0.55$
C (%)	0.04 ± 0.00[a]	0.05 ± 0.00[a]	$F_{1,79} = 1.38$, $P = 0.24$
pH			
O	5.60 ± 0.06[a]	5.75 ± 0.08[a]	$F_{1,90} = 2.45$, $P = 0.12$
A	4.99 ± 0.06[a]	5.16 ± 0.07[a]	$F_{1,90} = 3.38$, $P < 0.10$
C	**5.11 ± 0.06**[a]	**5.28 ± 0.06**[b]	$\boldsymbol{F_{1,79} = 6.72}$, $\boldsymbol{P < 0.05}$

Total = combined soil horizons to 20 cm, O = organic horizon, A = A mineral horizon, C = C mineral horizon. Numbers within rows followed by different superscript letters are significantly different at $P < 0.05$. Significant ANOVAs are in bold font. Values are means ± 1 SE ($N = 50$)

stands, where alder acidified O ($P < 0.05$), A ($P > 0.05$) and C ($P < 0.05$) horizon sub-canopy soils (Table 5). Across all stages, greater alder stem density was associated with lower C horizon pH ($r = -0.41$, $P < 0.05$). This relationship was most apparent within the mid-succession stage, where alder stem density was associated with lower soil pH in both the O ($r = -0.67$, $P < 0.05$) and C ($r = -0.60$, $P < 0.10$) horizons, and was also evident in white spruce stands but only for A horizon soils ($r = -0.65$, $P < 0.01$).

Across all stands, total soil P content ($P < 0.05$) and C horizon P content ($P < 0.05$) were lower under alder canopies than for interspace soils (Table 4). This effect was greatest in mid-succession where alder created islands of depleted total ($P < 0.10$) (Fig. 2; Table 5) and C horizon ($P < 0.05$) soil P content (g m^{-2}) (Table 5). Alder presence in white spruce

Table 5 Soil chemical characteristics under *A. viridis* canopies compared to interspace soils for post-fire, mid-succession and white spruce upland forest stages within Bonanza Creek Experimental Forest

Forest stage	Parameter	Subcanopy	Interspace	ANOVA
Post-fire	Organic soil			
	Mass (g m^{-2})	10143 ± 1487[a]	9787 ± 1348[a]	$F_{1,33} = 0.38$, $P = 0.54$
	Thickness (cm)	6.50 ± 0.59[a]	6.09 ± 0.44[a]	$F_{1,33} = 0.03$, $P = 0.85$
	Carbon			
	Total (g m^{-2})	4000 ± 401[a]	3347 ± 275[a]	$F_{1,33} = 1.90$, $P = 0.18$
	O (g m^{-2})	2126 ± 303[a]	1558 ± 215[a]	$F_{1,33} = 2.39$, $P = 0.13$
	A (g m^{-2})	1233 ± 134[a]	996 ± 119[a]	$F_{1,33} = 1.75$, $P = 0.20$
	C (g m^{-2})	907 ± 121[a]	1036 ± 114[a]	$F_{1,24} = 0.40$, $P = 0.53$
	O (%)	21.85 ± 2.00[a]	17.27 ± 2.14[a]	$F_{1,33} = 3.31$, $P < 0.10$
	A (%)	2.59 ± 0.47[a]	2.52 ± 0.47[a]	$F_{1,33} = 0.90$, $P = 0.90$
	C (%)	1.26 ± 0.15[a]	1.24 ± 0.11[a]	$F_{1,24} = 0.82$, $P = 0.45$
	Nitrogen			
	Total (g m^{-2})	258 ± 21[a]	225 ± 16[a]	$F_{1,33} = 1.40$, $P = 0.25$
	O (g m^{-2})	106 ± 17[a]	82 ± 10[a]	$F_{1,33} = 1.52$, $P = 0.23$
	A (g m^{-2})	102 ± 15[a]	76 ± 12[a]	$F_{1,33} = 1.65$, $P = 0.21$
	C (g m^{-2})	71 ± 9[a]	86 ± 13[a]	$F_{1,24} = 0.62$, $P = 0.44$
	O (%)	1.08 ± 0.10[a]	0.93 ± 0.10[a]	$F_{1,33} = 1.79$, $P = 0.19$
	A (%)	0.18 ± 0.02[a]	0.16 ± 0.02[a]	$F_{1,33} = 0.48$, $P = 0.49$
	C (%)	0.10 ± 0.01[a]	0.10 ± 0.01[a]	$F_{1,24} = 0.03$, $P = 0.87$
	Phosphorus			
	Total (g m^{-2})	76.0 ± 3.0[a]	81.0 ± 4.0[a]	$F_{1,33} = 0.88$, $P = 0.35$
	O (g m^{-2})	8.00 ± 0.0[a]	9.00 ± 1.0[a]	$F_{1,33} = 0.32$, $P = 0.58$
	A (g m^{-2})	36.0 ± 5.0[a]	32.0 ± 5.0[a]	$F_{1,33} = 0.27$, $P = 0.61$
	C (g m^{-2})	44.0 ± 4.0[a]	51.0 ± 5.0[a]	$F_{1,24} = 1.06$, $P = 0.45$
	O (%)	0.09 ± 0.00[a]	0.10 ± 0.00[a]	$F_{1,33} = 2.10$, $P = 0.16$
	A (%)	0.06 ± 0.00[a]	0.07 ± 0.00[a]	$F_{1,33} = 0.69$, $P = 0.41$
	C (%)	0.06 ± 0.00[a]	0.06 ± 0.01[a]	$F_{1,24} = 0.01$, $P = 0.91$
	C:N			
	Total	15.51 ± 0.85[a]	14.96 ± 0.73[a]	$F_{1,33} = 0.24$, $P = 0.63$
	O	20.70 ± 0.97[a]	18.55 ± 0.90[a]	$F_{1,33} = 2.63$, $P = 0.12$
	A	13.56 ± 1.13[a]	14.64 ± 1.24[a]	$F_{1,33} = 0.80$, $P = 0.38$
	C	12.73 ± 0.86[a]	12.81 ± 0.84[a]	$F_{1,24} = 0.00$, $P = 0.98$
	pH			
	O	**5.58 ± 0.10**[b]	**5.92 ± 0.15**[a]	$\boldsymbol{F_{1,33} = 5.09}$, $\boldsymbol{P < 0.05}$
	A	**4.95 ± 0.05**[b]	**5.30 ± 0.14**[a]	$\boldsymbol{F_{1,33} = 6.98}$, $\boldsymbol{P < 0.05}$
	C	**5.00 ± 0.05**[b]	**5.18 ± 0.09**[a]	$\boldsymbol{F_{1,24} = 4.82}$, $\boldsymbol{P < 0.05}$
Mid-succession	Organic soil			
	Mass (g m^{-2})	7692 ± 797[a]	8183 ± 1065[a]	$F_{1,33} = 0.26$, $P = 0.61$
	Thickness (cm)	7.21 ± 0.67[a]	6.76 ± 0.53[a]	$F_{1,33} = 0.13$, $P = 0.72$
	Carbon			
	Total (g m^{-2})	3890 ± 293[a]	3912 ± 330[a]	$F_{1,29} = 0.00$, $P = 0.96$
	O (g m^{-2})	1928 ± 249[a]	1947 ± 199[a]	$F_{1,29} = 0.00$, $P = 0.95$
	A (g m^{-2})	848 ± 116[a]	973 ± 152[a]	$F_{1,29} = 0.42$, $P = 0.52$

Table 5 continued

Forest stage	Parameter	Subcanopy	Interspace	ANOVA
	C (g m^{-2})	1113 ± 115[a]	991 ± 119[a]	$F_{1,29} = 0.65$, $P = 0.43$
	O (%)	25.06 ± 1.26[a]	24.33 ± 1.50[a]	$F_{1,29} = 0.15$, $P = 0.70$
	A (%)	3.86 ± 0.45[a]	3.76 ± 0.60[a]	$F_{1,29} = 0.02$, $P = 0.88$
	C (%)	1.54 ± 0.14[a]	1.29 ± 0.15[a]	$F_{1,29} = 2.00$, $P = 0.17$
	Nitrogen			
	Total (g m^{-2})	203 ± 16[a]	215 ± 18[a]	$F_{1,29} = 0.32$, $P = 0.58$
	O (g m^{-2})	88 ± 12[a]	91 ± 10[a]	$F_{1,29} = 0.06$, $P = 0.80$
	A (g m^{-2})	43 ± 4[a]	59 ± 8[a]	$F_{1,29} = 3.09$, $P < 0.10$
	C (g m^{-2})	72 ± 8[a]	64 ± 8[a]	$F_{1,29} = 0.57$, $P = 0.46$
	O (%)	1.15 ± 0.06[a]	1.14 ± 0.08[a]	$F_{1,29} = 0.01$, $P = 0.92$
	A (%)	0.22 ± 0.04[a]	0.22 ± 0.03[a]	$F_{1,29} = 0.02$, $P = 0.90$
	C (%)	0.10 ± 0.01[a]	0.08 ± 0.01[a]	$F_{1,29} = 1.37$, $P = 0.25$
	Phosphorus			
	Total (g m^{-2})	**47 ± 3**[b]	**61 ± 4**[a]	$\boldsymbol{F_{1,29} = 5.82}$, $\boldsymbol{P < 0.05}$
	O (g m^{-2})	6 ± 0[a]	8 ± 1[a]	$F_{1,29} = 1.55$, $P = 0.22$
	A (g m^{-2})	12 ± 2[a]	16 ± 1[a]	$F_{1,29} = 1.54$, $P = 0.23$
	C (g m^{-2})	**28 ± 2**[b]	**37 ± 3**[a]	$\boldsymbol{F_{1,29} = 4.93}$, $\boldsymbol{P < 0.05}$
	O (%)	0.09 ± 0.00[a]	0.10 ± 0.00[a]	$F_{1,29} = 2.48$, $P = 0.13$
	A (%)	0.05 ± 0.01[a]	0.06 ± 0.01[a]	$F_{1,29} = 0.63$, $P = 0.44$
	C (%)	0.04 ± 0.00[a]	0.05 ± 0.00[a]	$F_{1,29} = 0.18$, $P = 1.93$
	C:N			
	Total	19.8 ± 1.45[a]	18.31 ± 0.63[a]	$F_{1,29} = 1.04$, $P = 0.32$
	O	22.28 ± 1.26[a]	21.89 ± 1.14[a]	$F_{1,29} = 0.08$, $P = 0.78$
	A	20.76 ± 2.74[a]	16.35 ± 1.10[a]	$F_{1,29} = 2.23$, $P = 0.15$
	C	17.18 ± 2.2[a]	16.51 ± 1.54[a]	$F_{1,29} = 0.06$, $P = 0.80$
	pH			
	O	5.67 ± 0.06[a]	5.68 ± 0.09[a]	$F_{1,29} = 0.01$, $P = 0.90$
	A	4.92 ± 0.09[a]	5.04 ± 0.11[a]	$F_{1,29} = 0.72$, $P = 0.40$
	C	5.23 ± 0.12[a]	5.44 ± 0.11[a]	$F_{1,29} = 2.12$, $P = 0.16$
White spruce	Organic soil			
	Mass (g m^{-2})	**9899 ± 718**[b]	**12087 ± 1034**[a]	$\boldsymbol{F_{1,28} = 4.75}$, $\boldsymbol{P < 0.05}$
	Thickness (cm)	7.63 ± 0.43[a]	6.91 ± 0.57[a]	$F_{1,28} = 1.24$, $P = 0.28$
	Carbon			
	Total (g m^{-2})	4842 ± 223[a]	4801 ± 340[a]	$F_{1,26} = 0.06$, $P = 0.81$
	O (g m^{-2})	2550 ± 222[a]	2575 ± 222[a]	$F_{1,26} = 0.00$, $P = 0.98$
	A (g m^{-2})	1266 ± 209[a]	1048 ± 126[a]	$F_{1,26} = 0.50$, $P = 0.49$
	C (g m^{-2})	1024 ± 111[a]	1358 ± 213[a]	$F_{1,24} = 1.42$, $P = 0.25$
	O (%)	26.79 ± 1.77[a]	23.67 ± 1.95[a]	$F_{1,26} = 2.14$, $P = 0.16$
	A (%)	3.92 ± 0.49[a]	3.89 ± 0.57[a]	$F_{1,26} = 0.08$, $P = 0.77$
	C (%)	1.41 ± 0.11[a]	1.75 ± 0.35[a]	$F_{1,24} = 0.42$, $P = 0.52$
	Nitrogen			
	Total (g m^{-2})	277 ± 14[a]	271 ± 24[a]	$F_{1,26} = 0.00$, $P = 0.96$
	O (g m^{-2})	122 ± 10[a]	112 ± 10[a]	$F_{1,26} = 0.44$, $P = 0.52$
	A (g m^{-2})	78 ± 10[a]	87 ± 23[a]	$F_{1,26} = 0.39$, $P = 0.54$

Table 5 continued

Forest stage	Parameter	Subcanopy	Interspace	ANOVA
	C (g m^{-2})	76 ± 6[a]	82 ± 12[a]	$F_{1,24} = 0.73$, $P = 0.40$
	O (%)	**1.28 ± 0.07**[a]	**1.01 ± 0.07**[b]	$\boldsymbol{F_{1,26} = 9.80}$, $\boldsymbol{P < 0.005}$
	A (%)	0.27 ± 0.03[a]	0.27 ± 0.04[a]	$F_{1,26} = 0.00$, $P = 0.96$
	C (%)	0.11 ± 0.01[a]	0.10 ± 0.02[a]	$F_{1,24} = 0.01$, $P = 0.92$
	Phosphorus			
	Total (g m^{-2})	43 ± 5[a]	45 ± 3[a]	$F_{1,26} = 0.12$, $P = 0.73$
	O (g m^{-2})	7 ± 0[a]	8 ± 0[a]	$F_{1,26} = 0.24$, $P = 0.63$
	A (g m^{-2})	14 ± 3[a]	14 ± 2[a]	$F_{1,26} = 0.18$, $P = 0.68$
	C (g m^{-2})	20 ± 2[a]	25 ± 3[a]	$F_{1,24} = 3.21$, $P < 0.10$
	O (%)	0.08 ± 0.01[a]	0.08 ± 0.01[a]	$F_{1,26} = 1.73$, $P = 0.20$
	A (%)	0.04 ± 0.00[a]	0.04 ± 0.00[a]	$F_{1,26} = 0.78$, $P = 0.39$
	C (%)	0.03 ± 0.00[a]	0.03 ± 0.00[a]	$F_{1,24} = 0.31$, $P = 0.59$
	C:N			
	Total	17.80 ± 0.76[a]	18.76 ± 1.24[a]	$F_{1,26} = 0.12$, $P = 0.73$
	O	**20.86 ± 0.54**[b]	**23.49 ± 1.03**[a]	$\boldsymbol{F_{1,26} = 5.04}$, $\boldsymbol{P < 0.05}$
	A	16.31 ± 1.54[a]	16.25 ± 1.38[a]	$F_{1,26} = 0.02$, $P = 0.90$
	C	14.15 ± 1.23[a]	16.64 ± 1.59[a]	$F_{1,24} = 0.38$, $P = 0.54$
	pH			
	O	5.54 ± 0.13[a]	5.64 ± 0.15[a]	$F_{1,26} = 0.02$, $P = 0.89$
	A	5.12 ± 0.15[a]	5.12 ± 0.10[a]	$F_{1,26} = 0.17$, $P = 0.69$
	C	5.10 ± 0.08[a]	5.21 ± 0.08[a]	$F_{1,24} = 1.80$, $P = 0.19$

Total = combined soil horizons to 20 cm, O = organic horizon, A = A mineral horizon, C = C mineral horizon, C:N = total soil carbon to nitrogen ratio. Numbers within rows followed by different superscript letters are significantly different at $P < 0.05$. Significant ANOVAs are in bold font. Values are means ± 1 SE (N = 17)

stands was also associated with a marginally significant depletion of C horizon P content ($P < 0.10$) (Table 5).

Nodule biomass and N inputs

Nodule biomass was more variable within than among successional stages, averaging 0.65 ± 0.24, 0.60 ± 0.13, 0.77 ± 0.25 g nodule dry weight per soil core beneath alder shrubs from post-fire, mid-succession, and white spruce stages, respectively. Thus, for calculations of stand-level N inputs, we used a single average value for nodule biomass per core for all replicate stands within a given successional stage, and assumed nodule biomass was distributed evenly beneath the alder canopy. Stand-level nodule biomass was the product of nodule biomass per canopy, canopy area per shrub, and shrub density for a given replicate stand (Table 3). Because nodule biomass per canopy area was a constant for each successional stage, variation in nodule biomass at the stage level was driven primarily by differences in average canopy areas and shrub densities among stands across stages. This resulted in stand-level nodule biomass estimates of 6.4 ± 0.5, 11.9 ± 1.4, and 22.2 ± 3.3 g nodule m^{-2} for post-fire, mid-succession, and white spruce stages, respectively.

Estimates of N inputs (kg N ha^{-1} $year^{-1}$) averaged across years indicate greatest contribution of N by *A. viridis* to late-successional white spruce stands (6.6 ± 1.2), least to early-succession post-fire stands (2.5 ± 0.4), and intermediate to the mid-succession stands (3.2 ± 0.7) ($P < 0.05$) (Fig. 4).

Discussion

Alder interactions with soil parameters

Across the successional sequence in interior Alaskan upland forests, *A. viridis* displays substantial variation

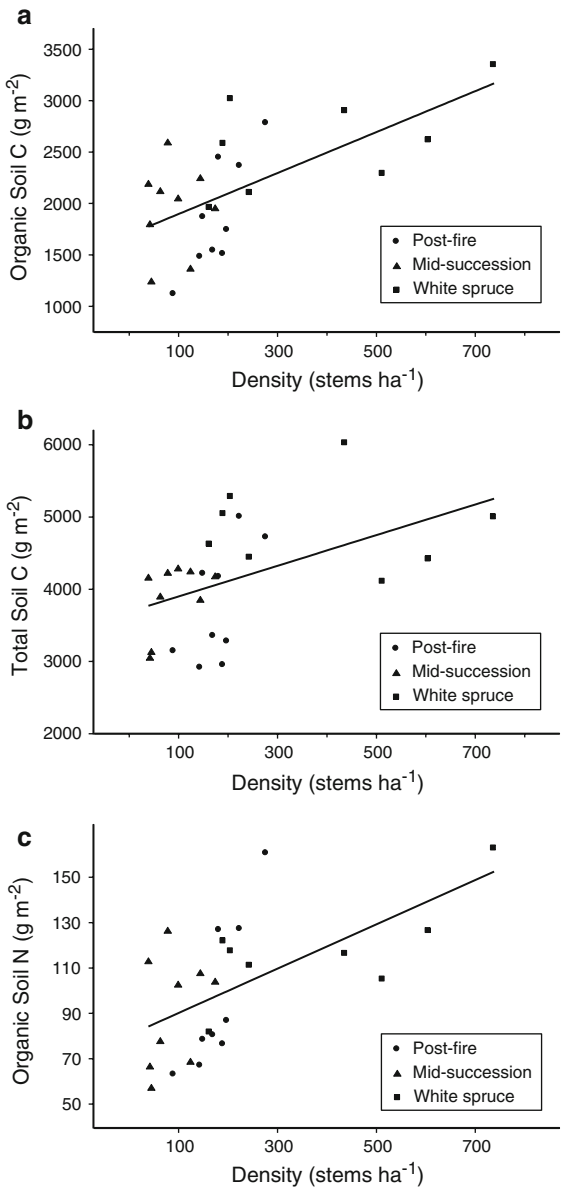

Fig. 3 Relationships between *A. viridis* stem density and (**a**) organic carbon content of the soil O horizon ($Y = 1.99X + 1699$, $r^2 = 0.37$, $P < 0.005$) (**b**) total soil organic carbon content (to 20 cm soil depth) ($Y = 2.10X + 3698$, $r^2 = 0.22$, $P < 0.05$), and (**c**) organic nitrogen content of the soil O horizon ($Y = 0.10X + 80.39$, $r^2 = 0.35$, $P < 0.005$) across upland forest stages within the Bonanza Creek Experimental Forest. Values are means ($N = 5$) for soil parameters

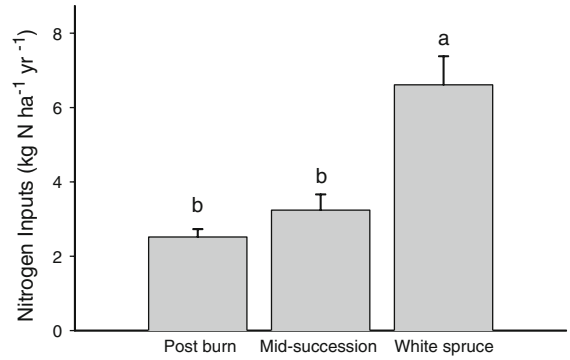

Fig. 4 Nitrogen inputs by *A. viridis* in upland forest stages within the Bonanza Creek Experimental Forest. *Letters* indicate differences between stages at $P < 0.05$. Values are means $\pm$ 1 SE ($N = 2$)

in physiology, growth dynamics, N_2 fixation, and influence on ecosystem function as it persists through changes in forest community composition and structure. Our data support the following generalizations concerning alder productivity in each successional stage. Alder growth rates are highest in post-fire stands where light availability is least limiting. During mid succession, where alder grows in the understory of paper birch and trembling aspen, alder stem density, growth rates, and N_2 fixation inputs are suppressed likely because of overstory closure and consequent resource limitation in accordance with the forest growth model proposed by Binkley et al. (2002). On drier south-facing slopes where aspen forms near monospecific stands during early- and mid-successional forest development, *A. viridis* is mostly absent, an effect we attribute primarily to water limitations (Hogg and Hurdle 1995). In late-successional white spruce stands where *A. viridis* exploits gaps in the overstory canopy, alder productivity increases, explaining the substantial increase in green alder stem density with the transition from mid- to late-succession forests (Table 3).

Alnus viridis alters soil microclimate (Sturm et al. 2005), rates of soil organic matter accumulation, and ecosystem N balance (Rhoades et al. 2001), changes that can lead to modified soil microbial processes (Mack et al. 2001). Shrubs, and N_2-fixing species in particular (Moro et al. 1997), create 'islands' or 'hot spots' of altered soil fertility (Schlesinger et al. 1996; Cross and Schlesinger 1999) such that a species' spatial distribution is mirrored by the spatial distribution of its effect on soil properties (Schlesinger et al. 1996). We identified alder effects on soil properties from relationships between plant parameters and soil characteristics beneath alder canopies that were not found for non-canopy soils. In contrast, relationships between plants traits and soils that were

similar for canopy and non-canopy soils were interpreted as stand-level effects on or by alder.

While plant effects on soil properties can diminish or vanish following shifts in species distribution, abundance, and/or vigor, it is also possible that vegetation legacies can persist long after a species is no longer present (Gallardo and Schlesinger 1995; Schlesinger et al. 1996; Mack et al. 2001; Seastedt and Adams 2001). Because alder genets persist by vegetative propagation, and occupy roughly the same spatial location throughout succession, such legacy effects may confuse interpretations of alder influences on, or response to, ecosystem function. Given that *A. viridis* grows rapidly from stump sprouts following fire (personal observation), and appears to spread mainly by vegetative propagation rather than by seed, it is conceivable that such island legacies may persist for decades, if not centuries.

The positive relationship between alder stem density and stand-level total soil C (Fig. 3b) across this successional sequence suggests that alder contributes to rates of soil C storage in these forests. This pattern was most pronounced among post-fire stands where increases in stand-level total soil C were related to increasing alder stem density. Although variation in organic horizon C concentration across all stands was explained principally by successional stage (Table 2), location (canopy vs. non-canopy) was also a significant predictor (Table 4). Together, these data suggest that the collective island effects of alder influence C accumulation rates, and that these effects continue with succession. Similar results have been reported for N_2-fixers in other ecosystems (Johnson 1992; Rhoades et al. 1998).

The influence of alder on ecosystem N balance within and among successional stages differed from that of C because alder N demand relative to soil N availability appears to vary across succession, and soil N is more subject to movement than is soil C. Among early succession stands, alder stem density was positively correlated with O horizon (Fig. 3c) and total soil N stocks; however, no significant "island effect" was detected, despite a non-significant difference between subcanopy (106.1 ± 17.1 g m^{-2}) and interspace (82.6 ± 10.2 g m^{-2}) O horizon N content (Table 5). Subsurface N transport has been shown to extend 15 m beyond alder canopies, ultimately coalescing into a stand-level N enrichment (Valentine 1990; Rhoades et al. 2001). Given that nitrification rates are highest under alder canopies (Rhoades et al. 2001) or in stands dominated by alders (Kielland et al. 2006), a portion of atmospheric N input by alder eventually ends up as nitrate. Leaching of nitrate into deeper horizons may persist into mid succession, where we detected a positive correlation between alder stem density and C horizon soil %N. A positive relationship between alder stem density and O horizon %N was found for both canopy and non-canopy soils in mid-succession stands. While these patterns may have indicated stand N influences on alder growth, we suspect that island N effects remain but were difficult to detect. During mid succession where alder productivity appeared to be suppressed, alder N demand may exceed N_2 fixation capacity; given that subcanopy A horizon N content was significantly lower than that of non-canopy soils (Table 5).

Alnus can lead to soil acidification as a byproduct of increased nitrification rates (van Miegroet and Cole 1984; Binkley and Sollins 1990; Rhoades et al. 2001). We detected subcanopy soil acidification only in post-fire stands, where pH beneath alder canopies was reduced by 0.1–0.5 units throughout the soil profile relative to non-canopy soils (Table 5). However, it is conceivable that legacies of soil acidification from post-fire stands may have persisted into mid- and late-succession stands within progressively deeper soil horizons. This pattern was suggested by the inverse relationship between alder stem density and soil pH in both A and C mineral horizons in mid-succession stands and within C mineral horizon soils in white spruce stands.

Similar to patterns for other successional forest sequences forests (Wardle et al. 2004), we found a significant decline in total soil P within the top 20 cm from post-fire (79 ± 2 g P m^{-2}), to mid-succession (54 ± 3 g P m^{-2}) to white spruce (44 ± 3 g P m^{-2}) stands (Fig. 2; Table 2). Given the high P requirement of N_2-fixing plants (Wall et al. 2000; Huss-Danell et al. 2002; Vitousek et al. 2002), we predicted strong effects of alder on, and in response to, soil P across this successional sequence. In post-fire stands, where P availability is highest because of mobilization from fire (Valentine et al. 2006), we found no significant effects of alder on %P or P content of any soil horizon. Uliassi and Ruess (2002) found significant increases in nodulation and N_2 fixation rates following P fertilization in *A. tenuifolia* growing in early and mid-succession floodplain stands along the

Tanana River, where most soil P is bound as insoluble inorganic complexes (Marion et al. 1993). We might expect similar responses in *A. viridis* to P fertilization in mid- and late-succession upland stands, where C horizon P content was 18 and 24% lower in canopy soils relative to non-canopy soils in white spruce and mid-succession stands, respectively (Table 5). Although we believe soil water was the primary factor limiting alder growth and N_2 fixation rates in upland stands, alder-P relations and the effects of soil water on these relations remain important, but poorly-studied, topics.

N inputs

Our estimates of annual N inputs by *A. viridis* to upland stands of the Bonanza Creek Experimental Forest (2.5–6.6 kg ha^{-1} $year^{-1}$) (Fig. 4) are substantially less than those reported for *A. tenuifolia* in early- and mid-successional floodplain forests along the Tanana River (38–107 kg ha^{-1} $year^{-1}$) (Uliassi and Ruess 2002; Ruess et al. 2009). Differences between species in N inputs are the product of lower *A. viridis* plant density (Table 3), nodule biomass, and rates of N_2 fixation relative to *A. tenuifolia*. However, several uncertainties in our estimates suggest that our values underestimate the actual potential for N_2 fixation inputs by *A. viridis* to these upland forests. First, we believe N_2 fixation was suppressed by drought in both study years (Mitchell and Ruess 2009). Secondly, we suspect that we may have underestimated nodule biomass, given our low sample size and the inherent variability in the spatial distribution of nodules. Our calculations assumed that nodule biomass was distributed evenly beneath alder canopies; however, when collecting nodules for acetylene reduction assays, we often observed declines in nodule biomass with distance from the main stem, and numerous nodule "hot-spots" throughout the sub-canopy. For example, nodule biomass ranged from 0.01 to 6.84 g per 15.24 cm diameter soil core, averaging 0.75 ± 0.15 g ($n = 59$, CV = 19.4%). Thirdly, there may be a number of errors propagated by the ARA method that mask actual fixation rates at the nodule level (Anderson et al. 2004; Mitchell and Ruess 2009).

Our data indicate that *A. viridis* contributed more N to late succession white spruce stands than to earlier post-fire and mid-succession stands (Fig. 4). This increase resulted primarily from greater alder abundance in late-compared to early- and mid-successional stages (Table 3). This pattern contradicts both predictions and observations of declining N inputs as a function of decreased abundance of N_2-fixing vascular plants during forest succession (Vitousek and Howarth 1991; Chapin et al. 1994; Vitousek and Field 1999; Vitousek et al. 2002). Interestingly, the factors identified by Rastetter et al. (2001) as those favoring N_2 fixers are all characteristics of our late-succession upland white spruce stands. The capacity of *A. viridis* to propagate vegetatively allows it to persist during the early development of white spruce dominance, where it creates and maintains canopy caps. Interspecific competition is reduced because of the inability of hardwood species to invade the moss ground cover, as well as the tendency of white spruce to self thin as it ages. The result is that alder stem density increases substantially during the transition from mid to late succession, resulting in moderate rates of N input that may be sustained for centuries.

Conclusions

We provide evidence that *A. viridis* was a modest but significant contributor of fixed N to this post-fire upland chronosequence and that N inputs were greatest in late succession spruce stands. While N_2-fixing non-vascular plants have been shown to maintain and even increase N inputs during late successional stages in both tropical (Matzek and Vitousek 2003) and boreal (DeLuca et al. 2002, 2008; Zackrisson et al. 2004) forests, to our knowledge, we are the first to estimate annual N_2 fixation inputs by *A. viridis*, and demonstrate an increase in N_2-fixation inputs across a successional sequence by any vascular plant species. We attribute the increase in total soil N from mid- to late-succession stands to greater alder stem density in late succession stands, because we did not detect changes in N_2 fixation rates or nodule biomass across the chronosequence. Our finding of high alder stem density in late succession stands contradicts theoretical models that predict diminishing N_2 fixer abundance over successional time in response to increasing competition for limiting resources (Vitousek and Howarth 1991; Chapin et al. 1994; Vitousek and Field 1999, Vitousek et al. 2002).

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References

Anderson MD, Ruess RW, Uliassi DD, Mitchell JS (2004) Estimating N_2 fixation in two species of *Alnus* in interior Alaska using acetylene reduction and $^{15}N_2$ uptake. Ecoscience 11:102–112

Binkley D (2003) Seven decades of stand development in mixed and pure stands of conifers and nitrogen-fixing red alder. Can J For Res 33:2274–2279

Binkley D, Sollins P (1990) Factors determining differences in soil pH in adjacent conifer and alder-conifer sands. Soil Sci Soc Am J 54:1427–1433

Binkley D, Sollins P, Bell R, Sachs D, Myrold D (1992) Biogeochemistry of adjacent conifer and alder-conifer stands. Ecology 73(6):2022–2033. doi:10.2307/1941452

Binkley D, Cromack JR, Baker D (1994) Nitrogen fixation by red alder: biology, rates, and controls. In: Hibbs DE, Debell DS, Tarrant RF (eds) The biology and management of red alder. Oregon State University Press, Corvallis

Binkley D, Stape JL, Ryan MG, Barnard HR, Fownes J (2002) Age-related decline in forest ecosystem growth: an individual-tree, stand-structure hypothesis. Ecosystems (N Y, Print) 5(1):58–67. doi:10.1007/s10021-001-0055-7

Binkley D, Senock R, Cromack K (2003) Phosphorus limitation on nitrogen fixation by *Facaltaria* seedlings. For Ecol Man 186(1/3):171–176

Bormann BT, Cromack K, Russell WO (1994) Influences of red alder on soils and long-term ecosystem productivity. In: Hibbs DE, Debell DS, Tarrant RF (eds) The biology and management of red alder. Oregon State University Press, Corvallis

Chapin FS, Walker LR, Fastie CL, Sharman LC (1994) Mechanisms of primary succession following deglaciation at Glacier Bay, Alaska. Ecol Monogr 64(2):149–175. doi:10.2307/2937039

Crews TE, Kitayama K, Fownes JH, Riley RH, Herbert DA, Mueller-Dombois DA, Vitousek PM (1995) Changes in soil-phosphorus fractions and ecosystem dynamics across a long chronosequence in Hawaii. Ecology 76(5):1407–1424. doi:10.2307/1938144

Cross AF, Schlesinger WH (1999) Plant regulation of soil nutrient distribution in the northern Chihuahuan Desert. Plant Ecol 145(1):11–25. doi:10.1023/A:1009865020145

Cumming SG, Schmiegelow FKA, Burton PJ (2000) Gap dynamics in boreal aspen stands: Is the forest older than we think? Ecol Appl 10(3):744–759

DeLuca TH, Zackrisson O, Nilsson MC, Sellstedt A (2002) Quantifying nitrogen-fixation in feather moss carpets of boreal forests. Nature 419(6910):917–920. doi:10.1038/nature01051

DeLuca TH, Zackrisson O, Gundale MJ, Nilsson MC (2008) Ecosystem feedbacks and nitrogen fixation in boreal forests. Science 320:1181. doi:10.1126/science.1154836

Gallardo A, Schlesinger WH (1995) Factors determining soil microbial biomass and nutrient immobilization in desert soils. Biogeochemistry 28(1):55–68. doi:10.1007/BF02178061

Giardina CP, Huffman S, Binkley D, Caldwell BA (1995) Alders increase soil-phosphorus availability in a Douglas-fir plantation. Can J Res 25(10):1652–1657. doi:10.1139/x95-179

Hart SC, Binkley D, Perry DA (1997) Influence of red alder on soil nitrogen transformations in two conifer forests of contrasting productivity. Soil Biol Biochem 29(7):1111–1123. doi:10.1016/S0038-0717(97)00004-7

Helfield JM, Naiman RJ (2002) Salmon and alder as nitrogen sources to riparian forests in a boreal Alaskan watershed. Oecologia 133(4):573–582. doi:10.1007/s00442-002-1070-x

Hogg EH, Hurdle PA (1995) The aspen parkland in western Canada: a dry-climate analog for the future boreal forest. Water Air Soil Pollut 82(1–2):391–400. doi:10.1007/BF01182849

Hu FS, Finney BP, Brubaker LB (2001) Effects of Holocene *Alnus* expansion on aquatic productivity, nitrogen cycling and soil development in southwestern Alaska. Ecosystems (N Y, Print) 4(4):358–368. doi:10.1007/s10021-001-0017-0

Huss-Danell K, Gentili F, Valverde C, Wall LG, Wiklund A (2002) Phosphorus is important in nodulation of actinorhizal plants and legumes. In: Finan TM, O'Brian MR, Layzell DB, Vessey JK, Newton W (eds) Nitrogen fixation: global perspectives. CAB International, Wallingford

Johnson DW (1992) Effects of forest management on soil carbon storage. Water Air Soil Pollut 64(1–2):83–120. doi:10.1007/BF00477097

Johnstone JF (2005) Effects of aspen (*Populus tremuloides*) sucker removal on postfire conifer regeneration in central Alaska. Can J Res 35(2):483–486. doi:10.1139/x04-171

Kielland K, Olson K, Ruess RW, Boone RD (2006) Contribution of winter processes to soil nitrogen flux in taiga forest ecosystems. Biogeochemistry 81(3):349–360. doi:10.1007/s10533-006-9045-3

Kurkowski TA, Mann DH, Rupp TS, Verbyla DL (2008) Relative importance of different secondary successional pathways in an Alaskan boreal forest. Can J Res 38(7):1911–1923. doi:10.1139/X08-039

Mack MC, D'Antonio CM, Ley RE (2001) Alteration of ecosystem nitrogen dynamics by exotic plants: a case study of C-4 grasses in Hawaii. Ecol Appl 11(5):1323–1335

Marion GM, Van Cleve K, Dyrness CT, Black CH (1993) The soil chemical environment along a forest primary successional sequence on the Tanana River floodplain, interior Alaska. Can J Res 23(5):914–922. doi:10.1139/x93-119

Matzek V, Vitousek PM (2003) Nitrogen fixation in bryophytes, lichens, and decaying wood along a soil-age gradient in Hawaiian montane rain forests. Biotropica 35(1):12–19

Mitchell JS (2006) Patterns of and controls over N inputs by green alder (*Alnus viridis* ssp. *fruticosa*) to a secondary successional chronosequence in interior Alaska. M.S. Thesis, University of Alaska Fairbanks

Mitchell JS, Ruess RW (2009) Seasonal patterns of climate controls over nitrogen fixation by *Alnus viridis* spp. *fruticosa* in a secondary successional chronosequence in interior Alaska. Ecoscience (in press)

Moro MJ, Pugnaire FI, Haase P, Puigdefabregas J (1997) Mechanisms of interaction between a leguminous shrub and its understory in a semi-arid environment. Ecography 20(2):175–184. doi:10.1111/j.1600-0587.1997.tb00360.x

Mulligan D (2006) Soil survey of the Fairbanks and North Star Borough areas. US Department of Agriculture Natural Resources Conservation Service, Palmer

Munsell Color Company (1992) Munsell soil color charts. Munsell Color, Baltimore

Pastor J, Binkley D (1998) Nitrogen fixation and the mass balances of carbon and nitrogen in ecosystems. Biogeochemistry 43(1):63–78. doi:10.1023/A:1006057428096

Rastetter EB, Vitousek P, Field CB, Shaver GR, Herbert D, Agren GI (2001) Resource optimization and symbiotic nitrogen fixation. Ecosystems (N Y, Print) 4(4):369–388. doi:10.1007/s10021-001-0018-z

Resh SC, Binkley D, Parrotta JA (2002) Greater soil carbon sequestration under nitrogen-fixing trees compared with *Eucalyptus* species. Ecosystems (N Y, Print) 5(3):217–231. doi:10.1007/s10021-001-0067-3

Rhoades C, Eckert GE, Coleman DC (1998) Effect of pasture trees on soil nitrogen and organic matter: implications for tropical montane forest restoration. Restor Ecol 6(3):262–270. doi:10.1046/j.1526-100X.1998.00639.x

Rhoades C, Oskarsson H, Binkley D, Stottlemyer B (2001) Alder (*Alnus crispa*) effects on soils in ecosystems of the Agashashok River valley, northwest Alaska. Ecoscience 8(1):89–95

Ruess R, McFarland J, Trummer LM, Rohrs-Richey JK (2009) Disease-mediated declines in N-fixation inputs by *Alnus tenuifolia* to early-successional floodplains in interior and south-central Alaska. Ecosystems (N Y, Print). doi:10.1007/s10021-009-9237-5

SAS Institute (2001) The SAS System for Windows, Version 8.2. SAS Institute, Inc., Cary

Schlesinger WH, Raikes JA, Hartley AE, Cross AF (1996) On the spatial pattern of soil nutrients in desert ecosystems. Ecology 77(4):1270. doi:10.2307/2265595

Seastedt TR, Adams GA (2001) Effects of mobile tree islands on alpine tundra soils. Ecology 82(1):8–17

Sturm M, Schimel J, Michaelson G, Welker JM, Oberbauer SF, Liston LE, Fahnestock J, Romanovsky VE (2005) Winter biological processes could help convert Arctic tundra to shrubland. Bioscience 55(1):17–26. doi:10.1641/0006-3568(2005)055[0017:WBPCHC]2.0.CO;2

Uliassi DD, Ruess RW (2002) Limitations to symbiotic nitrogen fixation in primary succession on the Tanana River floodplain. Ecology 83(1):88–103

Valentine D (1990) Influence of topography on soil acidity and hydrogen ion budgets in an Arctic landscape. Dissertation, Duke University

Valentine DW, Kielland K, Chapin FS, McGuire AD, Van Cleve K (2006) Patterns of biogeochemistry in Alaskan boreal forests. In: Chapin FS, Oswood MW, van Cleve K, Viereck LA, Verbyla DL (eds) Alaska's changing boreal forest. Oxford University Press, New York

Van Cleve K, Heal OW, Roberts D (1986) Bioassay of forest floor nitrogen supply for plant growth. Can J Res 16(6):1320–1326. doi:10.1139/x86-233

van Miegroet H, Cole DW (1984) The impact of nitrification on soil acidification and cation leaching in a red alder ecosystem. J Environ Qual 13(4):586–590

Viereck LA, Van Cleve K, Adams PC, Schlentner RE (1993) Climate of the Tanana River floodplain near Fairbanks, Alaska. Can J Res 23(5):899–913. doi:10.1139/x93-118

Vitousek PM, Field CB (1999) Ecosystem constraints to symbiotic nitrogen fixers: a simple model and its implications. Biogeochemistry 46(1/3):179–202. doi:10.1023/A:1006185020121

Vitousek PM, Hobbie S (2000) Heterotrophic nitrogen fixation in decomposing litter: patterns and regulation. Ecology 81(9):2366–2376

Vitousek PM, Howarth RW (1991) Nitrogen limitation on land and in the seas: how can it occur? Biogeochemistry 13(2):87–115. doi:10.1007/BF00002772

Vitousek PM, Cassman K, Cleveland C, Crews T, Field CB, Grimm NB, Howarth RW, Marino R, Martinelli L, Rastetter EB, Sprent JI (2002) Towards an ecological understanding of biological nitrogen fixation. Biogeochemistry 57(1):1–45. doi:10.1023/A:1015798428743

Wall LG, Hellsten A, Huss-Danell K (2000) Nitrogen, phosphorus, and the ratio between them affect nodulation in *Alnus incana* and *Trifolium pratense*. Symbiosis 29(2):91–105

Wardle DA, Lawrence R, Walker LR, Bardgett BD (2004) Ecosystem properties and forest decline in contrasting long-term chronosequences. Science 305(5683):509–513. doi:10.1126/science.1098778

Whitledge TE, Mallow SC, Patton CJ, Wirick CD (1981) Automated nutrient analysis in seawater. Ocean Science Division Brookhaven National Laboratory Technical Report

Wurtz TL (1995) Understory alder in 3 boreal forests of Alaska: local distribution and effects on soil fertility. Can J Res 25(6):987–996. doi:10.1139/x95-107

Wurtz TL (2000) Interactions between white spruce and shrubby alders at three boreal forest sites in Alaska. USDA Forest Service General Technical Report PNW-GTR-481

Zackrisson O, DeLuca TH, Nilsson MC, Sellstedt A, Berglund LM (2004) Nitrogen fixation increases with successional age in boreal forests. Ecology 85(12):3327–3334. doi:10.1890/04-0461

Zar JH (1998) Biostatistical analysis, 4th edn. Prentice-Hall, Englewood Cliffs

Zou XM, Binkley D, Caldwell BA (1995) Effects of dinitrogen-fixing trees on phosphorus biogeochemical cycling in contrasting forests. Soil Sci Soc Am J 59(5):1452–1458