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5 **Soil carbon, nitrogen and phosphorus stoichiometry (C:N:P) in relation to conifer species**

6 **productivity and nutrition across British Columbia perhumid rainforests**

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22 **Abstract**

23   Temperate rainforest soils of the Pacific Northwest are often carbon (C) rich and encompass a wide

24 range in fertility reflecting varying nitrogen (N) and phosphorus (P) availability. Soil resource stoichiometry

25 (C:N:P) may provide an effective measure of site nutrient status and help refine species-dependent patterns

26 in forest productivity across edaphic gradients. We described the nature of soil organic matter for mineral

27 soil and forest floor substrates across very wet (perhumid) rainforest sites of southwestern Vancouver

28 Island (Canada), and employed soil element ratios as covariates in a long-term planting density trial to test

29 their utility in defining basal area growth response of four conifer species. There were strong positive

30 correlations in mineral soil C, N and organic P (P_o) concentrations, and close alignment in C:N and C:P_o both

31 among and between substrates. Stand basal area after five decades was best reflected by soil C:N but

32 included a significant species-soil interaction. The conifers with ectomycorrhizal fungi had diverging growth

33 responses displaying either competitive (*Picea sitchensis*) or stress-tolerant (*Tsuga heterophylla*,

34 *Pseudotsuga menziesii*) attributes, in contrast to a more generalist response by an arbuscular mycorrhizal

35 tree (*Thuja plicata*). Despite the consistent patterns in organic matter quality we found no evidence via

36 foliar nutrition for increased P availability with declining element ratios as we did for N. The often high C:P_o

37 ratios (as much as 3000) of these soils may reflect a stronger immobilization sink for P than N, which, along

38 with ongoing sorption of PO_4^-, could limit the utility of C:P_o or N:P_o to adequately reflect P supply. The

39 dynamics and availability of soil P to trees, particularly as P_o, deserves greater attention as many perhumid

40 rainforests were co-limited by N and P, or, in some stands, possibly P alone.

41 **Keywords:** resource stoichiometry; temperate rainforest; soil organic matter; organic phosphorus; soil C:N

42 ratio; ectomycorrhizal conifers

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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 regime in certain soils

can be extremely rich 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, global 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

68   mineralization in soils are closely linked to microbial biomass stoichiometry (Manzoni et al., 2010;

69   Mooshammer et al., 2014; Zechmeister-Bolenstern et al., 2015). Element ratios (C:N and C:P) reach a

70   threshold where microbes shift from being C-limited to N- or P-limited and consequently the mineralization

71   and release of nutrients for plant uptake during decomposition should increase with declining C:N or C:P of

72   soil organic matter (e.g., Saggar et al., 1998; Prescott et al., 2000a; Heuck and Spohn, 2016). In addition,

73   N:P ratios of soil and plants can indicate the relative extent of N and P limitations on primary productivity,

74   as N:P tends to increase in older or well-weathered soils where P constraints might supersede those of N

75   (Güsewell, 2004; Wardle et al., 2004). The utility of resource stoichiometry in models of nutrient dynamics

76   and ecosystem productivity has spurred interest in quantifying these relationships for soil organic matter

77   across a range of landscapes (Bui and Henderson, 2013; Littke et al., 2014; Van Sundert et al., 2019).

78   Further details on the nature of soil organic matter across temperate rainforests would contribute to this

79   comprehensive depiction of global nutrient dynamics (Tipping et al., 2016; Achat et al., 2016).

80   Baseline relationships in soil resource stoichiometry and ecosystem productivity should also

81   consider the interaction of tree species. Temperate rainforests of the Pacific Northwest are exceptional

82   because of the prevalence of evergreen conifer species, many of which host ectomycorrhizal fungi (ECM)

83   (*Tsuga*, *Abies*, *Picea*, *Pseudotsuga* and *Pinus* spp.) or, alternatively, arbuscular (ARB) mycorrhiza (*Thuja* and

84   *Sequoia* spp.). Waring and Franklin (1979) postulated that most deciduous hardwood species were

85   extirpated from the Pacific Northwest by the early Pleistocene as the climate favoured evergreen trees and

86   their ability to photosynthesize during fall and winter months instead of through the driest parts of the

87   growing season. As a result, interspecific competition and adaptive traits related to soil fertility have arisen

88   primarily between the coniferous species of this landscape (Lacourse, 2009; Coates et al., 2013), and

89   exclude, with minor exceptions (*Acer*, *Prunus*), the deciduous ARB species that can dominate soils of high

90   fertility (low C:N) elsewhere (Phillips et al., 2013; Soudzilovskaia et al., 2015; Lin et al., 2017). It should also

91   be recognized that tree species, in turn, can influence soil C and nutrient cycling through differences in litter

92   (foliar and root) quality and mycorrhizal habit, which could eventually manifest as distinct species-soil

93   stoichiometry relationships (Prescott, 2002; Augusto et al., 2002; Cools et al., 2014). Quantifying both the

94   species response to soil fertility and possible feedback of tree species on soil resources is challenging in

95   uncontrolled settings and consequently well replicated, long-term field trials may be the best avenue for

96   better understanding these interactions (Binkley, 1995; Augusto et al., 2002).

97   The quintessential rainforests along the outer west coast of British Columbia are classified as

98   'perhumid', with relatively high summer rainfall, cool summers, and transient snowpacks (DellaSala et al.,

99   2011). In the early 1960's, the British Columbia Forest Service established a multi-species planting density

100   trial across several perhumid rainforest sites of southwest Vancouver Island (Omule, 1988). The study sites

101   encompassed a considerable range in forest productivity that provided a valuable opportunity to examine

102   ECM and ARB conifer species growth and nutrition in relation to soil C, N and P stoichiometry. We follow

103   the convention of Tipping et al. (2016) in this analysis by utilizing organic P (P_o) in stoichiometry

104   comparisons (rather than total P) to focus more directly on properties of soil organic matter. In addition,

105   we present nutrient concentration and stoichiometric ratios for both substrates of the soil profile because

106   of the typically stark differences in the C density of forest floors compared to mineral soils (e.g., 50 % vs. 5

107   % C, respectively). The objectives of our study were to 1) document the range and covariation in C, N and

108   P_o concentrations and element ratios across a variety of sites and between mineral soil and forest floor

109   substrates; 2) test the utility of soil C:N, C:P_o and N:P_o ratios as explanatory variables in relation to forest

110   productivity response; and 3) quantify any divergence in conifer growth response to soil fertility gradients

111   among ECM (*Tsuga*, *Picea*, *Pseudotsuga*) and ARB (*Thuja*) tree species.

112   **2 Methods**

113   **2.1 Site and study descriptions**

114   The planting density trial (EP571) was established along low elevations (< 300 m) at seven locations

115   in the Coastal Western Hemlock very wet maritime subzone (CWHvm; Green and Klinka, 1994) of western

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116   Vancouver Island (between Port Renfrew and Bamfield, B.C.), where mean annual precipitation averages

117   almost 3400 mm (Table 1). These areas supported old-growth forests before logging took place between

118   1958 and 1960, and cutblocks were subsequently slashburned in 1961. The study areas encompassed a

119   wide range in soil nutrient and moisture regimes (Green and Klinka, 1994): steep, well-drained upland sites

120   with poor to average nutrients; imperfectly-drained, nutrient-poor sites on modest slopes; steep, nutrient-

121   rich sites on base-rich colluvial material; and low-lying, nutrient-rich sites with seepage. Soils were derived

122   from glacial morainal, fluvial or colluvial deposits, with sandy loam to loam textures, moderate stone

123   content and well defined Bf or Bfh horizons (Humo-Ferric or Ferro-Humic Podzols, respectively; Soil

124   Classification Working Group, 1998).

125   The four conifer species utilized in the study are native to the Pacific Northwest: western hemlock

126   (*Tsuga heterophylla* [Raf.] Sarg.), Sitka spruce (*Picea sitchensis* [Bong.] Carr.), coastal Douglas-fir

127   (*Pseudotsuga menziesii* var. *menziesii* [Mirb.] Franco), and western redcedar (*Thuja plicata* Donn ex D. Don

128   in Lamb.). Single seedlots for each species were collected from the CWHvm on Vancouver Island and

129   planted as 2+0 bareroot stock in April of 1962 (Omule, 1988). The three planting density treatments were

130   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

131   consisted of 81 trees planted in rows of 9, with the inner 7 × 7 rows (49 trees) tagged for remeasurement.

132   Plot size ranged proportionally with planting density (0.037, 0.066, and 0.102 ha, respectively). All four

133   conifer species were planted at every site, but the density treatment was not fully replicated across the

134   study installations; San Juan and Branch 136 had only the 2.7 m spacing (n = 4), while WC1000 lacked the

135   4.6 m spacing (n = 8; Table 1).

136   **2.2 Soil and tree measures**

137   Individual tree heights and diameters at 1.3 m were measured most recently in 2014 (52 years in

138   age). In May of 2018 we sampled the upper soil profile for chemical properties mirroring the methodology

139   of Kranabetter et al. (2019). Forest floors were cut and removed over a 10 cm diameter area to the mineral

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140   soil interface, and the forest floor depth noted at each microsite. Mineral soils were sampled to a 20 cm

141   depth with a stony soil auger. Subsamples from 12 random microsites were composited into 3 forest floor

142   and 3 mineral soil samples per plot (an occasional plot had very thin forest floors [< 1 cm] so in those cases

143   we took only one or two bulked samples). Soils were air-dried, ground and sieved to 2 mm for chemical

144   analysis. Foliar samples were collected at the end of the growing season (mid-November 2018) by

145   searching each plot for fresh branches that had broken off during recent storms. We strove to obtain

146   needles from current year foliage off at least 12 separate branches and combined these into 3 samples per

147   plot. Foliar samples were oven-dried at 60° C for 24 hours and then ground for nutrient analysis.

148   Total C and N concentrations of soil and foliage were measured using combustion elemental

149   analysis with a Fisons/Carlo-Erba NA-1500 NCS analyzer (Thermo Fisher Scientific, Waltham, MA) (Carter

150   and Gregorich, 2008). Mineral soil and forest floors were finely ground to < 0.15 mm (100 mesh sieve)

151   before combustion analysis. Total P (P_t = inorganic P_i + organic P_o) of mineral soils and forest floors was

152   determined by an ignition method using sulfuric acid and an UV/visible spectrophotometer (O'Halloran and

153   Cade-Menum, 2008). Foliar P was determined by ICP-Atomic Emission Spectroscopy (Teledyne Leeman

154   Labs, Hudson, NH) following microwave digestion.

155   **2.3 Statistics**

156   Element ratios (C:N, C:P_o and N:P_o as molar ratios) were determined on each soil subsample and

157   then averaged by plot for statistical analysis. The covariation among average concentrations of C, N, P_o and

158   their element ratios was determined by pair-wise Pearson correlation coefficients (SAS Institute Inc., 2014).

159   Conifer productivity was assessed by stand basal area (m^2 ha^{-1} of live trees in 2014). Scaling factors in the

160   conversion to hectares (to account for differences in plot size) were 27.1 for 2.7 m spacing, 15.3 for 3.7 m

161   spacing, and 9.8 for 4.6 m spacing.

162   The experimental treatment effects (Species and Spacing) on soil nutrient concentrations, forest

163   floor depth, stand basal area and stocking (stems ha^{-1}) were tested by fitting separate linear mixed effect

164   models in SAS (Mixed Procedure, Method=REML) (SAS Institute 2014), with Site set as a random effect. We

165   examined the relationships between stand basal area and soils by including each element ratio as a single

166   continuous variable in the model, along with the full set of interactions. The interaction terms Spacing ×

167   Soil and Species × Spacing × Soil were consistently nonsignificant for all soil variables tested, so the final

168   models were refitted with these terms removed. Goodness of fit for the model was evaluated by the F

169   statistic of each parameter, as well as by the lowest overall model Akaike information criterion (AIC).

170   Model outputs were also assessed graphically by plotting the observed dependent variable versus predicted

171   values to ensure a relationship close to 1:1. Foliar N %, P % and N:P in relation to Species, Spacing and soil

172   element ratios were examined in the same manner but the final models were refitted without Species ×

173   Spacing, Spacing × Soil and Species × Spacing × Soil interaction terms as they were consistently

174   nonsignificant for all soil variables tested.

175   **4 Results**

176   **4.1 Soil nutrient concentrations and resource stoichiometry by substrate**

177   We found a considerable range in nutrient concentrations (e.g., 0.15-0.60 % N; Table 1) and strong,

178   positive correlations among C, N, and P_o for mineral soils (Pearson r > 0.7) across these temperate rainforest

179   sites (Table 2, Fig 1). Inorganic P_i concentrations of mineral soils were relatively limited, often < 200 mg kg^{-1}

180   ^{1}, which was substantially less than the contribution of P_o to total P for a majority of plots (53 of 64 plots

181   had P_o > 70 % of P_t). In addition to limited P_i, the extent of soil podzolization was reflected by typically low

182   pH and elevated concentrations of exchangeable Al and Fe (Table 1). Forest floors averaged 5.5 cm in

183   depth (SE 0.6) overall, and displayed a narrower range in C (31 – 55 %C, average = 46 % C [SE 0.7]) but also

184   exhibited a significant positive correlation between N and P_o concentrations (Table 2). Similar to mineral

185   substrates, the concentrations of inorganic P_i (average 110 mg kg^{-1} [SE 5.8]) were uniformly low in forest

186   floors, in contrast to P_o (average 970 mg kg^{-1} [SE 71]), and consequently contributed only a small proportion

187   of total P ($P_o \sim$ 90 % of P_t in forest floors).

188   C:N ratios of the mineral soils became narrower (declining from 44 to 23) with increasing % C (r = -

189   0.48; Fig. 2a), similar to $C:P_o$ (range approx. 300-1200; r = -0.36) (Table 2). In contrast, C:N of forest floors

190   widened with increasing % C (r = 0.51; Fig. 2b) but nevertheless C:N of both substrates were well aligned

191   across sites (r = 0.85, $p < 0.001$; Fig. 3a). The same symmetry in element ratios between substrates was

192   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 cases

193   the relationships in element ratios were not 1:1 as the organic horizons were less concentrated than

194   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.

195   3a). Lastly, there was typically a high degree of correlation (r > 0.7) in element ratios within a substrate,

196   such as C:N vs. $C:P_o$, for both mineral soils and forest floors (Table 2).

197   At this juncture in plantation age (52 years) we found no evidence that conifer species or planting

198   density had an effect on mineral soil nutrient concentrations or ratios (for Species, $p = 0.99$ for C:N, $p = 0.48$

199   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 $N:P_o$).

200   There was, however, a slight difference detected in N % of forest floors with Species ($p = 0.034$). Forest

201   floor N concentration under Douglas-fir averaged 1.52 % N (SE 0.06), which was slightly greater than the

202   other three species (combined average 1.35 % N), although forest floors also tended to be thinner under

203   Douglas-fir (4.7 cm [SE 0.8], on average, compared to 5.9 cm for the other three species; $p = 0.13$). Despite

204   the modification in N concentrations under Douglas-fir, this Species effect did not extend to element ratios

205   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 = $

206   0.25 for C:N, $p = 0.42$ for $C:P_o$, and $p = 0.25$ for $N:P_o$).

207   **4.2 Stand productivity in relation to soil resource stoichiometry**

208   Stand density (stems ha^{-1}) in 2014 was well aligned with initial planting spacing, and there were

209   significant differences among conifer species in stocking (Supplemental. Fig. 1). Western redcedar had the

210   least mortality (average 80 % survival), followed by Sitka spruce (76 %), western hemlock (71 %) and then

211   Douglas-fir (65 %). With the original study design we could only detect a significant effect of Spacing on

212   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

213   3). Including a soil element ratio of either substrate as a covariate in the analysis provided further details

214   on Species response, particularly with C:N (Table 3). Stand basal area was well aligned with mineral soil and

215   forest floor C:N for all four species, with a significant species interaction due to the sharper gains in Sitka

216   spruce basal area with decreasing C:N (Fig. 4a, b). Soil $C:P_o$ and $N:P_o$ were also mostly significant covariates

217   in the analysis of basal area, but neither ratio invoked the same degree of Species response (i.e., lower F

218   values) nor significant Species × Soil interactions, and both models had poorer AIC scores than C:N (Table

219   3). For comparison we also tested $C:P_t$ and $N:P_t$ of each substrate against basal area but found virtually

220   identical model outputs as $C:P_o$ and $N:P_o$ (data not shown).

221   **4.3 Foliar nutrition in relation to soil resource stoichiometry**

222   Foliage collections were not entirely successful as a few plots, particularly under Sitka spruce, had

223   insufficient branches to obtain three composite subsamples (n = 167 from a target of 192 subsamples, and

224   with 2 spruce plots removed from the analysis). Despite this more limited data set we were able to

225   demonstrate an overall gain in foliar N % with declining soil C:N ratio, both for mineral and forest floor

226   substrates, as well as a significant difference in foliar N % among Species due to the enhanced nutrition of

227   Sitka spruce (Table 4; Fig. 5a). In contrast, there was no relationship between foliar P % and $C:P_o$ ratio for

228   either substrate (Table 4, Fig. 5b). The better predictor of foliar P % was instead the concentration of P_i in

229   soils, with again significant differences among Species largely due to Sitka spruce (Table 4). We also tested

230   soil P_t and P_o concentrations in relation to foliar P % but neither of these attributes were significant (for P_t, p

231   = 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

232   floors). Foliar N:P ratios across the plots were for the most part greater than a proposed threshold of 16 (to

233   delineate N-only deficiencies; Güsewell, 2004), averaging 19.5 (SE 0.8) for western redcedar, 18.2 (SE 0.8)

234   for Douglas-fir, 20.6 (SE 0.8) for western hemlock, and 17.4 (SE 1.1) for Sitka spruce. We were unable to

235   find a significant relationship between foliar N:P and soil $N:P_o$ for either substrate (Table 4).

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5 Discussion

Our results provide further details on baseline nutrition and resource stoichiometry for soils of

perhumid rainforests along the southwest coast of British Columbia. Soil C and N regimes 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 (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, the

modest to high deficiencies in foliar P (0.10-0.15 %) for a large number of stands[1] and elevated range in

foliar N:P (16-25) suggests these perhumid rainforests were often limited by N and P together or, in some

stands, possibly P alone (Carter, 1992; Güsewell, 2004). 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 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

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[1] note that Douglas-fir, western hemlock and western redcedar averaged 0.20% P on less-weathered soils of eastern
Vancouver Island (Kranabetter et al. 2019 and unpub. data)

259   species growth response (and likely only significant as a surrogate for C:N) and not a significant predictor of

260   foliar P %, despite the expectation of positive correlations in net N and P mineralization rates (Heuck and

261   Spohn, 2016). Estimates of a critical $C:P_o$ for gross P mineralization of leaf litter range from 1400-1800

262   (Mooshammer et al., 2012; Heuck and Spohn, 2016), but thresholds for forest floor horizons and mineral

263   soil are likely much lower (perhaps < 500; Saggar et al., 1998; Heuck and Spohn, 2016). The substrate

264   distinction is important as very few of our study sites had $C:P_o$ ratios < 500, suggesting pervasive, low

265   quality organic matter in regards to P. Furthermore, the element ratios of saprotrophic fungi, as key

266   decomposers, in these perhumid rainforests averaged 120 and 10 for C:P and C:N, respectively (Kranabetter

267   et al., 2019), which when compared to soil organic matter would indicate a greater elemental imbalance for

268   P, especially in forest floors (Mooshammer et al., 2014). The biotic (microbes, plants) competition for P is

269   also very likely exacerbated by abiotic competition for phosphate (PO_4^-) via sorption to Fe and Al oxides,

270   much more so than would be present for NH_4^+ or NO_3^- (Olander and Vitousek, 2004). A greater sink

271   strength via immobilization and sorption for PO_4^- would require conifers to bypass mineralization of P by

272   decomposers to some degree and instead access organic P more directly for uptake. A concurrent study of

273   extracellular enzyme activity associated with ECM roots of Douglas-fir has revealed substantial increases in

274   P-acquiring enzymes (J. Meeds, pers. comm.) that are likely acting upon the orthophosphate monoesters

275   and diesters of organic P (Cade-Menum et al., 2000; Preston and Trofymow, 2000). Despite the expected

276   contribution of P_o to forest nutrition, however, we found it more effective to gauge P availability through

277   soil P_i concentrations (as the only significant correlate with foliar P %), but other methods may prove to be

278   more sensitive as a measure of plant-available P_o (DeLuca et al., 2015; Darch et al., 2016).

279   One unique aspect of soil organic matter found here was a decrease in mineral soil C:N and $C:P_o$

280   ratios with increasing soil C % (Fig 2a), in contrast to the inverse relationships described by Tipping et al.

281   (2016). This may reflect the significant legacy of N-fixing red alder (*Alnus rubra*) in coastal forest

282   ecosystems, which has been found to promote soil C sequestration and P mobilization while simultaneously

283   adding high quality (low C:N) litter (Binkley, 2005; Perakis and Pett-Ridge, 2019). A second key source of N-

284   rich litter could be from epiphytic cyanolichens and cyanobacteria-bryophyte associations (Antoine, 2004;

285   Lindo and Whiteley, 2011). Canopy lichens and bryophytes are noteworthy in low-frequency disturbance

286   ecosystems such as rainforests because they produce a steady input of N while growing independently of

287   the soil environment (Menge and Hedin, 2009). Red alder, in comparison, is an early-seral species that can

288   be hindered in its establishment and vigour by low P_i availability (Brown et al., 2011; Kranabetter et al.,

289   2013). Hedin et al. (2009) described a similar N paradox in tropical forests, and proposed N-fixing epiphytes

290   as one mechanism that allows soil N regimes to increase despite soil P_i deficiencies or physiological down-

291   regulation of N-fixation in high soil N environments.

292   The more significant differences in species productivity in relation to soil C:N was among the ECM

293   species rather than solely between mycorrhizal types. Western hemlock and Douglas-fir had the most

294   limited increase in basal area with declining C:N, a finding that was similar for these species in correlations

295   of site index with organic matter quality across a broader region of the US northwest (Edmonds and

296   Chappel, 2004). These two conifers would be considered relatively stress-tolerant under the C-S-R model

297   (Hodgson et al., 1999) as their growth on high C:N soils outperformed that of either spruce or cedar. Sitka

298   spruce, in contrast, would clearly be a strong competitor as exemplified by the impressive linear increase in

299   biomass with declining soil C:N. Perakis and Sinkhorn (2011) found coastal Douglas-fir productivity

300   plateaued with increasing N mineralization rates, but this relationship with N supply may be species-

301   dependent and not necessarily apply to Sitka spruce. A possible functional trait related to this growth

302   response is the low capacity of ECM roots of Douglas-fir to maximize uptake of NO_3^-, as would be in plentiful

303   supply on these richer soils (Prescott et al., 2000b; Perakis et al., 2006), but whether spruce ECM roots

304   would perform any differently has not been established (Boczulak et al., 2014; Hawkins and Kranabetter,

305   2017). As an aside, we noted some naturally-regenerated *Abies amabilis* within the study areas that had

306   the same girth as Sitka spruce, so it is likely *Abies* would be an equally competitive member of these

307   rainforest ecosystems. Western redcedar as the only ARB tree species in the trial was intermediate in

308   growth response to soil C:N, and displayed no particular advantage in foliar N % or P % over the ECM

309   conifers. Redcedar is recognized to have a wide ecological amplitude, from highly productive to very

310   nutrient poor or wet sites (Antos et al., 2016), and so would fit well within a generalist or intermediate C-S

311   strategy. These contrasting patterns in productivity emphasize a diversity of traits related to edaphic niches

312   within mycorrhizal guilds rather than a simple dichotomy in the distribution of ARB and ECM trees between

313   N-rich and N-poor soils (Koele et al., 2012; Dickie et al., 2014).

314   After five decades the possibility of tree species effects on soil nutritional status is also worth

315   considering. Enhanced N inputs via foliar litter are considered a positive reinforcement in sustaining soil

316   fertility (Prescott, 2002), which would be consistent with the overall trend in foliar N % across this

317   productivity gradient. The small difference in forest floor N concentrations under Douglas-fir may reflect

318   slightly better litter quality (lower lignin content) and potentially faster decomposition rates for this species

319   (Vesterdal and Raulund-Rasmussen, 1998; Thomas and Prescott, 2000). Overall, however, there were no

320   clear differences in element ratios of either forest floors or mineral soils by tree species, which leads us to

321   conclude these conifers lacked substantial enough differences in leaf or root litter to have more profoundly

322   and consistently diverged from inherent soil conditions. The glaciated landscape along Vancouver Island

323   has been in the current iteration of temperate perhumid rainforests for at least 7500 years (Brown and

324   Hebda, 2002; Lacourse, 2005), during which time the various site drivers (e.g., drainage, slope, soil

325   mineralogy, vegetation) have collectively produced the very wide disparity in soil fertility found today. It

326   would undoubtedly take a very sizable influence of tree species on C, N or P cycling to overcome the inertia

327   of site type in such complex terrain (Prescott et al., 2000b). For example, an ecologically minor shift in

328   forest floor C:N from 50 to 40 (equivalent to an average increase of foliar N from 1.17 % to 1.23 %; Fig. 5a),

329   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

330   cm^{-3}), which would seem implausible for coniferous stands to confer in mere decades. In addition, much of

331   the focus on tree species effects has focused on surface organic horizons, but given the symmetry in

332   element ratios between mineral and forest floor substrates we would argue that a true tree species effect

333   should extend throughout the rooting zone of the soil profile.

334   With mean annual precipitation near 3500 mm, these perhumid rainforests are at the extreme

335   range in rainfall for the Pacific west coast (Carpenter et al., 2014). The evidence for P constraints outlined

336   in this trial have been substantiated by fertilizer studies along northern Vancouver Island (Blevins et al.,

337   2006; Negrave et al., 2007), but other areas in the Pacific Northwest have shown more variation in growth

338   response to added P (Radwan et al., 1991; Mainwaring et al. 2014). Lower precipitation levels or

339   differences in soil mineralogy could mediate rates of soil podzolization and reductions in P_i so the full

340   regional extent of these presumed P deficiencies should be examined and tested more thoroughly. We

341   expected some utility in soil $N:P_o$ as a measure of forest productivity (Wardle et al., 2004) but it is possible

342   the mismatch in element thresholds for N and P_o turnover, as discussed above, reduced the efficacy of this

343   index. Phosphorus deficiencies are also relevant in the noted nutrient exchange between marine and

344   terrestrial environments through anadromous salmon biomass (Cederholm et al., 1999). Our results

345   support the likelihood that both salmon-derived N and P contribute to alleviating nutrient limitations of

346   Sitka spruce on riparian sites of the Pacific west coast (Reimchen and Arbellay, 2019).

347   **6 Conclusions**

348   Quantifying the fundamental relationships between soil element ratios and conifer species

349   productivity was facilitated in this study by the planting of single provenances at controlled densities,

350   alongside a uniform macroclimate and narrow elevation band among plot locales. Soil organic matter

351   content of perhumid rainforests was often high and displayed strong positive correlations in soil C, N and P_o

352   concentrations. Inorganic P was generally in low supply, reflecting soil podzolization processes, and

353   contributed a relatively minor proportion of total P. Element ratios of C:N and $C:P_o$ were well correlated in

354   forest floors and mineral soils, yet only C:N was an effective measure of forest productivity and foliar

355   nutrition. High C:P_o ratios (as much as 3000) may reflect a stronger immobilization sink for P than N, which,

356   along with ongoing sorption of PO_4^-, could limit the capacity of organic P turnover to meet tree

357   requirements. The interplay of conifers and soils after five decades suggests species growth response to

358   inherent soil C:N was more intrinsic to ecosystem productivity than any reciprocal effects of tree species on

359   soil resources. The conifers with ectomycorrhizal fungi had widely diverging responses in basal area over

360   the N gradient, illustrating the extent of both competitive (*Picea sitchensis*) and stress-tolerant (*Tsuga*

361   *heterophylla*, *Pseudotsuga menziesii*) traits for these tree species. The chemical nature and availability of

362   soil P to trees, particularly as P_o, deserves further investigation as many of these perhumid rainforests were

363   co-limited by both N and P, or, in some stands, possibly P alone.

364

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376   **Data Availability**

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

378   **Author Contribution**

379   LD was responsible for EP571 administration, including research site maintenance, tree measurements and

380   data archiving; JK conceived study design for soil covariates; JK and AS undertook field soil sampling and

381   laboratory preparation; JK and AS contributed statistical analysis; JK wrote manuscript with substantial

382   contributions by AS and LD.

383   **Competing interests**

384   The authors declare that they have no conflict of interest.

385

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589

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

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

592   concentrations.

593   Figure 3. Correlation in resource stoichiometry for a) C:N ratio, b) C:P_o ratio, and c) N:P_o ratio between

594   mineral soil and forest floor substrates.

595   Figure 4. a) Basal area by Species in relation to mineral soil C:N (all planting densities included), and b) linear

596   regressions between stand basal area and mineral soil C:N, fitted by Species and Species × Soil interactions

597   (model output averaged across planting density). Slope of the C:N regression was ranked highest for Sitka

598   spruce (Ss; -3.40), followed by western redcedar (Cw; -1.67), Douglas-fir (Fd; -0.84), and western hemlock

599   (Hw; -0.70).

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

601   ratio. Western redcedar = Cw; Douglas-fir = Fd; western hemlock = Hw; Sitka spruce = Ss.

602

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 (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

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

606   and associated 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***)

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608

Table 3. Conifer species basal area (m² 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 (p values < 0.05 in bold).

|	Df	No soil variable		Soil C:N		Soil C:P$_o$		Soil N:P$_o$	
		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	

612 Table 4. Conifer species foliar nitrogen (N) and phosphorus (P) concentrations and N:P ratio in relation to

613 planting density (1329, 748 and 479 stems ha^{-1}) and mineral soil (0-20 cm) or forest floor resource

614 stoichiometry (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*

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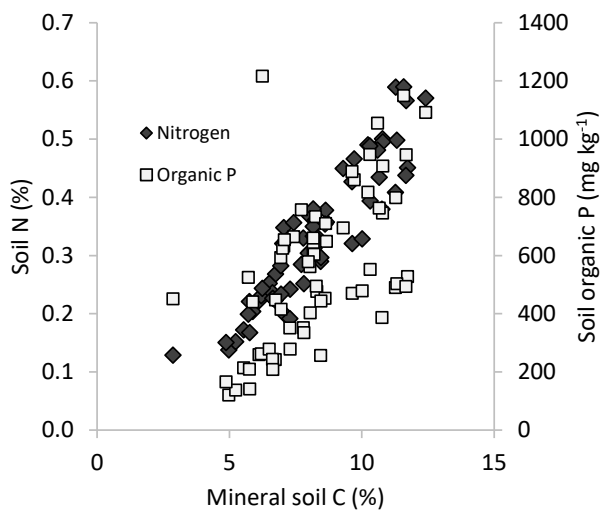
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618

Figure 1

619   (a)   (b)

620

Figure 2

621   (a)

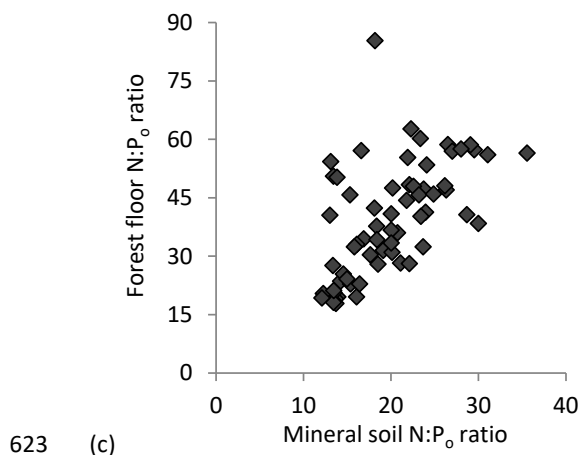622   (b)

623   (c)
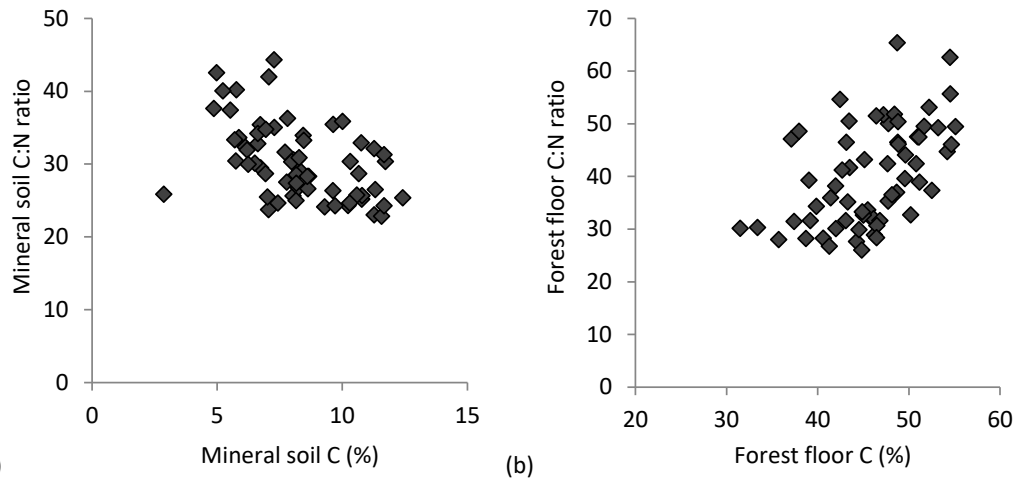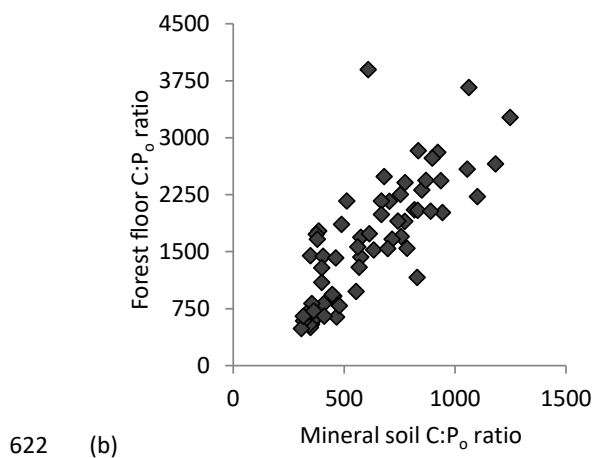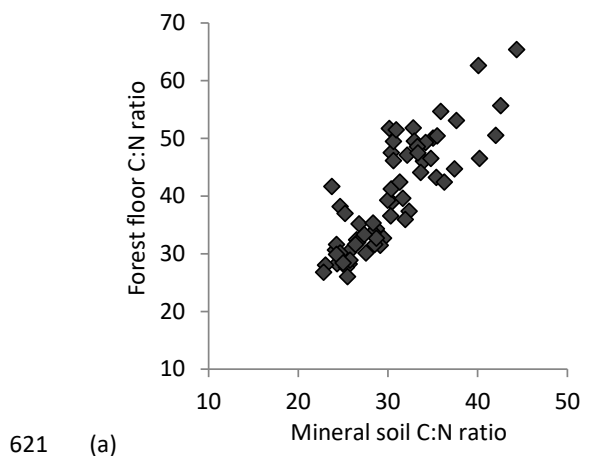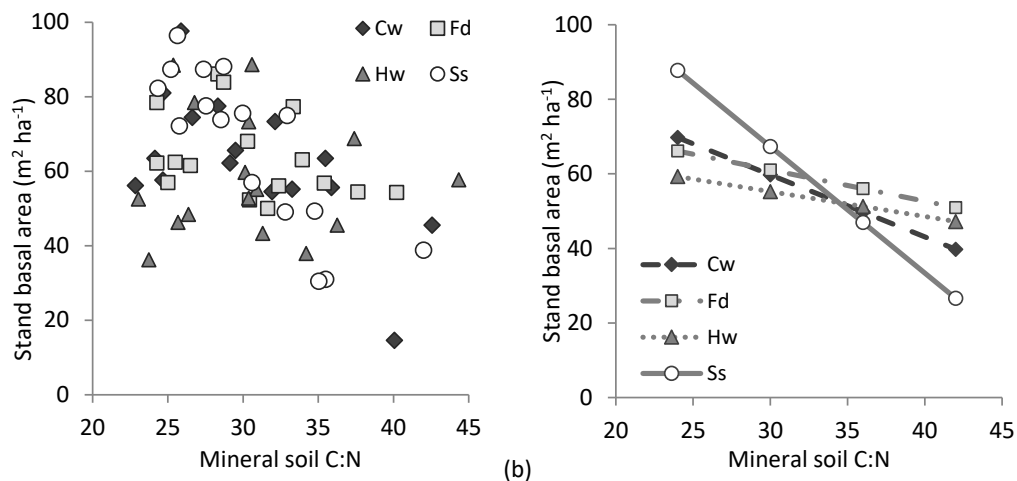
Figure 3

624   (a)   (b)

625

Figure 4

626   (a)   (b)

Figure 5