Contrasting conifer species productivity in relation to soil carbon, nitrogen and phosphorus stoichiometry of British Columbia perhumid rainforests

John Marty Kranabetter[1], Ariana Sholinder[2], Louise de Montigny[3]

[1]British Columbia Ministry of Forests, Lands and Natural Resource Operations

P.O. Box 9536, Stn Prov Govt, Victoria, B.C., Canada V8W 9C4

Tel: 1 778 698-9260; Fax: 1 250 952-4119

Marty.Kranabetter@gov.bc.ca

[2]Centre for Forest Biology, University of Victoria

P.O. Box 3020, Stn CSC, Victoria, B.C., Canada V8W 3N5

[3]British Columbia Ministry of Forests, Lands and Natural Resource Operations

P.O. Box 9512, Stn Prov Govt, Victoria BC, Canada V8W 9C2

Abstract

Temperate rainforest soils of the Pacific Northwest are often carbon (C) rich and encompass a wide range in fertility reflecting varying nitrogen (N) and phosphorus (P) availability. Soil resource stoichiometry (C:N:P) may provide an effective measure of site nutrient status and help refine species-dependent patterns in forest productivity across edaphic gradients. We determined mineral soil and forest floor nutrient concentrations across very wet (perhumid) rainforest sites of southwestern Vancouver Island (Canada), and employed soil element ratios as covariates in a long-term planting density trial to test their utility in defining basal area growth response of four conifer species. There were strong positive correlations in mineral soil C, N and organic P (P_o) concentrations, and close alignment in C:N and C:P_o both among and between substrates. Stand basal area after five decades was best reflected by mineral soil and forest floor C:N but in either case included a significant species-soil interaction. The conifers with ectomycorrhizal fungi had diverging growth responses displaying either competitive (*Picea sitchensis*) or stress-tolerant (*Tsuga heterophylla*, *Pseudotsuga menziesii*) attributes, in contrast to a more generalist response by an arbuscular mycorrhizal tree (*Thuja plicata*). Despite the consistent patterns in organic matter quality we found no evidence for increased foliar P concentrations with declining element ratios (C:P_o or C:P_{total}) as we did for N. The often high C:P_o ratios (as much as 3000) of these soils may reflect a stronger immobilization sink for P than N, which, along with ongoing sorption of PO_4^-, could limit the utility of C:P_o or N:P_o to adequately reflect P supply. The dynamics and availability of soil P to trees, particularly as P_o, deserves greater attention as many perhumid rainforests were co-limited by N and P, or, in some stands, possibly P alone.

Keywords: resource stoichiometry; temperate rainforest; soil organic matter; organic phosphorus; soil C:N ratio; ectomycorrhizal conifers

1 Introduction

One of the largest global expanses of temperate rainforest (approximately 25 million ha) is located along the Pacific coast of northwestern North America (DellaSala et al., 2011), an area renowned for towering, conifer-dominated forests of extraordinary productivity and longevity (Waring and Franklin, 1979; Smithwick et al., 2002; Keith et al., 2009). Carpenter et al. (2014) highlighted the high diversity of soil types across this region and some key attributes related to soil carbon (C), nitrogen (N), and phosphorus (P) status of these forests. Most notably, temperate rainforests often have substantial accumulations of organic matter at the soil surface (forest floors) and in mineral horizons that rank among the highest in global soil C stocks (Sun et al., 2004; Homann et al., 2005; McNicol et al., 2019). Secondly, the N concentrations of certain soils can be extremely high which, along with ample moisture, underpins the tremendous productivity of many forest stands (Perakis et al., 2006; Littke et al., 2011; Kranabetter et al., 2015). In contrast, areas with low relief and imperfect drainage can have deep organic soils and scrubby, less productive forests with very limited N availability (Sajedi et al., 2012; Kranabetter et al., 2013; Bisbing and D'Amore, 2018). Thirdly, intensive weathering under high rainfall combined with acidic leachate derived from coniferous vegetation has accelerated soil podzolization (Singleton and Lavkulich, 1987; Sanborn et al., 2011), resulting in limited supplies of P in some areas that likely co-limit forest growth (Preston and Trofymow, 2000; Blevins et al., 2006; Mainwaring et al., 2014; Kranabetter et al., 2019). Temperate rainforests with these combined attributes in soil organic matter, N and P may lack analogues in forest ecosystems elsewhere (Carpenter et al., 2014), and consequently a more detailed understanding of soil nutrient limitations and dynamics would better support land management decisions regarding wood production, C budgets, and conservation priorities.

Resource stoichiometry (C:N:P) of soils may be one avenue in which the combined constraints of N and P on ecosystem productivity can be effectively evaluated (Zechmeister-Boltenstern et al., 2015; Spohn, 2016). An essential premise of ecological stoichiometry is that rates of N and P immobilization or

mineralization in soils are closely linked to microbial biomass stoichiometry (Manzoni et al., 2010; Mooshammer et al., 2014; Zechmeister-Bolenstern et al., 2015). Element ratios (C:N and C:P) reach a threshold where microbes shift from being C-limited to N- or P-limited and consequently the mineralization and release of nutrients for plant uptake during decomposition should increase with declining C:N or C:P of soil organic matter (e.g., Saggar et al., 1998; Prescott et al., 2000a; Heuck and Spohn, 2016). In addition, N:P ratios of organic matter can indicate the relative extent of N and P limitations on decomposition and primary productivity, as N:P tends to increase in older or well-weathered soils where P constraints might supersede those of N (Wardle et al., 2004, Güsewell and Gessner, 2009). In comparison to nutrient stocks (e.g., kg N ha^{-1}), which require measures of soil bulk density, coarse fragment content and organic horizon thickness, resource stoichiometry presents a potentially simpler interpretation of nutrient dynamics across diverse landscapes (Bui and Henderson, 2013; Littke et al., 2014; Van Sundert et al., 2019). Further details on the nature of soil organic matter across temperate rainforests would contribute to this comprehensive depiction of global nutrient dynamics (Tipping et al., 2016; Achat et al., 2016).

Baseline relationships in soil resource stoichiometry and ecosystem productivity should also consider the interaction with tree species. Temperate rainforests of the Pacific Northwest are exceptional because of the prevalence of evergreen conifer species, many of which host ectomycorrhizal fungi (ECM) (*Tsuga*, *Abies*, *Picea*, *Pseudotsuga* and *Pinus* spp.) or, alternatively, arbuscular (ARB) mycorrhiza (*Thuja* and *Sequoia* spp.). Waring and Franklin (1979) postulated that most deciduous hardwood species were extirpated from the Pacific Northwest by the early Pleistocene as the climate favoured evergreen trees and their ability to photosynthesize during fall and winter months instead of through the driest parts of the growing season. As a result, interspecific competition and adaptive traits related to soil fertility have arisen primarily between the coniferous species of this landscape (Lacourse, 2009; Coates et al., 2013), and exclude, with minor exceptions (*Acer*, *Prunus*), the deciduous ARB species that can dominate soils of high fertility (low C:N) elsewhere (Phillips et al., 2013; Soudzilovskaia et al., 2015; Lin et al., 2017). It should also

92 be recognized that tree species, in turn, can influence soil C and nutrient cycling through differences in litter
93 (foliar and root) quality and mycorrhizal habit, which could eventually manifest as distinct species-soil
94 stoichiometry relationships (Prescott, 2002; Augusto et al., 2002; Cools et al., 2014). Quantifying both the
95 species response to soil fertility and possible feedback of tree species on soil resources is challenging in
96 uncontrolled settings and consequently well replicated, long-term field trials may be the best avenue for
97 better understanding these interactions (Binkley, 1995; Augusto et al., 2002).
98 The quintessential rainforests along the outer west coast of British Columbia are classified as
99 'perhumid', with relatively high summer rainfall, cool summers, and transient snowpacks (DellaSala et al.,
100 2011). In the early 1960's, the British Columbia Forest Service established a multi-species planting density
101 trial across several perhumid rainforest sites of southwest Vancouver Island (Omule, 1988). The study sites
102 encompassed a considerable range in forest productivity that provided a valuable opportunity to examine
103 ECM and ARB conifer species growth and nutrition in relation to soil C, N and P stoichiometry. We follow
104 the convention of Tipping et al. (2016) in this analysis by utilizing organic P (P_o) in stoichiometry
105 comparisons (rather than total P) to focus more directly on properties of soil organic matter. The element
106 enrichment of organic matter was compared by correlations among C:N, C:P_o and N:P_o (Manzoni et al.,
107 2010; Tipping et al., 2016) for each substrate because of the typically stark differences in the C density of
108 forest floors compared to mineral soils (e.g., 50 % vs. 5 % C, respectively). In addition, we relied upon foliar
109 N and P concentrations for the more conventional interpretation of stand nutrition (e.g., Carter, 1992)
110 rather than foliar C-nutrient ratios. The objectives of our study were to 1) document the range and
111 covariation in C, N and P_o concentrations and element ratios across a variety of sites and between mineral
112 soil and forest floor substrates; 2) test the utility of soil C:N, C:P_o and N:P_o ratios as explanatory variables in
113 relation to forest productivity response; and 3) quantify any divergence in conifer growth response to soil
114 fertility gradients among ECM (*Tsuga*, *Picea*, *Pseudotsuga*) and ARB (*Thuja*) tree species.
115 **2 Methods**

2.1 Site and study descriptions

The planting density trial (EP571) was established along low elevations (< 300 m) at seven locations in the Coastal Western Hemlock very wet maritime subzone (CWHvm; Green and Klinka, 1994) of western Vancouver Island (between Port Renfrew and Bamfield, B.C.), where mean annual precipitation averages almost 3400 mm (Table 1). These areas supported old-growth forests before logging took place between 1958 and 1960, and cutblocks were subsequently slashburned in 1961. The study areas encompassed a wide range in soil nutrient and moisture regimes (Green and Klinka, 1994): steep, well-drained upland sites with poor to average nutrients; imperfectly-drained, nutrient-poor sites on modest slopes; steep, nutrient-rich sites on base-rich colluvial material; and low-lying, nutrient-rich sites with seepage (Supplemental Table 1). Soils were derived from glacial morainal, fluvial or colluvial deposits, with sandy loam to loam textures, moderate stone content and well defined Bf or Bfh horizons (Humo-Ferric or Ferro-Humic Podzols, respectively; Soil Classification Working Group, 1998).

The four conifer species utilized in the study are native to the Pacific Northwest: western hemlock (*Tsuga heterophylla* [Raf.] Sarg.), Sitka spruce (*Picea sitchensis* [Bong.] Carr.), coastal Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* [Mirb.] Franco), and western redcedar (*Thuja plicata* Donn ex D. Don in Lamb.). Single seedlots for each species were collected from the CWHvm on Vancouver Island and planted as 2+0 bareroot stock in April of 1962 (Omule, 1988). The three planting density treatments were 2.7×2.7 m (1329 stems ha^{-1}), 3.7×3.7 m (748 stems ha^{-1}), and 4.6×4.6 m (479 stems ha^{-1}). Each plot consisted of 81 trees planted in rows of 9, with the inner 7×7 rows (49 trees) tagged for remeasurement. Plot size ranged proportionally with planting density (0.037, 0.066, and 0.102 ha, respectively). All four conifer species were planted at every site, but the density treatment was not fully replicated across the study installations; San Juan and Branch 136 had only the 2.7 m spacing (n = 4), while WC1000 lacked the 4.6 m spacing (n = 8; Table 1).

2.2 Soil and tree measures

Individual tree heights and diameters at 1.3 m were measured most recently in 2014 (52 years in age). In May of 2018 we sampled the upper soil profile (i.e., the predominant rooting zone) for chemical properties mirroring the methodology of Kranabetter et al. (2019). Forest floors were cut and removed over a 10 cm diameter area to the mineral soil interface, and the forest floor depth noted at each microsite. Mineral soils were sampled to a 20 cm depth with a stony soil auger. Subsamples from 12 random microsites were composited into 3 forest floor and 3 mineral soil samples per plot (an occasional plot had very thin forest floors [< 1 cm] so in those cases we took only one or two bulked samples). Soils were air-dried, ground and sieved to 2 mm for chemical analysis. Foliar samples were collected at the end of the growing season (mid-November 2018) by searching each plot for fresh branches that had broken off during recent storms. We strove to obtain needles from current year foliage off at least 12 separate branches and combined these into 3 samples per plot. Foliar samples were oven-dried at 60° C for 24 hours and then ground for nutrient analysis.

Total C and N concentrations of soil and foliage were measured using combustion elemental analysis with a Fisons/Carlo-Erba NA-1500 NCS analyzer (Thermo Fisher Scientific, Waltham, MA) (Carter and Gregorich, 2008). Mineral soil and forest floors were finely ground to < 0.15 mm (100 mesh sieve) before combustion analysis. Total P (P_t = inorganic P_i + organic P_o) of mineral soils and forest floors was determined by an ignition method using sulfuric acid and an UV/visible spectrophotometer (O'Halloran and Cade-Menum, 2008). Foliar P was determined by ICP-Atomic Emission Spectroscopy (Teledyne Leeman Labs, Hudson, NH) following microwave digestion.

2.3 Statistics

Element ratios (C:N, C:P_o and N:P_o as molar ratios) were determined on each soil subsample and then averaged by plot for statistical analysis. The covariation among average concentrations of C, N, P_o and their element ratios was determined by pair-wise Pearson correlation coefficients (SAS Institute Inc., 2014). Element ratios as a proportional rather than absolute metric are potentially prone to spurious correlations

(Jackson and Somers, 1991) so our purpose was to aid in data visualization and confirm direction of the relationships (Tipping et al., 2016), rather than implying causation. Conifer productivity was assessed by stand basal area (m^2 ha^{-1} of live trees in 2014). Scaling factors in the conversion to hectares (to account for differences in plot size) were 27.1 for 2.7 m spacing, 15.3 for 3.7 m spacing, and 9.8 for 4.6 m spacing.

The experimental treatment effects (Species and Spacing) on soil nutrient concentrations, forest floor depth, stand basal area and stocking (stems ha^{-1}) were tested by fitting separate linear mixed effect models in SAS (Mixed Procedure, Method=REML) (SAS Institute 2014), with Site set as a random effect. We examined the relationships between stand basal area and soils by including each element ratio as a single continuous variable in the model, along with the full set of interactions. The interaction terms Spacing × Soil and Species × Spacing × Soil were consistently nonsignificant for all soil variables tested, so the final models were refitted with these terms removed. Goodness of fit for the model was evaluated by the F statistic of each parameter, as well as by the lowest overall model Akaike information criterion (AIC). Model outputs were also assessed graphically by plotting the observed dependent variable versus predicted values to ensure a relationship close to 1:1. Foliar N, P and N:P in relation to Species, Spacing and soil element ratios were examined in the same manner but the final models were refitted without Species × Spacing, Spacing × Soil, Species × Soil, and Species × Spacing × Soil interaction terms as they were consistently nonsignificant for all soil variables tested.

4 Results

4.1 Soil nutrient concentrations and resource stoichiometry by substrate

We found a considerable range in nutrient concentrations (e.g., 0.15-0.60 % N; Table 1) and strong, positive correlations among C, N, and P_o for mineral soils (Pearson $r > 0.7$) across these temperate rainforest sites (Table 2, Fig. 1). Inorganic P_i concentrations of mineral soils were relatively limited, often < 200 mg kg^{-1}, which was substantially less than the contribution of P_o to total P for a majority of plots (53 of 64 plots had P_o > 70 % of P_t). In addition to limited P_i, the extent of soil podzolization was reflected by typically low

188 pH and elevated concentrations of exchangeable Al and Fe (Table 1). Forest floors averaged 5.5 cm in
189 depth (SE 0.6) overall, and displayed a narrower range in C (31 – 55 %C, average = 46 % C [SE 0.7]) but also
190 exhibited a significant positive correlation between N and P_o concentrations (Table 2). Similar to mineral
191 substrates, the concentrations of inorganic P_i (average 110 mg kg^{-1} [SE 5.8]) were uniformly low in forest
192 floors, in contrast to P_o (average 970 mg kg^{-1} [SE 71]), and consequently contributed only a small proportion
193 of total P ($P_o \sim 90$ % of P_t in forest floors).
194 C:N ratios of the mineral soils became significantly narrower (declining from 44 to 23) with
195 increasing % C (Table 2, Fig. 2a), similar to C:P_o (range approx. 300-1200) (Table 2). In contrast, C:N of forest
196 floors widened with increasing % C (Fig. 2b, Table 2) but nevertheless C:N of both substrates were well
197 aligned across sites ($r = 0.85$, $p < 0.001$; Fig. 3a). The same symmetry in element ratios between substrates
198 was found with C:P_o ($r = 0.78$, $p < 0.001$) and, to a lesser degree, N:P_o ($r = 0.58$, $p < 0.001$) (Fig. 3b,c). In all
199 cases the relationships in element ratios were not 1:1 as the organic horizons were less concentrated than
200 mineral soils (e.g., a forest floor C:N of 40 would be matched with a mineral soil C:N of 30, on average; Fig.
201 3a). Lastly, there was typically a high degree of correlation ($r > 0.7$) in element ratios within a substrate,
202 such as C:N vs. C:P_o, for both mineral soils and forest floors (Table 2).
203 At this juncture in plantation age (52 years) we found no evidence that conifer species or planting
204 density had an effect on mineral soil nutrient concentrations or ratios (for Species, $p = 0.99$ for C:N, $p = 0.48$
205 for C:P_o, and $p = 0.35$ for N:P_o; and for Spacing, $p = 0.61$ for C:N, $p = 0.65$ for C:P_o, and $p = 0.73$ for N:P_o).
206 There was, however, a slight difference detected in N % of forest floors with Species ($p = 0.034$). Forest
207 floor N concentration under *P. menziesii* averaged 1.52 % N (SE 0.06), which was slightly greater than the
208 other three species (combined average 1.35 % N), although forest floors also tended to be thinner under *P.*
209 *menziesii* (4.7 cm [SE 0.8], on average, compared to 5.9 cm for the other three species; $p = 0.13$). Despite
210 the modification in N concentrations under *P. menziesii*, this Species effect did not extend to element ratios

of forest floors (for Species, p = 0.30 for C:N, p = 0.97 for C:P_o, and p = 0.53 for N:P_o; and for Spacing, p = 0.25 for C:N, p = 0.42 for C:P_o, and p = 0.25 for N:P_o).

4.2 Stand productivity in relation to soil resource stoichiometry

Stand density (stems ha^{-1}) in 2014 was well aligned with initial planting spacing, and there were significant differences among conifer species in stocking (Supplemental. Fig. 1). *Thuja plicata* had the least mortality (average 80 % survival), followed by *P*. *sitchensis* (76 %), *T*. *heterophylla* (71 %) and then *P*. *menziesii* (65 %). With the original study design we could only detect a significant effect of Spacing on stand basal area (2.7 m Spacing = 70 m^2 ha^{-1}, 3.7 m = 61 m^2 ha^{-1}, and 4.6 m = 53 m^2 ha^{-1}, on average) (Table 3). Including a soil element ratio of either substrate as a covariate in the analysis provided further details on Species response, particularly with C:N (Table 3). Stand basal area was well aligned with mineral soil and forest floor C:N for all four species, with a significant species interaction due to the sharper gains in *P*. *sitchensis* basal area with decreasing C:N (Fig. 4a, b and Supplemental Fig. 2). Soil C:P_o and N:P_o were also mostly significant covariates in the analysis of basal area, but neither ratio invoked the same degree of Species response (i.e., lower F values) nor significant Species × Soil interactions, and both models had poorer AIC scores than C:N (Table 3). For comparison we also tested C:P_t and N:P_t of each substrate against basal area but found virtually identical model outputs as C:P_o and N:P_o (data not shown).

4.3 Foliar nutrition in relation to soil resource stoichiometry

Foliage collections were not entirely successful as a few plots, particularly under *P*. *sitchensis*, had insufficient branches to obtain three composite subsamples (n = 167 from a target of 192 subsamples, and with two *P*. *sitchensis* plots removed from the analysis). Carbon concentrations of the foliage were very uniform, averaging 52.9 (SE 0.17) for *T*. *plicata*, 52.3 for *P*. *menziesii* (0.17), 52.3 for *T*. *heterophylla* (0.18) and 51.9 (0.19) for *P*. *sitchensis*. We were able to demonstrate an overall gain in foliar N with declining soil C:N ratio, both for mineral and forest floor substrates, as well as a significant difference in foliar N among Species due to the enhanced nutrition of *P*. *sitchensis* (Table 4; Fig. 5a; note that Species × Soil interaction p

= 0.538 for mineral soil and p = 0.305 for forest floor). In contrast, there was no relationship between foliar P and C:P_o ratio for either substrate (Table 4, Fig. 5b; Species × Soil interaction p = 0.533 for mineral soil, p = 0.561 for forest floor). The better predictor of foliar P was instead the concentration of P_i in soils, with again significant differences among Species largely due to *P. sitchensis* (Table 4; Supplemental Fig. 3; Species × Soil interaction p = 0.468 for mineral soil, p = 0.425 for forest floor). We also tested soil P_t and P_o concentrations in relation to foliar P but neither of these attributes were significant (for P_t, p = 0.41 for forest floors and p = 0.12 for mineral soil; for P_o, p = 0.94 for mineral soil; p = 0.61 for forest floors). Foliar N:P ratios across the plots averaged 19.5 (SE 0.8) for *T. plicata*, 18.2 (SE 0.8) for *P. menziesii*, 20.6 (SE 0.8) for *T. heterophylla*, and 17.4 (SE 1.1) for *P. sitchensis*. We were unable to find a significant relationship between foliar N:P and soil N:P_o for either substrate (Table 4).

5 Discussion

5.1 Organic matter quality and conifer species productivity

Our results provide further details on baseline nutrition and resource stoichiometry for soils of perhumid rainforests along the southwest coast of British Columbia, and complement studies of temperate rainforests in the southern hemisphere (Parfitt et al., 2005; Turner et al., 2012). Soil C and N concentrations were at times very high (up to 12 % C and 0.6 % N for mineral soil), as has been reported previously across this region (Carpenter et al., 2014; Kranabetter, 2019; McNichol et al., 2019), while P_i was for the most part notably limited (< 200 mg kg^{-1}) in comparison to less-weathered soils on the drier east side of Vancouver Island (Kranabetter et al., 2019). The intense rainfall, acidic leachate (from coniferous vegetation), and, at some sites, possible NO_3^- losses (Perakis et al,. 2013) have combined to reduce soil pH and enhance the sorption of P_i with reactive (Fe and Al oxides) soil components (a sink-driven P limitation; Vitousek et al., 2010). Some differences in parent materials (e.g., colluvial slope, fluvial terrace, morainal till) may also have contributed to the inherent range in P content of these soils (Kranabetter and Banner, 2000). The high degree of positive correlations in C, N and P_o concentrations for mineral soils (and between N and P_o for

forest floors) was consistent with coniferous forests in Oregon (Perakis et al., 2013) and global datasets of soil organic matter (Xu et al., 2013; Tipping et al., 2016). Somewhat surprisingly we did not find evidence for decoupling of P_o from organic matter as suggested by Yang and Post (2011) for highly-weathered soils. Nevertheless, we surmise from the generally low soil P_i concentrations, modest to high deficiencies in foliar P (0.10-0.15 %; Carter, 1992) for a large number of stands[1] and elevated range (16-25) in foliar N:P (greater than a hypothesized threshold of 14 to delineate N-only deficiencies; Reich and Oleksyn, 2004) that these perhumid rainforests were often limited by N and P together (Blevins et al., 2006), or, in some stands, possibly P alone. The dynamics and availability of soil P to trees, particularly P_o, is challenging to reconcile given such strong and consistent patterns in soil organic matter quality.

The clear relationship between mineral soil and forest floor C:N with stand productivity and foliar N was consistent with many other biomes (Littke et al., 2014; Albertini et al., 2015; Van Sundert et al., 2018) and affirms the widely recognized relationship of increasing N availability with declining soil C:N (Booth et al., 2005). In contrast, $C:P_o$ and $N:P_o$ were less aligned with species growth response (and likely only significant as a surrogate for C:N) and not a significant predictor of foliar P, despite the expectation of positive correlations in net N and P mineralization rates (Heuck and Spohn, 2016). Estimates of a critical $C:P_o$ for gross P mineralization of leaf litter range from 1400-1800 (Mooshammer et al., 2012; Heuck and Spohn, 2016), but thresholds for forest floor horizons and mineral soil are likely much lower (perhaps < 500; Saggar et al., 1998; Heuck and Spohn, 2016). The substrate distinction is important as very few of our study sites had $C:P_o$ ratios < 500, suggesting pervasive, low quality organic matter in regards to P. Furthermore, the element ratios of saprotrophic fungi, as key decomposers, in these perhumid rainforests averaged 120 and 10 for C:P and C:N, respectively (Kranabetter et al., 2019), which when compared to soil organic matter would indicate a greater elemental imbalance for P, especially in forest floors (Mooshammer et al., 2014). The biotic (microbes, plants) competition for P is also very likely exacerbated by abiotic competition for

[1] note that *P. menziesii*, *T. heterophylla* and *T. plicata* averaged 0.20% P on less-weathered soils of eastern Vancouver Island (Kranabetter et al., 2019 and unpub. data)

282 phosphate (PO_4^-) via sorption to Fe and Al oxides, much more so than would be present for NH_4^+ or NO_3^-
283 (Olander and Vitousek, 2004). A greater sink strength via immobilization and sorption for PO_4^- would
284 require conifers to bypass mineralization of P by decomposers to some degree and instead access organic P
285 more directly for uptake. A concurrent study of extracellular enzyme activity associated with ECM roots of
286 *P. menziesii* has revealed substantial increases in P-acquiring enzymes (J. Meeds, pers. comm.) that are
287 likely acting upon the orthophosphate monoesters and diesters of organic P (Cade-Menum et al., 2000;
288 Preston and Trofymow, 2000). Despite the expected contribution of P_o to forest nutrition, however, we
289 found it more effective to gauge P availability through soil P_i concentrations (as the only significant
290 correlate with foliar P), but other methods may prove to be more sensitive as a measure of plant-available
291 P_o (DeLuca et al., 2015; Darch et al., 2016).
292 One unique aspect of soil organic matter found here was a decrease in mineral soil C:N and C:P_o
293 ratios with increasing soil C % (Fig 2a), in contrast to the inverse relationships described by Tipping et al.
294 (2016). This may reflect the significant legacy of N-fixing red alder (*Alnus rubra*) in coastal forest
295 ecosystems, which has been found to promote soil C sequestration and P mobilization while simultaneously
296 adding high quality (low C:N) litter (Binkley, 2005; Perakis and Pett-Ridge, 2019). A second key source of N-
297 rich litter could be from epiphytic cyanolichens and cyanobacteria-bryophyte associations (Antoine, 2004;
298 Lindo and Whiteley, 2011). Canopy lichens and bryophytes are noteworthy in low-frequency disturbance
299 ecosystems such as rainforests because they produce a steady input of N while growing independently of
300 the soil environment (Menge and Hedin, 2009). Red alder, in comparison, is an early-seral species that can
301 be hindered in its establishment and vigour by low P_i availability (Brown et al., 2011; Kranabetter et al.,
302 2013). Hedin et al. (2009) described a similar N paradox in tropical forests, and proposed N-fixing epiphytes
303 as one mechanism that allows soil N regimes to increase despite soil P_i deficiencies or physiological down-
304 regulation of N-fixation in high soil N environments.
305 **5.2 Conifer species interactions by ARB and ECM mycorrhizal guild**

306 The more significant differences in species productivity in relation to soil C:N was among the ECM
307 species rather than solely between mycorrhizal types. *Tsuga heterophylla* and *P*. *menziesii* had the most
308 limited increase in basal area with declining C:N, a finding that was similar for these species in correlations
309 of site index with organic matter quality across a broader region of the US northwest (Edmonds and
310 Chappel, 2004). These two conifers would be considered relatively stress-tolerant under the C-S-R model
311 (Hodgson et al., 1999) as their growth on high C:N soils outperformed that of either *P*. *sitchensis* or *T*.
312 *plicata*. *Picea sitchensis*, in contrast, would clearly be a strong competitor as exemplified by the impressive
313 linear increase in biomass with declining soil C:N. Perakis and Sinkhorn (2011) found *P*. *menziesii*
314 productivity plateaued with increasing N mineralization rates, but this relationship with N supply may be
315 species-dependent and not necessarily apply to *P*. *sitchensis*. A possible functional trait related to this
316 growth response is the low capacity of ECM roots of *P*. *menziesii* to maximize uptake of NO_3^-, as would be in
317 plentiful supply on these richer soils (Prescott et al., 2000b; Perakis et al., 2006), but whether *P*. *sitchensis*
318 ECM roots would perform any differently has not been established (Boczulak et al., 2014; Hawkins and
319 Kranabetter, 2017). As an aside, we noted some naturally-regenerated *Abies amabilis* within the study
320 areas that had the same girth as *P*. *sitchensis*, so it is likely *Abies* would be an equally competitive member
321 of these rainforest ecosystems. *Thuja plicata* as the only ARB tree species in the trial was intermediate in
322 growth response to soil C:N, and displayed no particular advantage in foliar N or P over the ECM conifers. .
323 *Thuja plicata* is recognized to have a wide ecological amplitude, from highly productive to very nutrient
324 poor or wet sites (Antos et al., 2016), and so would fit well within a generalist or intermediate C-S strategy.
325 The coexistence of ARB and ECM conifers affirms each mycorrhizal type is competent in the acquisition of
326 nutrients from organic and inorganic sources (Hodge, 2017), and the contrasting patterns in productivity
327 emphasize a diversity of traits within mycorrhizal guilds rather than a simple dichotomy in the distribution
328 of ARB and ECM trees between N-rich and N-poor soils (Koele et al., 2012; Dickie et al., 2014).

329 **5.3 Conifer species effects on soil organic matter quality**

After five decades the possibility of tree species effects on soil nutritional status is also worth considering. Enhanced N inputs via foliar litter are considered a positive reinforcement in sustaining soil fertility (Prescott, 2002), which would be consistent with the overall trend in foliar N across this productivity gradient. It was interesting to note that correlations between substrates for C:N were closer to a 1:1 relationship than $C:P_o$, indicating that P cycling through litterfall has been greatly impeded in comparison to N. The small increase in forest floor N concentrations under *P. menziesii* may reflect slightly better litter quality (lower lignin content) and potentially faster decomposition rates for this species (Vesterdal and Raulund-Rasmussen, 1998; Thomas and Prescott, 2000). Overall, however, there were no clear differences in element ratios of either forest floors or mineral soils by tree species, which leads us to conclude these conifers lack substantial enough differences in leaf or root litter to have more profoundly and consistently diverged from inherent soil conditions. The glaciated landscape along Vancouver Island has been in the current iteration of temperate perhumid rainforests for at least 7500 years (Brown and Hebda, 2002; Lacourse, 2005), during which time the various site drivers (e.g., drainage, slope, soil mineralogy, vegetation) have collectively produced the very wide disparity in soil fertility found today. It would undoubtedly take a very sizable influence of tree species on C, N or P cycling to overcome the inertia of site type in such complex terrain (Prescott et al., 2000b). For example, an ecologically minor shift in forest floor C:N from 50 to 40 (equivalent to an average increase in foliar N from 1.17 % to 1.23 %; Fig. 5a), would require a gain of approximately 200 kg ha^{-1} in N (based on a depth of 5 cm and bulk density of 0.14 g cm^{-3}), which would seem implausible for coniferous stands to confer in mere decades. In addition, much of the focus on tree species effects has focused on surface organic horizons, but given the symmetry in element ratios between mineral and forest floor substrates we would argue that a true tree species effect should extend throughout the rooting zone of the soil profile.

5.4 Regional significance of P deficiencies

With mean annual precipitation near 3500 mm, these perhumid rainforests are at the extreme range in rainfall for the Pacific west coast (Carpenter et al., 2014). The evidence for P constraints outlined in this trial have been substantiated by fertilizer studies of very similar perhumid forests along northern Vancouver Island (Blevins et al., 2006; Negrave et al., 2007), but other areas in the Pacific Northwest have shown more variation in growth response to added P (Radwan et al., 1991; Mainwaring et al. 2014). Lower precipitation levels or differences in soil mineralogy could mediate rates of soil podzolization and reductions in P_i so the full regional extent of these presumed P deficiencies should be examined and tested more thoroughly. We expected some utility in soil N:P_o as a measure of forest productivity (Wardle et al., 2004) but it is possible the mismatch in element thresholds for N and P_o turnover, as discussed above, reduced the efficacy of this index. Ultimately soil C:N and soil P_i together might best explain variations in rainforest productivity but the limitations in study size (64 plots distributed among 4 conifer species and 3 planting densities) prevented an adequate statistical analysis of all main factor interactions for two soil covariates. Phosphorus deficiencies are also relevant in the noted nutrient exchange between marine and terrestrial environments through anadromous salmon biomass (Cederholm et al., 1999). Our results support the likelihood that both salmon-derived N and P contribute to alleviating nutrient limitations of *P. sitchensis* on riparian sites of the Pacific west coast (Reimchen and Arbellay, 2019).

6 Conclusions

Quantifying the fundamental relationships between soil element ratios and conifer species productivity was facilitated in this study by the planting of single provenances at controlled densities, alongside a uniform macroclimate and narrow elevation band among plot locales. Soil organic matter content of perhumid rainforests was often high and displayed strong positive correlations in soil C, N and P_o concentrations. Inorganic P was generally in low supply, reflecting soil podzolization processes, and contributed a relatively minor proportion of total P. Element ratios of C:N and C:P_o were well correlated in forest floors and mineral soils, yet only C:N was an effective measure of forest productivity and foliar

377 nutrition. High C:P_o ratios (as much as 3000) may reflect a stronger immobilization sink for P than N, which,
378 along with ongoing sorption of PO_4^-, could limit the capacity of organic P turnover to meet tree
379 requirements. The interplay of conifers and soils after five decades suggests species growth response to
380 inherent soil C:N was more intrinsic to ecosystem productivity than any reciprocal effects of tree species on
381 soil resources. The conifers with ectomycorrhizal fungi had widely diverging responses in basal area over
382 the N gradient, illustrating the extent of both competitive (*Picea sitchensis*) and stress-tolerant (*Tsuga*
383 *heterophylla*, *P. menziesii*) traits for these tree species. The chemical nature and availability of soil P to
384 trees, particularly as P_o, deserves further investigation as many of these perhumid rainforests were co-
385 limited by both N and P, or, in some stands, possibly P alone.
386

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Data Availability

All data related to the study archived with Dryad at https://doi.org/10.5061/dryad.0gb5mkkwr

Author Contribution

LD was responsible for EP571 administration, including research site maintenance, tree measurements and data archiving; JK conceived study design for soil covariates; JK and AS undertook field soil sampling and laboratory preparation; JK and AS contributed statistical analysis; JK wrote manuscript with substantial contributions by AS and LD.

Competing interests

The authors declare that they have no conflict of interest.

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631 Figure 1. Mineral soil (0-20 cm) N and P_o concentrations in relation to mineral soil C across the study sites.

632 Figure 2. Trends in C:N molar ratios of a) mineral soil (0-20 cm) and b) forest floors in relation to substrate C

633 concentrations.

634 Figure 3. Correlation in resource stoichiometry for a) C:N molar ratio, b) C:P_o molar ratio, and c) N:P_o moliar

635 ratio between mineral soil and forest floor substrates. A 1:1 relationship is depicted by the gray lines.

636 Figure 4. a) Basal area by Species in relation to mineral soil C:N molar ratio (all planting densities included),

637 and b) linear regressions between stand basal area and mineral soil C:N, fitted by Spacing, Species and

638 Species × Soil interactions (output averaged across planting density; Species × Soil C:N $p = 0.009$, $r^2 = 0.56$).

639 Slope of the C:N regression was steepest for *Picea sitchensis* (Ss; -3.40), followed by *Thuja plicata* (Cw; -

640 1.67), *Pseudotsuga menziesii* (Fd; -0.84), and *Tsuga heterophylla* (Hw; -0.70).

641 Figure 5. a) Foliar N (%) in relation to forest floor C:N molar ratio, and b) foliar P (%) in relation to forest

642 floor C:P_o ratio. *Thuja plicata* (western redcedar) = Cw; *Pseudotsuga menziesii* (Douglas-fir) = Fd; *Tsuga*

643 *heterophylla* (western hemlock) = Hw; *Picea sitchensis* (Sitka spruce) = Ss.

644

Table 1. Study site location and selected plot features, including the range in mineral soil (0-20 cm) concentrations of total C, N, P_t (inorganic P_i + organic P_o), pH, and exchangeable Al + Fe. Number of plots (n) reflects the extent of conifer species × planting density treatments per site.

Site	n	Latitude (N)	Longitude (W)	Elev. (m)	MAT* (°C)	MAP (mm)	Soil C (%)	Soil N (%)	Soil P_t (mg kg^{-1})	pH (in H_2O)	Exch Al (cmol kg^{-1})	Exch Fe (cmol kg^{-1})
WC1000	8	48°33'12"	124°21'02"	250	8.1	3443	5.5 – 8.2	0.17 – 0.37	209 – 734	4.01-4.95	1.34-4.96	0.02-0.29
Fairy Lake	12	48°35'55"	124°19'18"	300	8.0	3537	5.0 – 11.7	0.14 – 0.45	121 – 527	3.86-5.02	2.05-9.99	0.08-0.48
San Juan	4	48°35'17"	124°11'59"	60	8.7	3035	6.2 – 7.7	0.24 – 0.36	633 – 1217	4.14-4.89	1.78-6.98	0.01-0.55
Klanawa	12	48°49'11”	124°46'29"	95	8.9	3258	7.0 – 12.4	0.32 – 0.59	625 – 1149	4.09-4.70	2.52-6.21	0.08-0.36
Branch 136	4	48°53'52"	124°54'41"	140	8.8	3189	8.3 – 11.3	0.33 – 0.50	477 – 746	4.38-4.78	2.12-5.95	0.05-0.24
Branch 167	12	48°54'51”	124°49'21"	220	8.4	3448	5.7 – 11.7	0.19 – 0.44	351 – 654	4.11-5.61	0.32-6.73	0.01-0.41
Branch 247	12	48°51'00”	124°53'02"	265	8.2	3557	2.9 – 10.8	0.13 – 0.50	166 – 907	3.84-4.88	1.31-9.72	0.02-0.58

* mean annual temperature (MAT) and precipitation (MAP) for the 30-yr period 1961-1990 were obtained for each location by querying ClimateWNA ver 4.72 (Wang et al., 2012) with latitude, longitude and elevation

647 Table 2. Pearson correlation r and *p* values (in brackets, < 0.05 in bold) among total C, N, P_o concentrations

648 and associated molar element ratios of the mineral soil (0-20 cm) and forest floor.

	N	P_o	C:N	C:P_o	N:P_o
Mineral soil					
C	0.92 (**< *0.001***)	0.71 (**< *0.001***)	-0.48 (**< *0.001***)	-0.36 (***0.004***)	-0.21 (0.101)
N	-	0.87 (**< *0.001***)	-0.75 (**< *0.001***)	-0.59 (**< *0.001***)	-0.38 (***0.002***)
P_o		-	-0.77 (**< *0.001***)	-0.82 (**< *0.001***)	-0.73 (**< *0.001***)
C:N			-	0.81 (**< *0.001***)	0.55 (***0.001***)
C:P_o				-	0.93 (**< *0.001***)
Forest floor					
C	-0.01 (0.91)	-0.32 (***0.011***)	0.51 (**< *0.001***)	0.61 (**< *0.001***)	0.52 (**< *0.001***)
N	-	0.74 (**< *0.001***)	-0.84 (**< *0.001***)	-0.59 (**< *0.001***)	-0.34 (***0.006***)
P_o		-	-0.71 (**< *0.001***)	-0.84 (**< *0.001***)	-0.82 (**< *0.001***)
C:N			-	0.77 (**< *0.001***)	0.48 (**< *0.001***)
C:P_o				-	0.91 (**< *0.001***)

649

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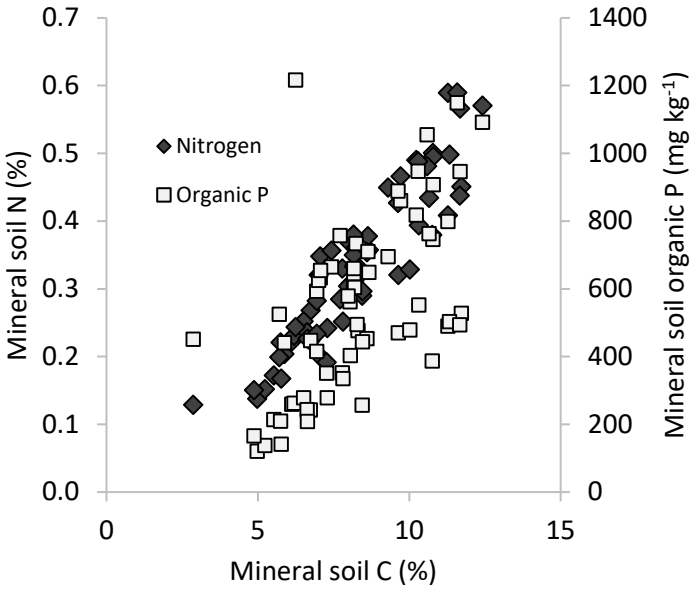
Table 3. Conifer species basal area (m^2 ha^{-1}) in 2014 (stand age 52 years) in relation to planting density (1329, 748 and 479 stems ha^{-1}) and mineral soil (0-20 cm) or forest floor resource stoichiometry (as molar ratios; *p* values < 0.05 in bold).

		No soil variable		Soil C:N		Soil C:P_o		Soil N:P_o	
	Df	F value	*p* value	F value	*p* value	F value	*p* value	F value	*p* value
Mineral soil									
Species	3	2.12	*0.110*	4.60	***0.007***	2.11	*0.113*	1.09	*0.363*
Spacing	2	7.12	***0.002***	11.94	***0.001***	10.06	***0.001***	7.88	***0.001***
Species × Spacing	6	0.72	*0.634*	0.91	*0.495*	0.72	*0.632*	0.54	*0.774*
Soil variable	1	na		20.85	***0.001***	15.15	***0.001***	6.61	***0.014***
Soil × Species	3			3.75	***0.018***	1.27	*0.296*	0.82	*0.491*
AIC fit		*450.2*		*422.8*		*460.0*		*437.4*	
Forest floor									
Species	3	Same as above		3.97	***0.014***	2.11	*0.114*	1.29	*0.290*
Spacing	2			10.92	***0.001***	7.29	***0.002***	6.80	***0.003***
Species × Spacing	6			0.82	*0.559*	0.51	*0.799*	0.46	*0.818*
Soil variable	1			14.49	***0.001***	7.62	***0.009***	3.15	*0.083*
Soil × Species	3			3.01	***0.041***	0.94	*0.431*	0.77	*0.547*
AIC fit				*420.7*		*463.7*		*435.9*	

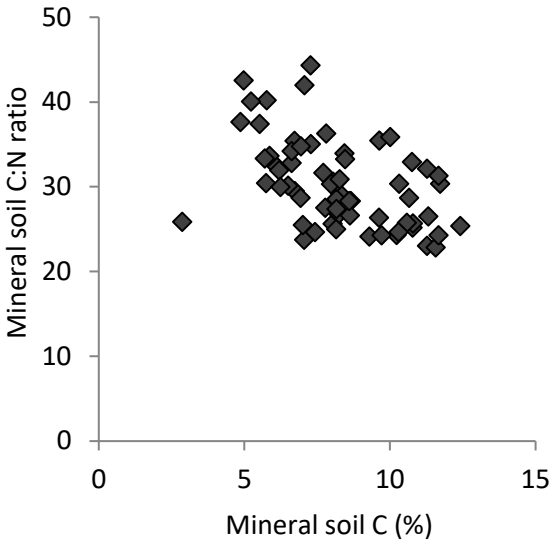
Table 4. Conifer species foliar nitrogen (N) and phosphorus (P) concentrations and molar N:P ratios in relation to planting density (1329, 748 and 479 stems ha^{-1}) and mineral soil (0-20 cm) or forest floor resource stoichiometry (as molar ratio; *p* values < 0.05 in bold).

		Mineral soil		Forest floor	
	Df	F value	*p* value	F value	*p* value
Foliar N%					
Species	3	9.32	***< 0.001***	7.72	***0.001***
Spacing	2	0.39	*0.677*	0.97	*0.387*
Soil C:N	1	8.13	***0.006***	19.16	***< 0.001***
Foliar P%					
Species	3	12.56	***< 0.001***	11.94	***< 0.001***
Spacing	2	0.32	*0.729*	0.36	*0.703*
Soil C:P_o	1	2.00	*0.164*	0.01	*0.984*
Foliar P%					
Species	3	11.00	***< 0.001***	12.59	***< 0.001***
Spacing	2	0.91	*0.408*	0.70	*0.503*
Soil P_i	1	13.45	***0.001***	6.76	***0.012***
Foliar N:P					
Species	3	5.02	***0.004***	4.21	***0.010***
Spacing	2	1.15	*0.324*	1.10	*0.340*
Soil N:P_o	1	2.10	*0.154*	0.61	*0.439*

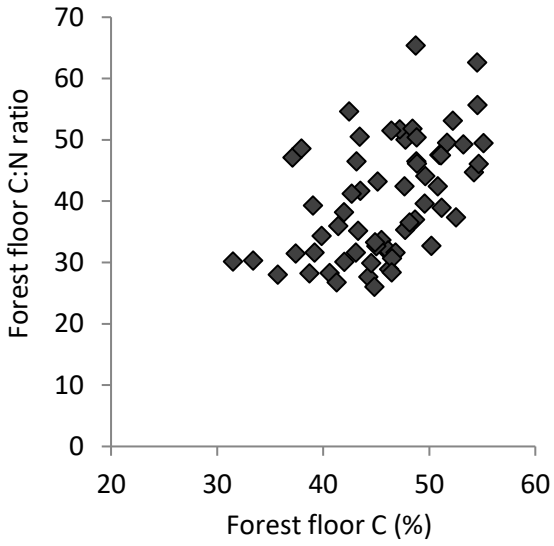

0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
1400
1200
1000
800
600
400
200
0
0
5
10
15
Nitrogen
Organic P
Mineral soil N (%)
Mineral soil organic P (mg kg-1)
Mineral soil C (%)

659

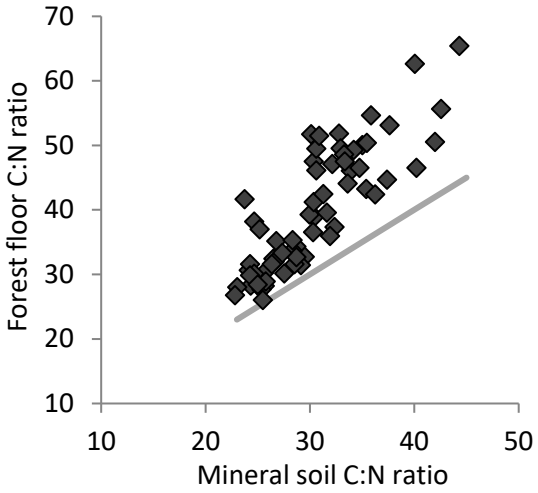
660


Mineral soil C:N ratio
Mineral soil C (%)
0
10
20
30
40
50
0
5
10
15

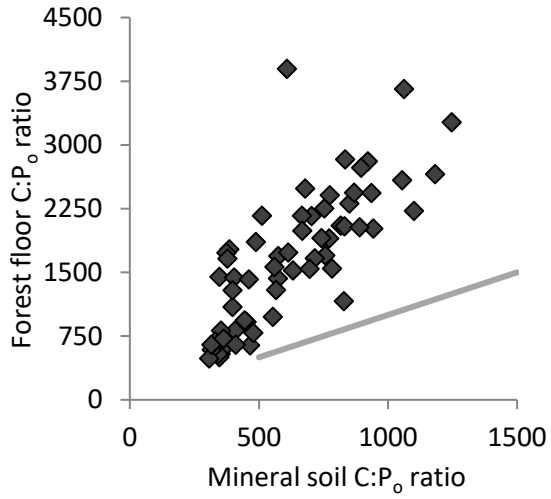
(a)


Forest floor C:N ratio
Forest floor C (%)
0
10
20
30
40
50
60
70
20
30
40
50
60

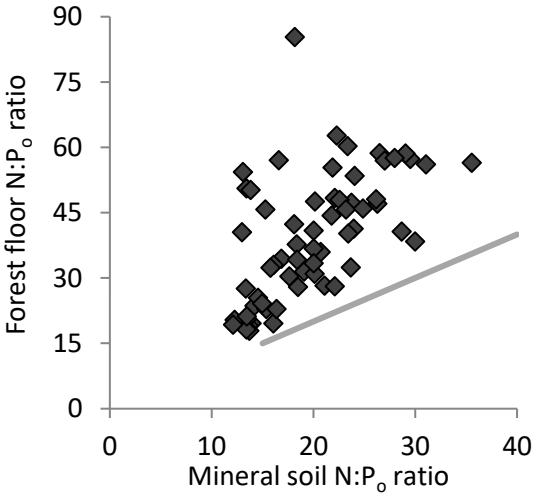
(b)



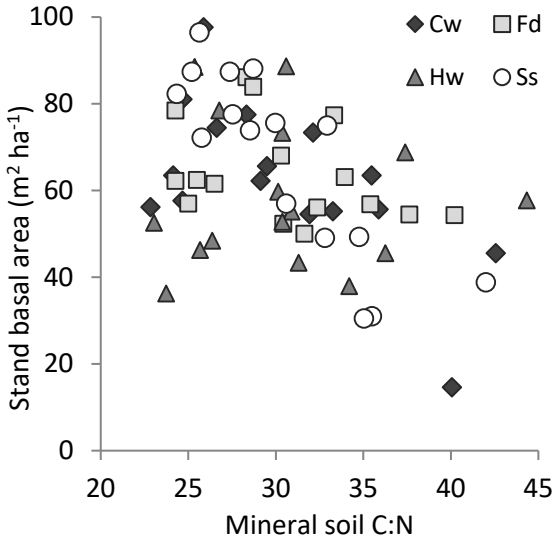
663 (a)



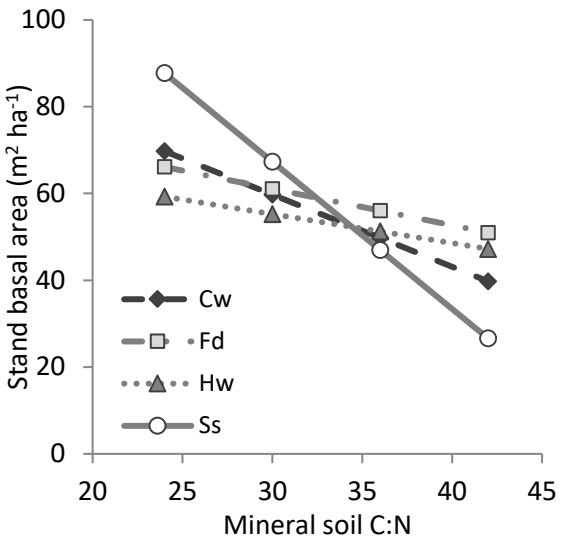
664 (b)



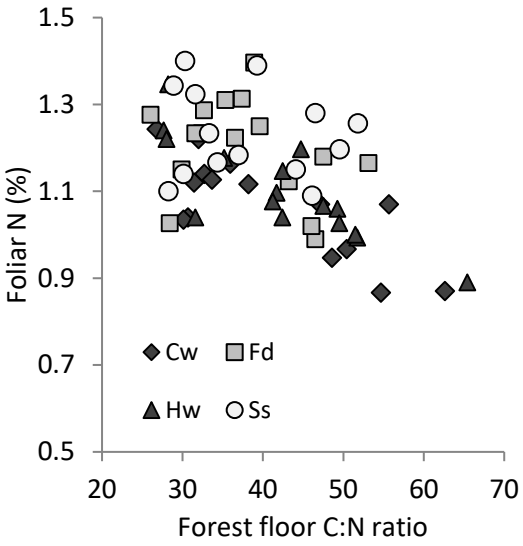
665 (c)


Cw
Fd
Hw
Ss
Stand basal area (m² ha⁻¹)
Mineral soil C:N
0
20
40
60
80
100
20
25
30
35
40
45

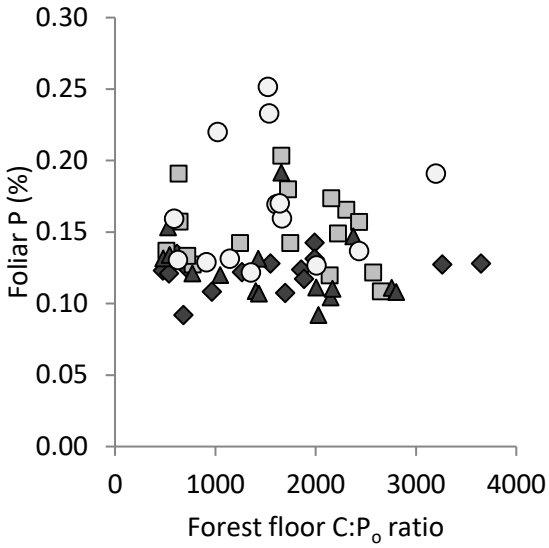
(a)


Cw
Fd
Hw
Ss
Stand basal area (m² ha⁻¹)
Mineral soil C:N
0
20
40
60
80
100
20
25
30
35
40
45

(b)


1.5
1.3
1.1
0.9
0.7
0.5
Foliar N (%)
Cw
Fd
Hw
Ss
20
30
40
50
60
70
Forest floor C:N ratio

(a)


0.30
0.25
0.20
0.15
0.10
0.05
0.00
Foliar P (%)
0
1000
2000
3000
4000
Forest floor C:P$_o$ ratio

(b)