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Nutrient uptake and use efficiency in co-occurring plants along a disturbance and nutrient availability gradient in the boreal forests of the southwest Yukon, Canada

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Summary

Aim: In boreal forest ecosystems plant productivity is typically constrained by mineral nutrient availability. In some boreal regions changes in nutrient availability have led to limited changes in productivity but large changes in plant composition. To determine the impact that a change in nutrient availability has on the plant communities it is important to understand how species use nutrients. Here we explore how plant species and functional types in a cold-dry boreal forest community use available nutrients by quantifying their respective nutrient utilisation and response efficiency.

Location: Boreal forests in the southwest corner of the Yukon Territory, Canada.

Methods: We collected soil samples and total plant biomass from 29 plots from nine locations subjected to fire, harvesting or bark beetle disturbances. Nutrient analysis of all vegetation and soil samples were conducted to determine the concentration of macro- and micronutrients from both plant biomass and soils collected. Nutrient pools between stands with different disturbance histories are compared. Nutrient uptake, use and response efficiencies were then calculated and nutrient response profiles were developed for each species/ functional type.

Results: We found few differences between nutrient pools in plots with different disturbance histories. A clear separation of species and functional groups in elemental hyperspace suggesting divergent nutrient use in co-occurring species was identified. The use efficiency analysis highlighted that the species with the highest uptake efficiency have lowest use efficiency and vice versa. Species

showed either a monotonic or constant relationship between nutrient response efficiency and N, P, K, reflecting a lack of relationship between plant productivity and resource availability or a linear increase in productivity with increasing nutrient availability, respectively;

Conclusions: Our findings indicate that species are maximising nutrient use along different parts of the resource gradient which has implications for understanding how species respond to changes in nutrient availability. Our findings also show that nutrient use by some species may be governed more by uptake efficiency than use efficiency allowing them to respond to increases in resource availability by increasing uptake rather than use.

Keywords: *Picea glauca*, boreal, nutrient, nitrogen, nutrient response efficiency, phosphorus, potassium, nutrient use efficiency

Nomenclature: USDA Plants Database (http://plants.usda.gov/java/; accessed on 4 Dec 2014)

Introduction

In boreal forest ecosystems plant productivity is typically constrained by nutrient availability (Turkington et al. 1998; Hobbie et al. 2002). Nutrient availability is typically low as nitrogen (N) and phosphorus (P) are immobilised in soil organic matter due to temperature limited decomposition (Schulze et al. 1994; Hobbie et al. 2002; Rohrs-Richey & Mulder 2007). Due to the low nutrient status of the boreal forest, changes in nutrient availability could have a large impact on this ecosystem. The changes in nutrition of boreal forest induced by fertilisation or atmospheric deposition have been found to increase productivity in trees, shrubs, herbs while also instigating changes in plant species abundance and composition (Turkington et al. 1998, 2002; Manninen et al. 2009). Hobbie et al. (2002) suggested that an increase in nutrient mineralisation, and thus nutrient availability, due to climate change would likely drive changes in net primary productivity particularly if species composition changes as result of nutrient enrichment. Disturbances such as fire, bark beetle outbreaks and harvesting, all frequent in boreal forest, can also lead to changes in the species composition and nutrient pools and nutrient cycles of affected stands (Smithwick et al. 2002; Huber et al. 2004; Palviainen et al. 2005a; Bond-Lamberty et al. 2006; Duchesne & Houle 2008; Morehouse et al. 2008; Manninen et al. 2009).

To determine the impact that a change in nutrient availability has on the boreal communities it is important to understand how different species and plant life forms coexist and to what extent species competition for nutrients is limiting their abundance, distribution and productivity. The plant species in the boreal forests of north-western Canada have evolved under low nutrient conditions but even in nutrient poor communities species may exist that are able to take advantage of nutrient

enrichment and show an increase in productivity, while others may not (Turkington et al. 1998, 2002; Shaver et al. 2001). For example, Turkington et al. (1998, 2002) found that NPK fertilisation caused changes in shrub and herb communities in the southwest Yukon, whereas Boonstra et al. (2008) found that *Picea glauca* (Moench) Voss productivity only marginally increased due to fertilisation with productivity returning to control conditions following the termination of the fertilisation. They suggested that the added nutrients could be tied up and cycled within the grasses, herbs and shrubs, becoming unavailable to the trees of the stand. On the other hand, species from low productivity or infertile environments tend to exhibit a lower degree of plasticity compared to species from fertile environments and as such are able to persist in nutrient poor environments but unable to take up additional nutrients under high availability (Chapin III 1980). In the above mentioned study (Boonstra et al. 2008), it is unclear whether *P. glauca* had limited access or limited up-take of the added nutrients. What is evident though is that any imbalances generated by increased nutrient availability can lead to significant changes in community composition and structure. Shaver et al. (2001) also observed a shift in species composition from a mix of graminoid, shrub and moss species to dominance by the deciduous shrub *Betula nana* L. that was able to outcompete the other species by increasing its productivity in response to nutrient enrichment. Therefore, the flexibility of the species to adapt to different nutritional availability is a key factor to understand if we are to disentangle the inter-specific competitive relationships that regulate community composition.

The coexistence between competing plant species relies on them accessing similar resources within the same habitat; for example, plants all require water, CO_2, light, macronutrients, and micronutrients (Peñuelas et al. 2008). Co-occurring plants species can have different nutrient requirements and nutrient uptake efficiencies, due to physiological and environmental interactions, that are reflected in their mineral composition (Woodwell et al. 1975, Garten Jr. 1978). Inter-specific differences in the mineral element composition of co-occurring plants relates to the concept of resource partitioning within a community (Peñuelas et al. 2008). Differential use of nutrients by co-occurring species has been identified in a semi-aquatic environment in South Carolina, USA (Garten Jr. 1978); in a Mediterranean shrub community (Peñuelas et al. 2008); in a Mediterranean oak forest (Aponte et al. 2011); in the Brookhaven oak-pine forest (Woodwell et al. 1975); and, in the Mojave Desert of the USA (El-Ghonemy et al. 1978). Garten Jr. (1978) concluded that species overlapping in "elemental space" could be competing for the same nutrient resources if they co-occur in the same habitat. Species can also show a distinct nutrient use efficiency, which in turn might fluctuate along a resource availability gradient. An inter-specific difference in nutrient uptake and nutrient use efficiency translates into different nutrient response efficiency (NRE), i.e. net productivity per unit

nutrient available (Pastor & Bridgham 1999). The patterns of NRE along resource availability gradients can give insight into potential changes in community composition and species abundance. Thus separating species based on nutrient uptake and use could be useful in explaining how species can co-exist when they are limited by the same resources (Schulze et al. 1994).

In the nutrient limited ecosystems of the cold-dry boreal forests of the southwest Yukon, how species co-exist with one another may be explained by differences or similarities in their mineral composition. In this study, overlapping nutrient composition is hypothesized to represent competition for similar nutrient requirements since species are occupying the same environmental space in a nutrient limited environment (cf. Garten Jr. 1978). Here we seek to identify if co-occurring species utilise nutrient elements differently along a nutrient availability gradient and between stands with different disturbance histories. We further seek to asses if the nutrient response efficiency theory of Pastor & Bridgham (1999) can be used to determine how species use nutrients across a resource gradient in the region.

Methods

Study Area

The study area is located around Haines Junction (60° 45'N and 137° 30'W) within the Champagne and Aishihik Traditional Territory (CATT) of the southwest Yukon Territory, Canada (see Figure S1 in online supplement). The climate in the area is characterized by cold winters and warm and dry summers (for details cf. Chavardès et al. 2013; and references therein). Soil texture in the region varies from mixtures of sandy and silty fluvial deposits by rivers and lakes in lowland areas to mixtures of sandy and silty clays in the rest of the area (Paudel et al. 2015). Permafrost is also common but discontinuous in the study area (Paudel et al. 2015). The forests in the study region are dominated by *Picea glauca* (Moench) Voss, which occurs as both an early and late successional species. *Populus tremuloides* Michx. is the second most abundant tree species in the region and the primary early seral species occupying warm and dry sites following fire and partial harvesting disturbances. The tall shrub community is dominated by *Salix* spp. (typically *Salix glauca* L.), *Shepherdia canadensis* (L.) Nutt. and *Rosa acicularis* Lindl., while the dwarf shrub community is dominated by *Arctostaphylos uva-ursi* (L.) Spreng., *Arctostaphylos rubra* (Rehder & Wilson) Fernald, *Linnaea borealis* L., *Empetrum nigrum* L., *Vaccinium vitis-idaea* L. and/ or *Rhododendrum groenlandicum* (Oeder) Kron & Judd. The herb and non-vascular layers are dominated by a variety of graminoids, sedges, wildflowers, mosses and lichens (all species information is summarised in Table

S1 in the Supplement). Elevation ranges from about 650 m above sea level (a.s.l.) to 850 m a.s.l in the study area. Terrain is level to gently sloping (<10°) and aspects range from northeast to southwest (90° to 240°).

The study area has recently been affected by an unprecedented spruce bark beetle (SBB) (*Dendroctonus rufipennis* Kirby) outbreak which has affected over 85% of the region's forests (270,000 ha) between 1993 and 2006 (Waeber et al. 2013, and references therein). In response to the recent bark beetle outbreak, salvage harvesting of beetle affected stands and fuel reduction thinning to reduce the increased fire risk to communities has been initiated (Paudel et al. 2015). Concurrent with the bark beetle outbreak, the region has also been experiencing increases in wildfire severity and frequency (Hogg & Wein 2005). The extensive impact of the SBB outbreak in conjunction with fires and harvesting has left little of the region's forests unaffected by disturbances in the last 25 years.

Research Design and Nutrient Extraction

Twenty nine plots located along nine 200–300 meter transects within nine stands were sampled in 2009 within the study area (Fig. S1). Transects were located in stands that had experienced a fire (n=3), spruce bark beetle (n=3), or harvesting (n=3) disturbance within the last 11–14 years. Along each transect, three to four one m^2 plots were sampled; plots along each transect were a minimum of 100 m apart and at least 50 m away from roads, edges and power lines to avoid edge-effects. Fine scale plot location at each 100 m point along the transect was determined based on two sampling rules: (1) the presence of S*. canadensis*; and, (2) the presence of seedlings or saplings of *P. glauca*. This was done to capture the dominant tree species and shrub species in the region (95% of plots sampled by Paudel et al. (2016) in the region had *P. glauca* and 68% had *S. canadensis*) and to remove the potential confounding effect of having plots with and without the nitrogen fixing *S. canadensis*.

All aboveground vegetation existing at each one m^2 plot was cut at the base and placed in paper bags (sensu Wilmking et al. 2006). All samples were oven-dried at 70 °C for 48 hours. To allow for species specific testing of shrub-tree relations, *S. canadensis*, *S. glauca*, *P. tremuloides* and *P. glauca* samples were separately stored, dried, weighed and analysed. Ages for *S. canadensis*, *P. tremuloides* and *P. glauca* were determined by counting the number of rings formed at time of sampling. From each plot, one 15 cm soil core was sampled from the centre of each plot. Soil samples were bagged in the field in zip lock bags; air dried and stored in a cool and dry place for less than 10 days prior to processing. In order to address our research questions we determined the concentration of macro-

(N,P,K,Ca, Mg, S) and micro- (B, Mn, Zn) nutrients from plant biomass and soils collected from the 29 plots. Nutrient analysis of all vegetation and soil samples was done by the Ministry of Forests, Victoria, British Columbia, Canada. For plant material the oven-dried samples were milled, total N was analysed using Combustion Elemental Analysis with an Elemental analyser; B, Ca, Mg, Mn, P, K, S and Zn were analysed using VHP Closed Vessel Microwave Acid Digestion by ICP Spectrometer. For soils, bulk density was calculated as the dry weight of the sampled divided by the core volume; available P was measured through colorimetric determination following extraction by the Bray P-1 procedure (1 minute shake). Mineralizeable N was determined by incubating the sample anaerobically under water-logged conditions (2 weeks at 30°C) followed by extraction in 1M KCl and analysis of the ammonium-N using an Alpkem Flow System IV automated chemistry analyzer. Total C and N were measured using either a Fisons (Carlo-Erba) NA-1500 elemental analyzer for the mineral soils (ground to -100 mesh), or the Leco Truspec elemental analyzer for organic soils. Mehlich extractables were measured on a Teledyne/Leeman Labs "Prodigy" dual-view ICP following extraction with the Mehlich III universal extractant (5 minute shake). Microwave digestions were carried out in a closed vessel digestion system (Questron QLab 6000) using concentrated nitric acid and peroxide. The digests were analyzed for nutrient elements on the Teledyne/Leeman Labs "Prodigy" dual-view ICP. The overall biomass of the plant species was analysed versus individual tissues to reduce the possible confounding influence of the timing and degree of nutrient translocation that occurs within boreal species (Chapin III & Kedrowski 1983). The resulting analysis thus does not address nutrient cycling of the species but the nutritional characteristics of the species within the studied communities (cf. Woodwell et al. 1975).

Nutrient Uptake, Use and Response Efficiency

To assess nutrient uptake, use and response efficiency we followed the methods outlined by Bridgham et al. (1995) and Pastor & Bridgham (1999). In this study, the total production in a given plot was sampled and separated into distinct 'species pools' for analysis. We calculated 'nutrient uptake efficiency' as the ratio of plant nutrient concentration (g N g^{-1} m^{-2}) to soil nutrient availability (g N m^{-2}), which reflects the ability of a plant to acquire nutrients from the soil. 'Nutrient use efficiency' (NUE) relates to the net production of biomass (g m^{-2}) per unit of nutrients acquired by plants (g N m^{-2}) and is the inverse of plant nutrient concentration. 'Nutrient response efficiency' (NRE) was calculated as the net production of biomass (g m^{-2}) divided by the soil nutrient availability (g N m^{-2}). NRE is useful for analysing ecosystem and species responses to resource gradients as it integrates the ability of a species to acquire resources (nutrients) with its ability to use them for growth (Bridgham et al. 1995). The use of this metric complements the uptake and use efficiency

metrics particularly for studies where the total production is the sum total of all species' responses along a resource gradient (Bridgham et al. 1995). NRE curves for N, P, and K were developed for each species/ functional group to determine their NRE relationships along the studied resource gradient. The curves were developed using general additive modelling (GAM) to determine the nature of the relationship (monotonic, linear, bimodal) between NRE and resource availability using the package *mgcv* in R (Wood 2004, 2011). Prior to these analyses, outlier tests were conducted on plant NRE values for plots located between the poorest and richest sites along the identified nutrient gradients using boxplots, Grubbs test, Chi-square test and Dixon's test (Dixon 1950, 1951; Grubbs 1950; Rorabacher 1991). Outliers were only removed if determined to be significant by all tests. For the "shrub" analysis, two plots were excluded as they contained only a single species; the remaining plots were composites of multiple species. The response curves are not to be interpreted as predictive models; they are provided to illustrate the general pattern of response.

Statistical Analysis

Differences in plot structure, soil, plant and total nutrient pools between stands with different disturbance histories were tested using Single Random Factor ANOVA (following Logan 2010) with stand considered as a random factor. Single Random Factor ANOVA was selected to account for the nested structure of our study design, 29 plots within 9 stands, suggests that plots within each stand are likely to be more related than values from plots between stands (Zuur et al. 2009). This analysis was conducted in R 3.2.1 (R Core Team 2015) using the *nlme* (Pinheiro et al. 2015) package. Multiple comparison tests were conducted using Tukey tests where necessary. The normality of all data was checked and where necessary the data were transformed to adjust for normality. To determine the impact of changes in the resource availability on nutrient pools we used linear and non-linear regression in R following Logan (2010). To determine if nutrient availability was explained by other site factors we also tested the influence of soil pH (H+ ions), organic soil layer depth (cm) and proportion of plant community occupied by different species/ functional groups, all of which have been found to affect nutrient availability (Smithwick et al. 2005; Mallon et al. 2016).

Two multivariate methods were used to analyse different aspects of the variation in our datasets. Discriminant function analysis (DFA) and principal component analysis (PCA) were used to identify the elemental space occupied by each species/ species group (n=141). Prior to analyses the normality of the concentration data was checked and where necessary the data were ln(x+1) transformed to adjust for skewness. All data was standardised to a unit of variance to allow for cross species/ functional group comparisons. DFA ordinates the species by minimising within-group

variation and maximizing between-groups variation providing information on which variables are best suited for discriminating between the species/ functional groups (Kourtev et al. 2002). DFA was used to classify species into elemental space. Differences between species/ functional groups in their mineral element composition were based on the mean position of the centroids and the degree of overlap amongst polygons in the discriminant space (Garten Jr. 1978; Quinn & Keough 2002). The elemental space occupied by each species/group was measured as the mean square distance of the scores to the centroid of the polygon (Carnes & Slaid 1982). PCA maximises the variation within a dataset (Kourtev et al. 2002) and was used to explore the relationships among concentrations of elements within the plants and where species are dispersed within this multivariate space (Garten Jr. 1978). The significance of the extracted component was assessed using the eigenvalues (greater than 1.5) and the broken stick method (Quinn & Keough 2002). PCA is a commonly used approach for quantifying the elemental space each species occupies (see Gerloff et al. 1966; Woodwell et al. 1975; El-Ghonemy et al. 1978; Garten Jr. 1978; Peñuelas et al. 2008). The DFA supplements the PCA by identifying the variables best suited for discriminating between the predefined species/ functional groups (Kourtev et al. 2002). The ordination of species using the DFA and PCA approach allows for the interpretation of the breadth / plasticity of a species' nutrient use. Differences between species on the extracted DFA and PCA ordination axes were tested using both one-way analysis of variance (ANOVA) PCA; ANOVA analyses were conducted in R. DFA was conducted in R using the MASS package (Venables & Ripley 2002).

Results

Disturbance History and Nutrient Pools

No significant differences in plot age, density and height were detected for *Picea glauca*, *Populus tremuloides* and *Shepherdia canadensis* across stands with different disturbance histories (Table 1). Soil physical properties varied across stands as did species composition; a summary of species occurrence (Table S1 in Supplement) and soil data (Table S2 in Supplement) are provided in the online Supplemental Material. Total nutrient pools between disturbance histories were found to vary significantly for Al, B, Ca and S ($P \leq 0.05$) but not for the remaining elements (see Table 2). Differences in Ca and S were found between fire and harvest affected stands and differences for Al between fire and spruce bark beetle (SBB) affected stands. Boron differed between fire and SBB and fire and harvest effected stands but not between SBB and harvested stands. Differences in the elemental pools within both organic and mineral soil horizons by disturbance history were also

detected. Fire affected stands had significantly higher B, Ca, Fe, Mg, S, and available P but significantly less Al in the mineral soil pool. Significantly larger pools of Ca and Mg were also found in the organic soil pool of fire affected stands ($p \leq 0.05$; Table S3). Significant difference in Cu pools between harvest and fire affected stands was detected and SBB effected stands were found to have significantly less cation exchange capacity (CEC) in the organic soil layer than fire and harvest affected stands ($p \leq 0.05$; Table S3). The majority of variance explained for all elements was due to disturbance effects with S the only element have a greater proportion of its variance explained by stand effects suggesting that location has a greater influence than disturbance history. Significant differences were also found between organic and mineral soil pools when all stands were combined for all elements except Ca, Mg, and S and soil pH. The mineral soil pool had significantly more Al, Fe and Cu while the organic soil pool had significantly more B, C, K, Mn, N, mineralized N, P, available P, Zn and a significantly higher CEC ($p \leq 0.05$; Table S4). Significant differences were detected in plant nutrient pools with the biggest difference occurring in non-vascular plant pools between fire affected and SBB/ salvage harvested stands for all elements except K, N and C ($p \leq 0.05$; Table S5). *S. canadensis* had significantly higher N and C pools in harvested stands while *P. glauca* had significantly higher N, P and S pools in harvest affected stands ($P \leq 0.05$; Table S5).

<Table 1>

<Table 2>

A nutrient availability gradient was detected across the 29 plots with soil nitrogen ranging from 69 to 951 g/m^2, phosphorus from 1.9 to 15.8 g/m^2, and potassium from 10 to 89 g/m^2. Availability of B, Ca, Mg, and S were found to exhibit significant logarithmic relationships ($p \leq 0.05$, R^2: 0.60, 0.57, 0.52 and 0.48% respectively) with decreasing pH in the study area (see Figure S2 in Supplement); all other elements were not found to vary significantly. The response of Ca and Mg are similar to the findings of Dryness et al. (1989) for boreal stands in Alaska. Availability of N and mineralized N were found to exhibit significant quadratic relationships ($p \leq 0.05$, R^2: 0.56 and 0.67 respectively, Figures 2 and S3 in Supplement) with increasing depth of the organic soil horizon, while Mn, Al, and Zn were found exhibit significant linear relationships ($p \leq 0.05$, R^2: 0.32, 0.32 and 0.19 respectively) (see Figure S3 in Supplement); other elements were not found to vary significantly. Carbon was also found to exhibit a significant quadratic relationship ($p \leq 0.05$, R^2: 0.54) with increasing organic layer depth; however, the C:N ratio was not found to significantly change ($p \leq 0.35$, R^2: 0.03) (Figure 1). Significant relationships between proportion of plant biomass for both *P. glauca* ($p \leq 0.001$, R^2: 0.71) and non-vascular plants ($p \leq 0.001$, R^2: 0.43) and availability of mineralized N were found (Figure 2). Mineralized N was found to increase with increasing proportion of biomass comprised of *P. glauca*

but decrease with increasing proportion of biomass comprised as non-vascular plants (bryophytes and lichens).

<Fig 1>

<Fig 2>

Discriminant Function Analysis

The discriminant analysis showed the interspecific differences between species/ functional groups. The two discriminate functions accounted for 58% (DF1) and 22 % (DF2) of the variability. Nitrogen followed by S contributed the most to DF1 while Ca and B were moderate contributors (N>S>Ca>B). Potassium, B, and P (K>B>P) contributed the most to DF2. *S. canadensis* was nearly unique in its mineral element composition (Figure 3). It showed a significant ($p < 0.001$) separation from the other species and functional groups along DF1 with higher concentrations of N (and to some extent B) and lower concentrations of S, P and Ca. It also showed different values along DF2, i.e. different concentrations of K, B and P ($p < 0.05$ to 0.001), than the herbs, non-vascular plants (bryophytes and lichens) and *P. glauca* although it overlapped with *S. glauca*, *P. tremuloides* and shrubs ($p > 0.05$).

Salix glauca, P. tremuloides, P. glauca and shrubs showed a partial overlapping of elemental space. *Salix glauca* and *P. tremuloides* showed similar elevated concentration of S compared to the levels found in *P. glauca* and shrubs as indicated by the separation of the two groups along DF1 ($p < 0.001$). However, *S. glauca* and *P. tremuloides* occupied a different space along DF2: *Populus tremuloides* was separated from the majority of the other species, including *S. glauca*, due to its higher concentration of Ca. *S. glauca* showed concentrations of P higher than that found in *P. tremuloides* but similar to the one found for *P. glauca* and shrubs.

The non-vascular plants and herbs comprised several species (Table S1) and thus showed a large variability in their chemical composition, i.e. they occupied a large area in the elemental space (Fig. 3). Nevertheless, these two groups showed a significantly different chemical composition between them and amongst all other groups ($p \leq 0.01$ to 0.001). The biplot of elements (Fig.3) indicates that non-vascular plants were characterized by a higher concentration of P, S, Zn, and Mn and shared their space with *S. glauca*, shrubs and *P. glauca*, whereas herbs showed a large concentration of K, B and Ca and shared their space with *P. tremuloides* and shrubs.

<Fig 3>

Principal Component Analysis (PCA)

Two significant principal components (PC) were extracted from the PCA, which explained 44 % (PC1) and 20.5 % (PC2) of the variance respectively. Species and functional groups were segregated along the two PCs reflecting differences in their chemical composition (see Figure S4 in Supplement). PC1 was related to an enrichment of all nutrients with the strongest loadings for Ca, S, P, Mg, B, and K (0.43, 0.41, 0.41, 0.37, 0.37, and 0.33; respectively). *P. glauca* and shrubs had the lowest scores along this axis ($p<0.05$) thus showing lower nutrient concentrations as compared to the other species/functional groups. *S. glauca*, *P. tremuloides*, *S. canadensis* and non-vascular plants occupied a similar space along the nutrient gradient while herbs, located at the positive end of PC1, showed significantly higher scores ($p<0.05$) and tended to have a higher nutrient content than the other species (but not *P. tremuloides*). PC2 was positively related to Mn and Zn (0.51 and 0.48) and negatively correlated to N (-0.49). PC2 clearly separated *S. canadensis*, which had the lowest scores ($p<0.05$) due to its higher N content, from all the other groups (see Fig S4).

Nutrient Uptake, Use and Response Efficiency

The PCA and DFA provided evidence of nutrient use partitioning based on species nutrient composition but do not provide an indication of the nutrient efficiency of the plants nor the community outcomes of this apparent partitioning. The nutrient efficiency results disentangle the species capacity to uptake and use nutrients to produce biomass (see species-specific results in Figure S5 in Supplement) while Fig. 4 reveals how species' productivity, based on nutrient efficiency, responds to changes in nutrient availability. Two types of responses can be observed from the NRE patterns in Fig. 4 (sensu Pastor & Bridgham 1999): (1) a monotonically increase in NRE with declining nutrient availably, and (2) a constant NRE across the nutrient availability gradient, which is defined by no relationship between NRE and the nutrient gradient.

The nutrient efficiency patterns of *S. canadensis* showed the highest N uptake efficiency and the lowest N use efficiency (Fig. S5). The opposite was found for other nutrients such as P, K and Ca. The slow decrease in NRE with increasing N, P, and K availability (Fig. 4c, d, e) suggests however that its productivity is not constrained by NPK availability. Herbs were found to have the highest uptake efficiency for P, K, B, and Ca, but showed the lowest response efficiency for all nutrients (Fig. S5). The monotonic response of their NRE to nutrient availability gradient suggest that a lack of relationship between herb productivity and NPK availability exists (Fig. 4h, i, j). Non-vascular plants had the highest Mg, Mn, S, and Zn uptake efficiencies and the highest response efficiency to all nutrients (three to four fold higher response efficiency than the other plants within the studied community); however, these response efficiencies are skewed towards the poor end of the nutritional gradient suggesting that at low nutrient availability levels their biomass is very high but

significantly decreases at intermediate and high levels (Fig. 4k, l, m). The monotonic increase in NRE with declining nutrient availability was also found for non-vascular plants suggesting a lack of relationship between productivity and N, P and K availability (Fig. 4k, l, m). The shrub community also exhibited monotonic responses to N and P (Fig. 4f, g) but no response to K. This suggests that shrub productivity increases linearly with increasing K but not with N or P. The response efficiency of *P. tremuloides* and *S. glauca*, which showed average nutrient uptake and use efficiencies (Fig. S5), also had the highest minimal nutrient availability at which any production can occur, which should reflect a higher maximum productivity (sensu Pastor & Bridgham 1999). *P. tremuloides* exhibited a weak monotonic relationship with K (Fig 4b) but no relationship with N or P, while *S. glauca* exhibited no relationship with N, P or K. This suggests that both *P. tremuloides* and *S. glauca* increase productivity with increasing N and P availability and with increasing K availability for the latter. Overall *P. glauca* had the lowest uptake efficiencies but the highest nutrient use efficiency. *Picea glauca* also exhibited the highest response efficiency (after the non-vascular) which followed a monotonic curve across the N availability gradient (Fig 4a); however, no relationship with P or K was detected suggesting that its productivity increases linearly with increasing P and K availability.

<Fig 4>

Discussion

Nutrient Pools and Disturbance

No consistent trends in the impact of disturbance type on total nutrient pools were found across the study area. The main macronutrients N, P, and K all were found to be in similar abundance across all three disturbance types while other nutrients showed congruent abundances across at least two disturbance histories. A possible explanation could be that total nutrient pools are back to pre-disturbance levels as it had been 10 years since perturbation. This is supported by the findings of Palviainen et al. (2005b) who found nutrient levels were back to pre-disturbance levels within 5 years of harvesting in the boreal forests of Finland and by Morehouse et al. (2008) who found only short-term increases in N in *Pinus ponderosa* stands following bark beetle attack. The results could also indicate that disturbance has had a limited effect on nutrient pools; for example, Dryness et al. (1989) found that N content of mineral soils in burnt *P. glauca* stands did not vary from unburnt stands in Alaska. The significant increases in Ca and Mg in fire affected stands is congruent with the findings of Thiffault et al. (2008) who found that fire affected sites had more Ca and Mg in the forest floor compared to harvested and control sites. The increase in available P in the mineral soil of fire affected stands was also found by Dryness et al. (1989) in Alaska. The differences in available P may

be due to the changes in the Al and Fe pools observed in fire affected stands. Reduced P availability in boreal stands has been attributed to high Al and Fe pools (Geisler et al. 2002); Al pools in particular were significantly higher in SBB and harvest affected stands. The lack of response in C:N ratios between plots suggests that any benefits of disturbance to soil N pools that have been observed following bark beetle attack (Morehouse et al. 2008), fire (Dryness et al. 1989) or harvesting (Bock & Van Rees 2002; Palviainen et al. 2005b) are no longer evident 10 years post disturbance. In addition, the similar C:N ratios between plots with varying depths of soil organic matter suggest that N pools across all sites are all largely recalcitrant and have slow turnover rates (Thiffault et al. 2008). The similarity in pH, cation exchange capacity (CEC), C:N ratios, mineralizable N, and total concentrations of N, P, K, across stands with different disturbance histories suggests that an underlying gradient of site fertility exists across stands with varying disturbance histories and varying depths of soil organic matter.

Nutrient differentiation and response profiles of co-occurring species

We found a clear separation of co-occurring species and functional groups in the elemental hyperspace (sensu Garten 1978). Interspecific differences in the mineral element composition of co-occurring plants have rarely been done for the boreal forest (Schulze et al. 1994; Rohrs-Richey & Mulder 2007). Resource partitioning is particularly relevant in nutrient limited ecosystems, such as the boreal forest, where species are expected to diverge in their nutrient requirements to reduce competition and partition the resources within the community (Garten Jr. 1978; Peñuelas et al. 2008). Our findings suggest that interspecific differences in nutrient uptake, use and response efficiencies are occurring within our study area and likely facilitate the partitioning of resources. Despite this partitioning it is likely that competition for nutrients does occur as considerable overlap in elemental composition (cf. Garten 1978) and NRE were identified.

The use efficiency analysis highlights that the species with the highest uptake efficiency have lowest use efficiency and vice versa. Herbs and non-vascular plants showed the highest nutrient concentrations and the largest breadth in elemental space. Both herbs and non-vascular plants showed a high capacity to acquire nutrients but a low efficiency in using them. Prescott et al. (1989) found that herbaceous plants were able to uptake and retain high amounts of nutrients but had limited nutrient reabsorption capacity leading to low nutrient use efficiencies. Herbs exhibited monotonic responses to N, P and K suggesting that this functional group shows no relationship between nutrient availability and productivity. This suggests that herbs uptake nutrients and

accumulate them in their tissues, but do not invest in growth across the nutrient gradient (Pastor & Bridgham 1999). The shrub community showed a relatively low concentration of nutrients and occupied a narrow elemental space, reflecting a low plasticity of their stoichiometry. The skewed monotonic response of their NRE to N and P availability suggests that only at very poor sites will shrubs be highly efficient in their nutrient use, whereas their response efficiency will decrease as N and P availability increases. Chapin III (1983) found that understorey shrubs play an important part in N and P cycling in the boreal forest in Alaska which our finding suggest would be the case on sites with the lowest N and P availability. Interestingly, the shrub community was found to exhibit no response to K availability suggesting that the shrub community is able to increase productivity in response to increases in K. Similarly to shrubs, non-vascular plants exhibited a high level of response efficiency at low fertility levels, which rapidly decayed with increasing nutrient availability suggesting that increases in N, P, and K do not result in increased productivity. The skewed monotonic response of their NRE to N availability suggests that only on N poor sites are non-vascular plants highly efficient in their nutrient use. This suggests that non-vascular plants and shrubs in the region may have a competitive advantage; particularly on N poor sites, but that they likely become less efficient and poorer competitors as nutrient availability increases. Studies in the Arctic tundra have shown that shrubs productivity can be stimulated by low levels of fertilization but higher levels of fertilization has a negative impact on their growth, leading to mortality (Chapin III & Shaver 1985, 1996; Kellner & Marshagen 1991). Schulze et al. (1994) however found that ericaceous shrubs have a competitive advantage in boreal communities for N under N limited conditions. Our results suggest this may be the case in our study area where NRE for the ericaceous dominated shrub community increases rapidly on N poor sites but show limited ability to increase productivity as N increases.

Among all studied species, *S. canadensis* was clearly differentiated into its own elemental space specifically due to its higher N concentration and uptake efficiency and its lower concentration and higher use efficiency of P, Ca and S. The relationship between NRE and nutrient availability suggests that *S. canadensis* productivity is not sensitive to changes to NPK. *Shepherdia canadensis* is a nitrogen-fixing shrub that has been found to play a significant role in N accretion in Alaskan floodplain ecosystems (Rhoades et al. 2008), so its ordination into a separate space based on N is not surprising.

Populus tremuloides and *S. glauca* overlapped with most of others species and they had average nutrient concentrations and nutrient uptake, use and response efficiencies. Their NRE across the gradient of nutrient availability were also similar from one another. According to the nutrient

response efficiency theorem (Pastor & Bridgham 1999), both species are able to increase productivity in response to increasing N and P availability while *S. glauca* can also capitalise on increasing K to increase productivity. Their capacity to respond to increases in NPK compared to other species, suggests that these species would be favoured by increasing N, P and N, P, K availability respectively.

Picea glauca had the lowest nutrient concentrations and nutrient uptake efficiencies of all other co-occurring plants across the study area. The NUE and NRE analyses however suggest that it is one of the more efficient users; enabling it to maintain its productivity in sites with limited nutrient availability; in particular, for N where a monotonic relationship between resource availability and productivity was detected. *P. glauca* was found to exhibit a null response to P and K which highlights that productivity likely increases with a change in P and K availability. The NRE profiles thereby provide some insight into the limited response of *P. glauca* stands in the region to NPK fertilization observed by Boonstra et al. (2008). The NRE profiles can also aid in explaining the contradictory results obtained by Prescott et al. (1989, 1992), who found that regenerating *P. glauca* (13 years old) in the Montane Cordilleran forests of the Rocky Mountains in southwest Alberta was an inefficient user of N and P with high uptake but low use efficiency. Our results suggest that the response observed by Prescott et al. (1989, 1992) would be independent of soil N but dependent upon soil P. If soil P on their sites is low enough then both N and P uptake would occur without any compensatory increase in productivity thus leading to their conclusion that the species is an inefficient user of N and P.

Based on the nutrient response theorem of Pastor & Bridgham (1999) inter and intra specific differences in uptake and in use and response efficiencies suggest that co-existing plant species in the nutrient-limited boreal forests of the southwest Yukon use nutrients differently. Species' nutrient use efficiency also appears to be varying with changing nutrient availability. As a result changes in nutrient availability within the study region could lead to changes in the plant communities. In fertilization studies within the low-nutrient boreal forests of the region, Turkington et al. (1998, 2002) observed an "increase in biomass of all components of the vegetation, with the most immediate response being detected in the herbaceous layer and the slowest response by the trees". The higher N, P and K uptake efficiency of the herbs as compared to *P. glauca* found in this study may explain this response. Finzi et al. (2007) found that uptake increases versus NUE as

resource availability increases in N-limited systems which suggest that herbs with their higher uptake efficiency will benefit more than *P. glauca* from nutrient enrichment. In the same studies, Turkington et al. (1998, 2002) found that the growth of *S. glauca* significantly increased with fertilization whereas the growth of *P. glauca* showed marginal increments compared to the control. Based on our results, in the context of the nutrient response theorem of Pastor & Bridgham (1999), we would expect *S. glauca* and *P. tremuloides* to be able to increase productivity to N and K fertilisation over *P. glauca* as both *S. glauca* and *P. tremuloides* showed higher response efficiencies (particularly for P) than *P. glauca* and null relationships between NRE and NPK and NP availability, respectively. The results of Turkington et al. (1998, 2002) support our findings and highlight that the nutrient responses identified in the co-occurring species in this study increase our understanding of how boreal forest communities respond to changes in nutrient availability.

Conclusion

Species from low productivity or infertile environments tend to exhibit a lower degree of plasticity and as such are able to persist in nutrient poor environments but may be unable to take up additional nutrients under high availability (Chapin III 1980). Our findings suggest that most species have a narrow window at which they are able to effectively uptake and utilise nutrients along a resource gradient though this response will vary between nutrients. Our findings also show that some species exhibit broad nutrient use which may be governed more by uptake efficiency than use efficiency allowing them to respond to increases in resource availability by increasing uptake rather than use. For some species, such as *P. glauca*, their narrower use of nutrients may be governed by use efficiency not uptake efficiency thus they are unable to take up additional nutrients under high availability but are able to tolerate the increasing nutrient limitations imposed on boreal species during succession.

Growing concerns and aspirations in the CATT region are the occurrence of wildfire, the development of a local forest industry to stimulate economic development, climate change and the occurrence of future spruce bark beetle outbreaks (Waeber et al. 2013). Disturbances such as fire or harvesting will change species composition but will largely keep the nutrient cycle intact as the plant community is made up of species that are able to take advantage of nutrient pulses and ones that can tolerate low nutrient conditions. The community thus comprises species that utilize different nutrient use strategies which drives competition for nutrients but also prevents nutrient leaching and promotes nutrient storage (cf. Chapin III 1983). In this nutrient-limited environment, driven by

change and disturbance, it is likely the character of their nutrient use that allows some species, such as *Picea glauca*, to persist in coexistence with a constantly changing community.

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Appendix B: Nutrient Pools and Availability

Table S3: Soil nutrient pools and pH and CEC by disturbance history

Table S4: Mean values for organic and mineral soil nutrient pools and pH and CEC

Table S5: Plant nutrient pools by disturbance history

Figure S2: Relationships between nutrient availability and pH

Figure S3: Relationship between nutrients and organic soil depth (cm)

Appendix C: Nutrient Use and Efficiency of Plants

Figure S4: Position of species and functional groups in the "elemental space" based on PCA

Figure S5: Nutrient uptake, use and response efficiency of the studied species/ functional groups

Table S6: P values for tests between nutrient uptake, use and response efficiency

Table 1: Density, height and age data for dominant tree and shrub species in sampled plots. P. tremuloides was not detected in Spruce bark beetle (SBB) as indicated by a density of zero and null values for age and height.

	Disturbance History			
	SBB	**Fire**	**Harvesting**	**Overall**
Density (m^2)				
Populus tremuloides	0.0	1.1	0.2	0.4
	(0.0)	(1)	(0.6)	(0.8)
Sheperdia canadensis	1.0	1.3	1.0	1.1
	(0.0)	(0.7)	(0.0)	(0.4)
Picea glauca	2.2	1.6	1.7	1.8
	(1.7)	(0.7)	(0.9)	(1.2)
Height (m)				
Populus tremuloides		0.9	1.1	0.9
		(0.8)	(0.4)	(0.7)
Sheperdia canadensis	0.6	0.8	0.7	0.7
	(0.1)	(0.5)	(0.1)	(0.2)
Picea glauca	0.5	0.5	1.3	0.8
	(0.2)	(0.2)	(1.3)	(0.9)
Age (years)				
Populus tremuloides		7.3	8.0	7.4
		(1.3)	(2.8)	(1.2)

Sheperdia canadensis	10.7	4.3	12.0	8.6
	(3.5)	(1.2)	(1.4)	(4.1)
Picea glauca	11.8	6.6	11.9	10.0
	(7.7)	(2.8)	(1.5)	(5.2)

Table 2: Mean values and standard deviation (SD) of total nutrient pools (g/m^2) by disturbance history (spruce bark beetle (SBB), n=9; Fire, n= 10; harvest n=10). Differences between disturbance histories are shown within rows; different letters indicate significant differences and significance level of Single Random Factor ANOVA indicated by: * P ≤ 0.05; ** P ≤0.01. Bolded values identify disturbance significantly different than other two histories.

	SBB				**Fire**				**Harvest**			
	mean		**SD**		**mean**		**SD**		**mean**		**SD**	
Al**	189.4	±	51.3	a	105.3	±	47.9	b	152.72	±	31.94	ab
B*	0.19	±	0.10	a	**0.29**	±	0.19	b	0.18	±	0.06	a
C	7897	±	5668	a	5450	±	3198	a	7831	±	3785	a
Ca*	553.5	±	375.7	ab	987.8	±	844.3	a	449.1	±	257.7	b
Cu	0.57	±	0.20	a	0.45	±	0.18	a	0.39	±	0.12	a
Fe	73.3	±	21.7	a	68.1	±	25.2	a	61.0	±	13.0	a
K	37.7	±	22.8	a	40.1	±	19.1	a	39.7	±	17.8	a
Mg	60.2	±	43.2	a	104.0	±	91.3	a	50.9	±	16.5	a
Mn	6.8	±	3.2	a	5.93	±	2.87	a	8.7	±	4.7	a
N	325.3	±	254.9	a	229.6	±	158.0	a	304.4	±	135.6	a
P	6.6	±	3.1	a	8.0	±	3.6	a	6.6	±	3.1	a
S**	2.3	±	1.4	ab	4.0	±	3.4	a	1.8	±	0.62	b

Zn	0.30	±	0.12	a	0.22	±	0.10	a	0.61	±	0.49	a

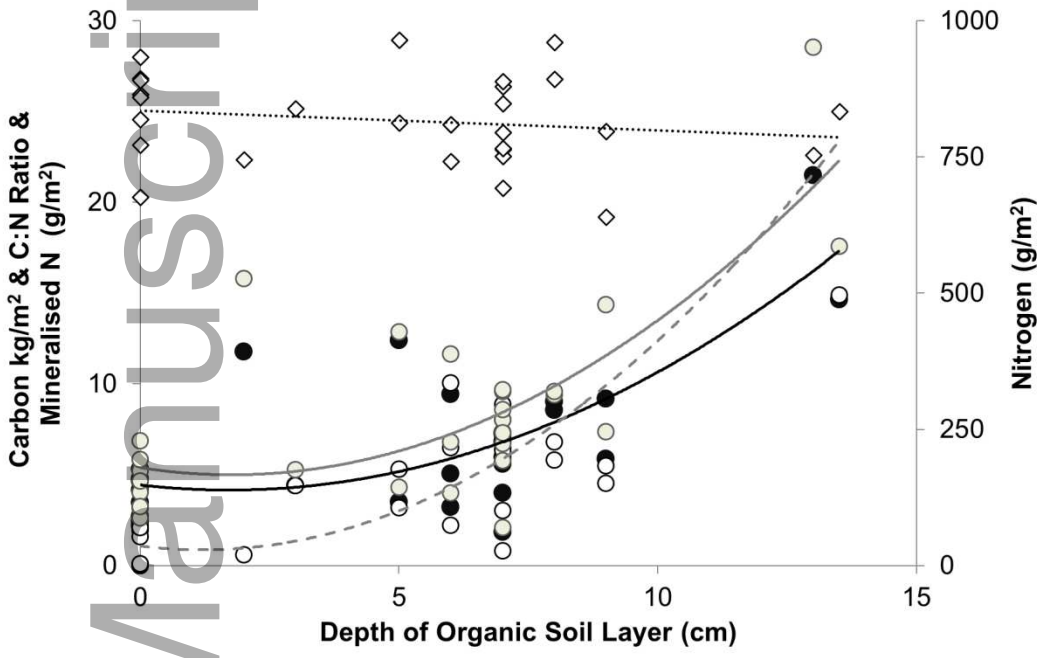

Figure 1: Change in Nitrogen (N, solid grey line and circles), Mineralised N (dashed line, open circles), carbon (C, black line and circles); and, C:N ratio (dotted line, open triangles) with changes in organic soil depth. Significant quadratic relationships (P < 0.001) found for N (r^2: 0.56), Min N (r^2: 0.67), and C (r^2: 0.54). No significant relationship found between C:N ratio and organic soil depth (P 0.35; r^2: 0.03).

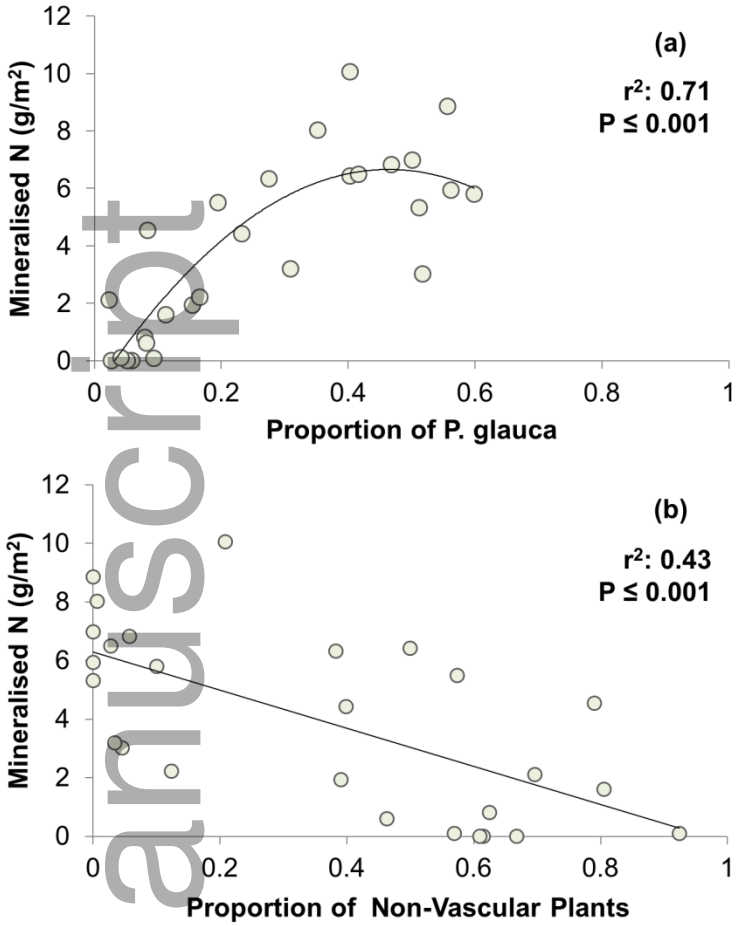

Figure 2: Relationship between Mineralised Nitrogen (N) and proportion of plant biomass comprised of Picea glauca (a) or non-vascular plants (b). Stepwise regression modelling identified the P. glauca relationship as the sole predictor of mineralised N over other species for the study region.

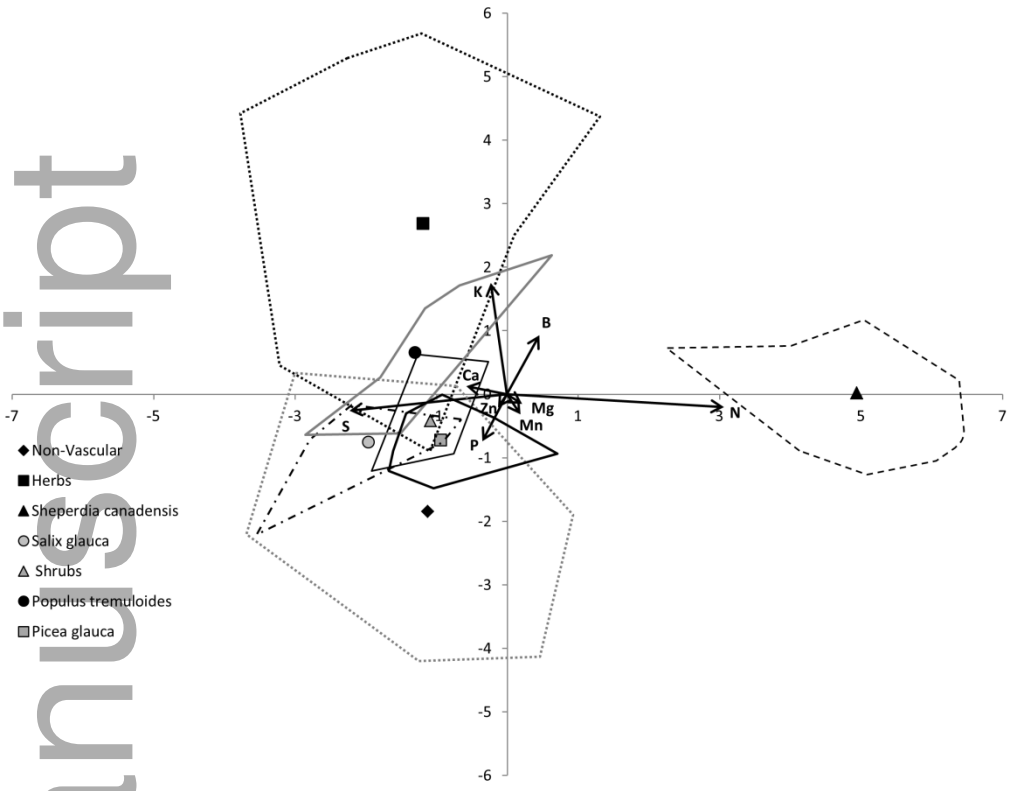

Figure 3: Mean position of species and functional groups in the "elemental space" based on discriminant function analysis of the nine mineral elements. The mean position represents the group centroid and the polygons represent the area covered by the observations of each species/ functional group. Differences between species/ functional groups in their mineral element composition are interpreted from the mean position of the centroids and the degree of overlap amongst polygons in the discriminant space (Garten Jr. 1978; Quinn & Keough 2002). DF1 is represented by the x-axis and DF2 by the y-axis. Biplot represent the relationship between mineral elements and discriminant functions. The direction of the element vectors indicates an increase in the values of the element towards which the vector is pointing and the length of the vector indicates the rate of increase (Quinn & Keough 2002). Vectors were rescaled from one to four to facilitate interpretation of the data.

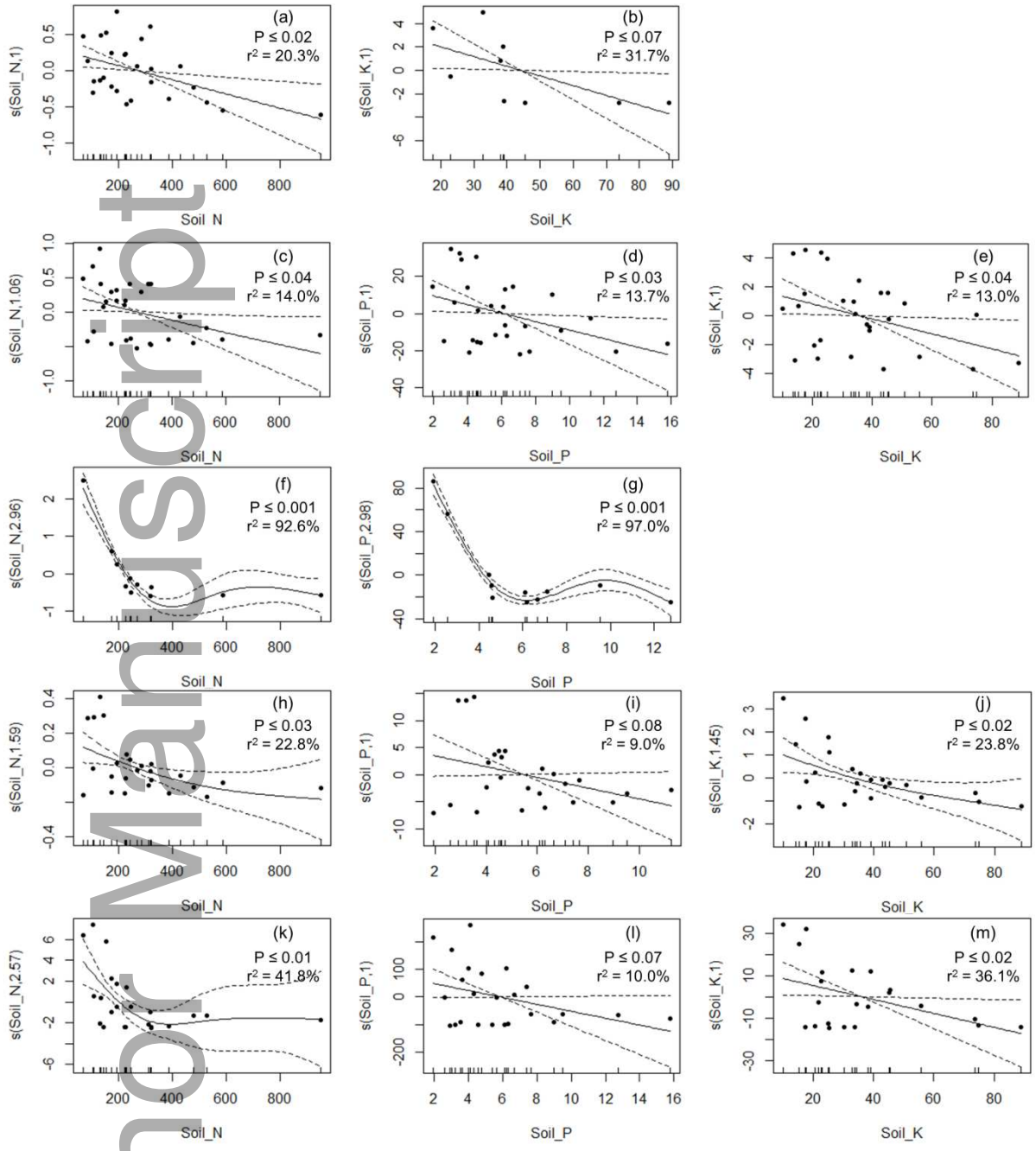

Figure 4: Significant (P< 0.10) nutrient response efficiency (NRE) relationships for *P. glauca*: nitrogen (N) (a); *P. tremuloides*: K (b): *S. canadensis*: N (c) ,Phosphorus (d), K (e); shrubs: N (f), P (g); herbs: N (h), P (i), K (j); and non-vascular plants: N (k), P (l), K (m). A monotonic increase in NRE with declining nutrient availability reflects a lack of relationship between plant productivity and resource availability and is illustrated in all graphs. P. glauca (PK); *P. tremuloides* (NP); *S. glauca* (NPK); and, shrubs (K) (not illustrated) all showed a constant NRE (i.e. no significant relationship) across the nutrient availability gradient indicating a linear increase in productivity with increasing availability for a respective nutrient.