Reviewer 1

A lot of attention is given to the potentially important role of P. Although the authors have attempted to provide support for their statements on P (co-)limitation based on multiple lines of evidence (relatively high foliar N:P, high soil C:Po vs low soil C:N, low soil Pi, low leaf P, literature + comparison with data from other parts of the island), I am not yet fully convinced. For example, there was only mediocre evidence for a role of soil C:Po in explaining variation in basal area (and the apparent + effect that occurred may have been caused by a mere confounding effect of soil C:N, as acknowledged by the authors), and no link between leaf P and soil C:Po, in sharp contrast to its analogue with N. I suggest to reinforce the evidence by performing some additional analyses you can do based on the data you already have (e.g. test for effects of Pi, test soil C:N*C:Po if no collinearity, plot foliar N:P vs forest floor and mineral soil C:N), and by referring better to any existing literature discussing P limitation on this region of the island, or other comparable systems.

We would disagree with the reviewer that results regarding organic P weaken the case for P limitations. A decline in element ratios has been typically matched to gains in plant-available nutrients, and consequently has been proposed as fundamental relationship in forest soils (e.g., Mooshammer et al. 2014; Zechmeister-Bolenstern et al. 2015; Spohn 2016). The fact that $C:P_o$ and $N:P_o$ were poor variables in explaining basal area or foliar nutrition is a very important finding as it underscores the uncertainty as to where these stoichiometry concepts can be successfully applied. This does not undermine the evidence for P deficiencies in these forests, but emphasizes instead how organic P is not behaving as ecological theory postulates. All the other lines of evidence for P limitations (low soil Pi, low foliar P%, high foliar N:P, fertilizer responses etc.) are collectively quite compelling, and underscore how $C:P_o$ should by all accounts be a useful metric. As we outlined in the Discussion, it is possible the fairly high values for $C:P_o$, elemental imbalance with microbial biomass, and abiotic immobilization of PO_4 have collectively reduced the effectiveness of P_o to supply plant-available P in these ecosystems. One could argue that in this case a 'negative' (or nonsignificant) result is as interesting as a 'positive' one would be.

Here and elsewhere was a request for much more attention to inorganic P in the manuscript. We certainly examined soil P_i in our preparations but felt it was a poor covariate. The distribution of P_i was skewed, being generally low for most sites with a few outlier plots with high P_i (see Supplemental Figure S3 as an example). This created an issue because the main treatment factors of Spacing and Species were not evenly balanced among the upper range in P_i, leading to possible spurious relationships. Arguably a second covariate should be added to the analysis (e.g., C:N plus P_i) but the statistical model is overwhelmed with two main treatments (Spacing, Species), two covariates and all the interaction terms. We were advised our study design was not suitable for multiple covariates. Given the range in soils and constraints of the study design we felt the questions to be best answered were focused entirely on organic matter stoichiometry and how well these relationships matched the ecological literature (as mentioned above). We only added one P_i statistic in regards to foliar P%, to at least establish some relationship with soil P, but would argue a fuller analysis of P_i would be unwise and possibly misleading. We included a comment in the Discussion on this matter (line 362) "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"

The manuscript has a strong focus on these particular perhumid forest ecosystems of western Vancouver Island. The eventual paper might attract a broader audience if more reference is made to other possible P (co-)limited coniferous and temperate ecosystems worldwide. One short section in

the Discussion, plus perhaps mentioning it in the Abstract and/or Conclusion may suffice. In the Introduction, the authors explain why the forest ecosystems of Vancouver Island are unique, but still I think some parallels can be made with other forests globally.

We added comments in the Discussion (line 248) on how our results complement studies of rainforests from the southern hemisphere, and also added a second reference (Xu et al. 2013) with global C, N and P datasets to facilitate comparison of these sites with ecosystems elsewhere.

Line 5 – Consider changing the title to reflect the main conclusion of this work, e.g. the different responses among tree species to variation in soil stoichiometry, or on the possible importance of P (the latter only if evidence is strong enough, see my other comments).

We changed the title to emphasize the contrasting patterns in conifer productivity. Since foliar nutrition was a secondary objective (along with conifer species effects on soils) we thought it best to remove that word from the title.

Line 6 – I assume that "nutrition" refers to foliar stoichiometry?

Yes, but nutrition has now been removed from the title

Line 26 – "We described the nature of soil organic matter (...)": this is a bit confusing, could also refer to SOM properties not measured in this study. I suggest you immediately indicate that you determined the forest floor thickness, and forest floor + soil nutrient concentrations and stoichiometry.

We changed this to nutrient concentrations as suggested. Forest floor depth was measured but did not contribute much to our analysis so we felt it was unnecessary to include that detail in the Abstract.

Line 31 – At this point, it is not clear whether you refer to forest floor or mineral soil C:N. In practice, both explained well spatial variation in basal area. I suggest to specify that.
We made it clear that both substrate C:N were related to basal area as suggested.

Line 36 – "(...) no evidence via foliar nutrition for increased P availability with declining element ratios (...)": this refers to the lack of a relationship between foliar P and soil C:Po ratio. Looking at Table 4 and Fig. 5b, this seems to be correct definitely when combining species. But maybe there is a significant correlation between foliar P and soil C:Po within species? Foliar stoichiometry is typically strongly taxonomy-dependent (Sardans et al., 2015).

Under Methods (line 179) we note that the model was first run with all interactions and then the insignificant terms removed to solve for the remaining terms (we inadvertently did not specify Species × Soil in the first draft, it is included now). We at no time found a significant Species × Soil interaction for foliar nutrients. To emphasize this point we included the interaction *p* values for each of the foliar nutrients throughout Results.

Line 36 – Throughout the manuscript, C:Po ratio is used instead of C:P ratio. The rationale behind this is mentioned in the text, and the text also explains that results for C:Po and C:P are very similar. I suggest to at least once also mention C:P in the Abstract, and making clear that in this case results are very analogous anyway.

A comment was added to include C:P_{total} as suggested.

Line 40 – A lot of attention is given to the potentially important role of P, but it was not possible to detect a clear effect of soil C:Po ratio on foliar P, nor productivity. My feeling is that this is to a great extent because N is still the primary nutrient limiting productivity across most of the gradient, yet I agree that P may become more important as a limiting factor at plots with low C:N. Since soil P availability is strongly influenced by soil pH, and pH seems to have been measured at all plots, you may consider testing relationships between productivity and pH, foliar P and pH, soil C:Po and pH, soil Pi and pH, ... Since curves of P availability vs pH typically show an optimum, first try fitting a quadratic function (although pH is generally low in this dataset and may eventually be below the optimum anyway).

Nitrogen varied widely to include both low N availability to high N availability (foliar N% of 0.9 to 1.5%). In contrast, P was almost a 'blanket' constraint across the landscape, as indicated by a large number of plots with low P_i and moderate foliar P% (often 0.10 - 0.13%). What the reviewer is suggesting in regards to pH and P optima would have been more suitable to an earlier publication (2019. New Phytologist 221, 482-492) on Vancouver Island where we compared a more balanced array of plots across wet to dry maritime forest soils with low to high P_i. Our focus in this manuscript is largely the quality of soil organic matter and how well these element ratios reflect forest productivity and nutrition. Details on soil P_i were included to fully characterize the soils, but a full analysis of inorganic P optima is beyond the scope of this study.

Line 80 – "Baseline relationships in soil resource stoichiometry and ecosystem productivity should also consider the interaction of tree species.": I agree, and this is also the case for foliar stoichiometry. While different species are shown in Fig. 5, the analyses in Table 4 do not test for the interaction between soil stoichiometry and species. Why?

As mentioned above, all interaction terms were tested and we found no significant Species × Soil terms for foliar nutrients. We now include the interaction *p* values for each of the foliar nutrients under Results.

Line 110 - A lot of attention is paid to the different responses among species, and a distinction between ECM and ARB trees is made. Moreover, in the discussion, a link with CSR strategies is made. I agree with the authors that these differential responses should be discussed, and I support the idea of explicitly stating a hypothesis or objective on this aspect. However, I would like to see a bit more of an explanation (in Intro and/or Discussion) of why you expect responses to differ between ECM and ARB. Some elements are in the text, but for example, in general, ectomycorrhizae are rather associated with enhanced N uptake, whereas arbuscular mycorrhizae rather for the uptake of P, which may influence (hypothesized) slopes like those in Fig. 4b. Having said that, these ECM-N vs AM-P links may be an overgeneralization; you for instance already mention the potential role of arbuscular mycorrhizae in N uptake in the manuscript.

An excellent review by Hodge (2017) demonstrates ample evidence for both mycorrhizal types to access inorganic and organic sources of nutrients. I suspect the distinction currently in vogue with differential mycorrhizal abilities is overstressed, as reviewer alludes to. We added the Hodge reference to the Discussion (line 325) to make the point that the coexistence of ARB and ECM conifers demonstrates some shared competence in nutrient uptake from these soils.

Lines 118-124 – Add this information to Table 1 (or make a Table S1 in SI and refer to it). Then it is clear which site has what conditions. While this is not relevant to the main messages of the manuscript, it may be practical in case researchers want to use the data of the paper in the future, e.g. for reviews, meta-analyses, ...

A Supplemental Table was added to the manuscript with a more thorough description of landforms and ecological classification as suggested.

Line 140 – Add forest floor depths to Table 1 or S1.

This was added to S1 as suggested.

Line 156 – ! molar ratios ! In terrestrial ecology, some studies use mass-based ratios, others use molar. Please clarify that molar ratios were used at least in the description of every table and figure.

Molar was added to Tables and Figures

Line 232-233 – Foliar N:P ratios are used in the manuscript as one line of evidence suggesting P (co-)limitation. However, caution is needed when using such critical N:P ratios, since they depend on species. Also, I did not immediately find the proposed threshold of 16 in the given reference Güsewell et al., 2004. As explained under "general comments", please try to find some stronger evidence for (co-)limitation of P. Then for me, mentioning a critical foliar N:P ratio can remain in the manuscript if justified (but you note the taxonomy-dependence), but it should be one piece of the evidence, together with other arguments.

A number of papers have discussed this critical N:P ratio and the reviewer is correct, it was not addressed as directly in Güsewell. I have added the Reich and Oleskyn 2004 paper to reference this proposed threshold in N:P (which suggests 14, rather than 16, to delineate N-only constrained ecosystems; this change was made). I believe we have stressed a number of lines of evidence for P limitations as the reviewer suggested, and we have not over-relied upon a hypothetical threshold in foliar N:P.

Line 236 – For clarity, consider subdividing Discussion into sections with titles, like in Results or referring to the three objectives.

Subheadings were added as suggested

Line 238 – Like in the Introduction, the authors refer here to "high C and N regimes". In contrast to what was written in the Introduction, however, the sentence here discusses TOTAL N, whereas in the Introduction, reference is rather made to the AVAILABILITY of N. I suggest to (i) rephrase the vague mentioning of "high regimes" (e.g. total C and N concentrations were high), and (ii) not use total N as an argument to suggest that P may be as or even more limiting than N. Only a small proportion of the total N is plant-available, in the form of small organic molecules, ammonia and/or nitrate.

True, we revised to total C and N concentrations rather than regime as suggested. Our comment that stands are co-limited by N and P was based mostly on the interpretation of foliar nutrients, not total N.

Line 256-258 – The cited synthesis paper (Booth et al., 2005) indeed focuses on the link between C:N and N availability, among other things. It however not explicitly refers to the influence on soil C:N ratio on stand productivity and/or foliar N. I suggest adding a few references of gradients/large-scale studies exploring Productivity/foliar N _ soil C:N ratio, e.g. Alberti et al., 2014; Van Sundert et al., 2018, ... –> "The clear relationship between mineral soil and forest floor C:N with stand productivity and foliar % was consistent with many other biomes (NEW REFERENCES) and (...) with declining soil C:N (Booth et al., 2005)."

These two references were added as suggested

Line 276 – "(...) we found it more effective to gauge P availability through soil Pi concentrations (as the only significant correlate with foliar P %)": overall, the evidence for P (co-)limitation based on soil C:Po is limited (except from the facts that C:Po was comparatively high, and it had a significant + influence on basal area in Table 3, but a confounding effect with soil C:N cannot be excluded). Table 4 confirms the potential of Pi to explain variation in foliar P instead. So, why didn't you further check whether Pi was perhaps a better indicator of the soil P status than soil Po or C:Po? Would spatial variation in Pi, even within plots, be too high, and also seasonal variation, as can be argued for available N (depending on the application)? I suggest you to either perform additional analyses using Pi, or explain in the manuscript why it is not a suitable indicator.

We felt P_i was generally an unsuitable soil covariate for our analysis of stand productivity as discussed earlier. We maintain that questions related to organic matter stoichiometry are much better suited to the nature of this dataset. A larger geographical area in the region that encompassed a more balanced array of plots between low and high P_i soils would be better suited to this line of enquiry.

Line 336 – I strongly support your reference to additional nearby fertilizer application studies. However, to what extent are soils on N Vancouver Island comparable to W Vancouver Island, where the current study was performed? Earlier in the Discussion, you note based on your own data that the East of the island at least has soils differing from those in the West, as reflected in different foliar P.

The fertilizer study took place in very similar perhumid rainforest sites (the CWHvm, 01 HwBa-Blueberry site series) on the north Island. We revised this comment to note the relevance as suggested.

Line 352 – See also my earlier comment. Inorganic P was generally in low supply, and contributed a relatively minor proportion of total P. Please perform additional analyses on basal area vs Pi etc., or explain why this would not be a good idea.
Table 2 – Please include Pi or argue why not.
Table 3 – Please include Pi or argue why not.

Please note that the objectives of our study were to better characterize organic matter quality (C:N, $C:P_o$ $N:P_o$) and test whether these gradients in element ratios would parallel the trends postulated by the ecological literature. To fully explore how all soil properties might influence tree growth (Pi, but also Ca, K, Mg, B, Cu, Fe, pH etc.) would be much better suited to a simpler design (e.g., one tree species at one planting density replicated across 50 test sites). We recognize that regionally the role of P_i could be substantial, and have commented on that, but we are unable to prove that with any confidence with this data set.

Table 3 – Why exactly was the 0-20 cm interval used for sampling mineral soil? Is this roughly corresponding to the main rooting zone? Please specify in the M&M section.

This depth captures enough of the critical rooting zone to adequately quantify site effects. A comment was added as suggested.

Table 4 – It would be interesting to see how foliar and soil stoichiometry relate within species. Separate species were visualized in Fig. 5, but separate analyses (or analogous: soil*species interaction) were not performed. You could show that not only the link basal area _ soil stoichiometry depends on species, but also foliar stoichiometry _ soil stoichiometry. If you make a new table for this, perhaps place it in SI, and refer briefly to it.

Table 4 lists the final model output for foliar attributes so, as mentioned previously, the Species × Soil interaction terms were listed in Results.

Figure 4b – I do not understand why mineral soil C:N was preferred here as a predictor over forest floor C:N. Table 3 suggests both are good explanatory variables. Please add and discuss panels using forest floor C:N, or explain why mineral soil C:N is the better alternative.

Depicting both mineral soil and forest floor C:N results seemed redundant as they were strongly correlated and produced very similar model outputs in relation to basal area. To streamline the manuscript we will include forest floor as a Supplemental Figure.

Figure 4b – Add test statistics (P, R_2, ...)

I included the p value for the Species X Soil interaction for this fitted model and the overall r^2 as suggested in the Figure caption.

Figure 5 - Why was foliar N and P chosen, and not foliar C:N and C:P (here and throughout the whole manuscript)?

Nutritional data in forest ecology has long been interpreted via concentrations rather element ratios (e.g. Carter 1992) and we chose to continue with this approach as it is far more informative (e.g, foliar P of 0.12% has much more interpretive value than a foliar C:P of 850). We included a comment on this in the Introduction (line 109) but added average C concentrations of the foliage under Results in case readers want to be able to calculate element ratios.

Figure 5 – Figs. 4 and 5 confirm to me the role of N as a primary determinant of forest structure and function. In order to find stronger evidence for the role of P, you may consider (i) testing the interaction soil C:N*soil C:Po on basal area, and perhaps other response variables, and (ii) plotting foliar N:P (within and among species) vs mineral/forest floor C:N. My feeling is that (i) may fail, because soil C:N and C:Po may induce collinearity in the statistical model. If so, try checking the single influence of soil C:Po for data points only where C:N is low (_ high N availability). For (ii), we may expect an increase in foliar N:P, and thus P (co-)limitation, with decreasing soil C:N.

We indeed played with many of these multiple covariates but upon plotting residuals and discussions with our statistician we felt the study design was not robust enough to expand upon one soil covariate. Species interactions in particular can be potentially spurious with this many model terms for a relatively

small data set. In regards to foliar N:P, we found weak patterns in relation to C:N but our analysis was constrained by some of the difficulties in getting adequate foliage for every plot. We felt it best to limit our discussion to the simpler, broad trends in foliar N% and P% in relation to soil C:N, $C:P_o$ and $N:P_o$.

Figure 5b – I would be curious to see this graph with Pi as an explanatory variable (cf. Table 4).

We added that Figure as a Supplemental since the lack of relationship between foliar P and soil $C:P_o$ is the more critical finding.

TECHNICAL CORRECTIONS
Line 5 – Perhaps the abbreviation C:N:P is not necessary in the title, or only provide the abbreviation and not the full words at this place.

C:N:P was removed from the title as suggested

Line 35 – "(...) no evidence via foliar nutrition (...)": please rephrase, Line 36 - "(...) no evidence via foliar nutrition for increased P availability with declining element ratios as we did for N.": "declining element ratios" is vague; this refers to soil C:Po ratio in the first place. Please rephrase.

Line 35 and 36 were simplified to 'no increase in foliar P concentrations with declining element ratios…'

Line 52 – "the N regime in certain soils can be extremely rich": somewhat weird way of expressing that some soils can be rich in available N = exhibit high N availability. Please rephrase.

In ecological classification the word 'rich' in terms of nutrient regime is used regularly but in any case we revised this to 'high'

Line 63 – Remove the word "global".

OK

Line 80 – "Baseline relationships in soil resource stoichiometry and ecosystem productivity should also consider the interaction of tree species.": you mean the statistical interaction between soil stoichiometry with species. As written now, with the word "of", it may seem as if the paragraph would discuss biological interactions between species. I suggest to replace "of" by "with".

OK

Line 188 – Sometimes P-values are given along with the correlations in brackets, sometimes not. Please add P-values everywhere.

The Pearson r values for the comparison of soil C and C:N were redundant as all the correlation statistics are in Table 2 so this text was removed. The comparison of substrates (Fig. 3) was not part of Table 2 so for these we have kept the *p* and r values

Line 277 – Remove the "%", from the data it is clear that foliar P is expressed in % (also apply this to analogous cases elsewhere).

This was done

Line 317 – "The small difference in forest floor N concentrations under Douglas-fir": you mean it was higher than for the other species. Please rephrase.

OK

Line 601 – At some places in the manuscript, Latin names were used, yet at others, tree species were named in English. Please use one of the two throughout the manuscript, including Tables and Figures.

All text in the manuscript regarding the tree species is now with Latin names as suggested

Figure 1 – Please add "mineral" to the titles of both vertical axes.

OK

Reviewer 2

The study is largely based on correlations analyses. In particular, the authors correlated element contents and element ratios (Table 2 and Figure 2). This is problematic in most cases because one precondition of a correlation analysis is that the variables are independent. By definition the C:N ratio is not independent of the C content, thus the pre-condition of independence is not fulfilled. Therefore, the two variables should not be correlated

This portion of the manuscript followed the example of Tipping et al. 2016, who said "…previous analyses considered the C, N, P and S contents of the soil as a whole rather than SOM, whereas a more informative approach might to compare N:C, P:C, and S:C ratios, which are direct measures of the element enrichment of organic matter. Mazoni et al. (2010) for example, in a meta-analysis of litter stoichiometry, constructed plots of C:P against C:N as a way to visualise the data, and thereby demonstrated a strong pattern…"
The reviewer is correct in that correlations of ratios are more prone to spurious correlations, but we argue that they can still be useful if care is taken not to overinterpret the relationships. We included the ratio correlations in Table 2 as it confirms the direction of these patterns and how closely it matches absolute C, N and P_o correlations (e.g. consistent these patterns in organic matter quality). Note, for example, that C:N and C:P_o are quite strongly aligned (r = 0.8), which by ecological theory should mean that plant-available N and P increase in lockstep. That this does not appear to happen in reality is a key finding of the study. Also the relationship between soil C and C:N was again promoted by Tipping et al. (2006) and so our finding of the inverse relationship is well worth highlighting here. We revised the Introduction (line 106) to explain how the correlations follow the Tipping et al. (2016) protocol, and added a comment under Statistics to emphasize some of the issues in correlations of ratios (line 163) "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".

One asset of the dataset is that the authors have collected data on stand productivity. This kind of information is many times not available in datasets on soil nutrient dynamics in forests and the authors should make better use of this data. The authors found negative correlations between the stand basal area and the soil C:N ratio which is interesting. However, to explain the observed pattern it would very likely be more meaningful to look at the relationship between soil N stocks and productivity. I recommend to not only consider the element ratios but to calculate the element stocks. The element stocks are likely also useful in explaining the foliage element contents.

A significant challenge with soil N stocks is that nutrient concentrations of each substrate have to be converted to content (kg ha^{-1}) so that the total amount of N can be deployed. This requires accurate measures of bulk density for each substrate, plus coarse fragment content. In addition, some sites with deep forest floors will be compared to sites with thin forest floors and so the researcher has to decide whether N stocks needs to be scaled accordingly (e.g., sample deeper into the mineral soil profile when forest floors are thin). Soil stoichiometry bypasses all of these issues by focusing on organic matter quality. A number of studies have shown the utility of this approach (e.g. Littke et al. 2014; Albertini et al. 2015; Van Sundert et al. 2018), including the current work, and it seems increasingly likely that these ratio parameters will be of the most utility in largescale comparisons. We would also point out that the correlations in Table 2 clearly indicate that N% of either substrate are in any case very closely related to C:N ratios. But to partially answer your question, we tested mineral soil %N and forest floor %N against basal area and found them to be inferior to C:N, both in the AIC score and in the F values. Species

effects and species interactions were also weaker or nonsignificant with soil %N. As we commented in regards to the previous reviewer, please keep in mind that our goal in this study was not simply to find the absolute best predictors of stand productivity, particularly since multiple nutrients might be at play and we have no way of testing all the possible interactions. Instead, we wanted to contribute to the growing interest in soil resource stoichiometry as a tool in understanding ecosystems (Zechmeister-Boltenstern et al. 2015; Spohn 2016). So we prefer to keep that focus in the manuscript and not add further sections examining possible model outcomes for nutrient stocks. A comment as to why resource stoichiometry might be preferable to nutrient stocks was added to the Introduction (line 75) "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)".

The results shown in Fig 3 are interesting. It would be helpful to see the 1:1 line in all three plots. The authors should discuss the question why the difference in the C:N ratio between organic horizon and mineral soil is smaller than the difference in the C:P ratio.

The graphs were revised to include the 1:1 line. We included a comment on substrates as suggested in the Discussion (line 333) "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".

~~Soil~~Contrasting conifer species productivity in relation to soil carbon, nitrogen and phosphorus stoichiometry ~~(C:N:P) in relation to conifer species productivity and nutrition across~~of British Columbia perhumid rainforests

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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 ~~described the nature of soil organic matter for~~determined mineral soil and forest floor ~~substrates~~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 ~~via foliar nutrition~~ for increased foliar P ~~availability~~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 ~~regime in~~concentrations of certain soils can be extremely ~~rich~~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, ~~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 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 ~~soil and plants~~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 (~~Güsewell, 2004;~~ Wardle et al., ~~2004). The utility~~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 ~~in models~~presents a potentially simpler interpretation of nutrient dynamics ~~and ecosystem productivity has spurred interest in quantifying these relationships for soil organic matter~~ across ~~a range of~~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 ~~of~~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 be recognized that tree species, in turn, can influence soil C and nutrient cycling through differences in litter (foliar and root) quality and mycorrhizal habit, which could eventually manifest as distinct species-soil stoichiometry relationships (Prescott, 2002; Augusto et al., 2002; Cools et al., 2014). Quantifying both the species response to soil fertility and possible feedback of tree species on soil resources is challenging in uncontrolled settings and consequently well replicated, long-term field trials may be the best avenue for better understanding these interactions (Binkley, 1995; Augusto et al., 2002).

The quintessential rainforests along the outer west coast of British Columbia are classified as 'perhumid', with relatively high summer rainfall, cool summers, and transient snowpacks (DellaSala et al., 2011). In the early 1960's, the British Columbia Forest Service established a multi-species planting density trial across several perhumid rainforest sites of southwest Vancouver Island (Omule, 1988). The study sites encompassed a considerable range in forest productivity that provided a valuable opportunity to examine ECM and ARB conifer species growth and nutrition in relation to soil C, N and P stoichiometry. We follow the convention of Tipping et al. (2016) in this analysis by utilizing organic P (P_o) in stoichiometry comparisons (rather than total P) to focus more directly on properties of soil organic matter. ~~In addition, we present nutrient concentration and stoichiometric ratios for both substrates of the soil profile~~The element enrichment of organic matter was compared by correlations among C:N, C:P_o and N:P_o (Manzoni et al., 2010; Tipping et al., 2016) for each substrate because of the typically stark differences in the C density of forest floors compared to mineral soils (e.g., 50 % vs. ~~5 % C, respectively).~~5 % C, respectively). In addition, we relied upon foliar N and P concentrations for the more

conventional interpretation of stand nutrition (e.g., Carter, 1992) rather than foliar C-nutrient ratios.

The objectives of our study were to 1) document the range and covariation in C, N and P_o concentrations and element ratios across a variety of sites and between mineral 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 relation to forest productivity response; and 3) quantify any divergence in conifer growth response to soil fertility gradients among ECM (*Tsuga*, *Picea*, *Pseudotsuga*) and ARB (*Thuja*) tree species.

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 pH and elevated concentrations of exchangeable Al and Fe (Table 1). Forest floors averaged 5.5 cm in depth (SE 0.6) overall, and displayed a narrower range in C (31 – 55 %C, average = 46 % C [SE 0.7]) but also exhibited a significant positive correlation between N and P_o concentrations (Table 2). Similar to mineral substrates, the concentrations of inorganic P_i (average 110 mg kg^{-1} [SE 5.8]) were uniformly low in forest floors, in contrast to P_o (average 970 mg kg^{-1} [SE 71]), and consequently contributed only a small proportion of total P (P_o ~ 90 % of P_t in forest floors).

C:N ratios of the mineral soils became significantly narrower (declining from 44 to 23) with increasing % C (~~r = -0.48;~~Table 2, Fig. 2a), similar to C:P_o (range approx. 300-1200~~; r = -0.36~~) (Table 2). In contrast, C:N of forest floors widened with increasing % C (~~r = 0.51;~~ Fig. 2b, Table 2) but nevertheless C:N of both substrates were well aligned across sites (r = 0.85, p < 0.001; Fig. 3a). The same symmetry in element ratios between substrates 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 cases the relationships in element ratios were not 1:1 as the organic horizons were less concentrated than 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. 3a). Lastly, there was typically a high degree of

correlation ($r > 0.7$) in element ratios within a substrate, such as C:N vs. $C:P_o$, for both mineral soils and forest floors (Table 2).

At this juncture in plantation age (52 years) we found no evidence that conifer species or planting density had an effect on mineral soil nutrient concentrations or ratios (for Species, $p = 0.99$ for C:N, $p = 0.48$ 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 $N:P_o$). There was, however, a slight difference detected in N % of forest floors with Species ($p = 0.034$). Forest floor N concentration under ~~Douglas-fir~~*P. menziesii* averaged 1.52 % N (SE 0.06), which was slightly greater than the other three species (combined average 1.35 % N), although forest floors also tended to be thinner under ~~Douglas-fir~~*P. menziesii* (4.7 cm [SE 0.8], on average, compared to 5.9 cm for the other three species; $p = 0.13$). Despite the modification in N concentrations under ~~Douglas-fir~~*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). ~~Western redcedar~~*Thuja plicata* had the least mortality (average 80 % survival), followed by ~~Sitka spruce~~*P. sitchensis* (76 %), ~~western hemlock~~*T. heterophylla* (71 %) and then ~~Douglas-fir~~*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 ~~Sitka spruce~~*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 ~~Sitka spruce~~*P. sitchensis*, had insufficient branches to obtain three composite subsamples (n = 167 from a target of 192 subsamples, and with ~~2 spruce~~two *P. sitchensis* plots removed from the analysis). ~~Despite this more limited data set we~~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 ~~Sitka spruce~~*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).~~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 ~~Sitka spruce~~*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 ~~were for the most part greater than a proposed threshold of 16 (to delineate N-only deficiencies; Güsewell, 2004), averaging~~averaged 19.5 (SE 0.8) for ~~western redcedar~~*T. plicata*, 18.2 (SE 0.8) for ~~Douglas-fir~~*P. menziesii*, 20.6 (SE 0.8) for ~~western hemlock~~*T. heterophylla*, and 17.4 (SE 1.1) for ~~Sitka spruce~~*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~~. Soil C and N regimes~~, 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, ~~the~~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

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

foliar N:P (~~16-25) suggests~~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 ~~(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 (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 phosphate (PO_4^-) via sorption to Fe and Al oxides, much more so than would be present for NH_4^+ or NO_3^- (Olander and Vitousek, 2004). A greater sink strength via immobilization and sorption for PO_4^- would require conifers to bypass mineralization of P by decomposers to some degree and instead access organic P more directly for uptake. A concurrent study of extracellular enzyme activity associated with ECM roots of ~~Douglas-fir~~*P. menziesii* has revealed

substantial increases in P-acquiring enzymes (J. Meeds, pers. comm.) that are likely acting upon the orthophosphate monoesters and diesters of organic P (Cade-Menum et al., 2000; Preston and Trofymow, 2000). Despite the expected contribution of P_o to forest nutrition, however, we found it more effective to gauge P availability through soil P_i concentrations (as the only significant correlate with foliar P ~~%),),~~ but other methods may prove to be more sensitive as a measure of plant-available P_o (DeLuca et al., 2015; Darch et al., 2016).

One unique aspect of soil organic matter found here was a decrease in mineral soil C:N and C:P_o ratios with increasing soil C % (Fig 2a), in contrast to the inverse relationships described by Tipping et al. (2016). This may reflect the significant legacy of N-fixing red alder (*Alnus rubra*) in coastal forest ecosystems, which has been found to promote soil C sequestration and P mobilization while simultaneously adding high quality (low C:N) litter (Binkley, 2005; Perakis and Pett-Ridge, 2019). A second key source of N-rich litter could be from epiphytic cyanolichens and cyanobacteria-bryophyte associations (Antoine, 2004; Lindo and Whiteley, 2011). Canopy lichens and bryophytes are noteworthy in low-frequency disturbance ecosystems such as rainforests because they produce a steady input of N while growing independently of the soil environment (Menge and Hedin, 2009). Red alder, in comparison, is an early-seral species that can be hindered in its establishment and vigour by low P_i availability (Brown et al., 2011; Kranabetter et al., 2013). Hedin et al. (2009) described a similar N paradox in tropical forests, and proposed N-fixing epiphytes as one mechanism that allows soil N regimes to increase despite soil P_i deficiencies or physiological down-regulation of N-fixation in high soil N environments.

5.2 Conifer species interactions by ARB and ECM mycorrhizal guild

The more significant differences in species productivity in relation to soil C:N was among the ECM species rather than solely between mycorrhizal types. ~~Western hemlock~~*Tsuga heterophylla* and ~~Douglas-fir~~*P. menziesii* had the most limited increase in basal area with declining C:N, a finding that was

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

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

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

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

Figure 3. Correlation in resource stoichiometry for a) C:N molar ratio, b) C:P_o molar ratio, and c) N:P_o moliar ratio between mineral soil and forest floor substrates. A 1:1 relationship is depicted by the gray lines.

Figure 4. a) Basal area by Species in relation to mineral soil C:N molar ratio (all planting densities included), and b) linear regressions between stand basal area and mineral soil C:N, fitted by Spacing, Species and Species × Soil interactions (~~model~~ output averaged across planting density~~).~~; Species × Soil C:N $p = 0.009$, $r^2 = 0.56$). Slope of the C:N regression was ~~ranked highest~~steepest for ~~Sitka spruce~~*Picea sitchensis* (Ss; -3.40), followed by ~~western redcedar~~*Thuja plicata* (Cw; -1.67), ~~Douglas-fir~~*Pseudotsuga menziesii* (Fd; -0.84), and ~~western hemlock~~*Tsuga heterophylla* (Hw; -0.70).

Figure 5. a) Foliar N (%) in relation to forest floor C:N molar ratio, and b) foliar P (%) in relation to forest floor C:P_o ratio. ~~Western~~ *Thuja plicata* (western redcedar) = Cw; *Pseudotsuga menziesii* (Douglas-fir) = Fd; *Tsuga heterophylla* (western hemlock) = Hw; *Picea sitchensis* (Sitka spruce) = Ss.

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

Table 2. Pearson correlation r and *p* values (in brackets, < 0.05 in bold) among total C, N, P_o concentrations and associated molar element ratios of the mineral soil (0-20 cm) and forest floor.

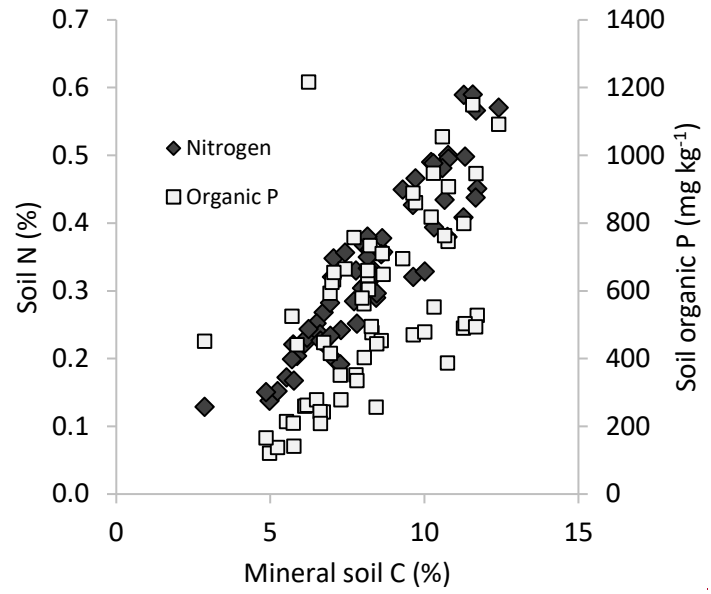
	N	P_o	C:N	C:P_o	N:P_o
Mineral soil					
C	0.92 (**< *0.001***)	0.71 (**< *0.001***)	-0.48 (**< *0.001***)	-0.36 (***0.004***)	-0.21 (0.101)
N	-	0.87 (**< *0.001***)	-0.75 (**< *0.001***)	-0.59 (**< *0.001***)	-0.38 (***0.002***)
P_o		-	-0.77 (**< *0.001***)	-0.82 (**< *0.001***)	-0.73 (**< *0.001***)
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***)

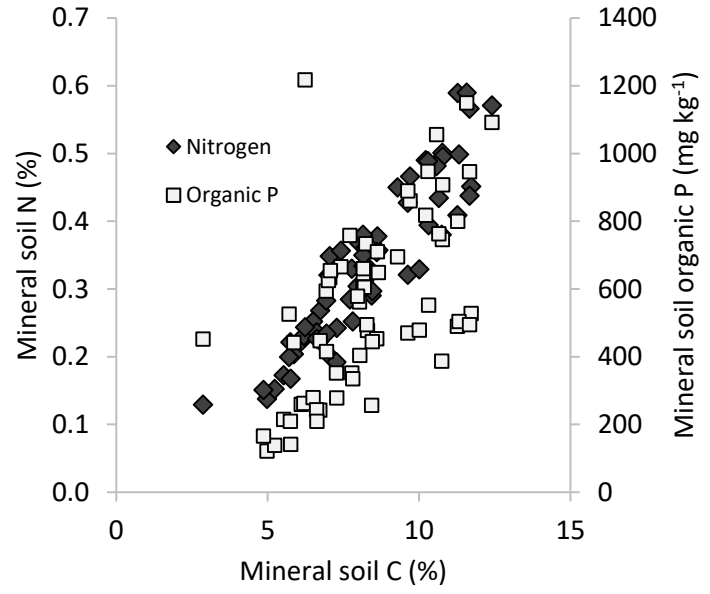
Table 3. Conifer species basal area (m^2 ha^{-1}) in 2014 (stand age 52 years) in relation to planting density (1329, 748 and 479 stems ha^{-1}) and mineral soil (0-20 cm) or forest floor resource stoichiometry (as molar ratios; *p* values < 0.05 in bold).

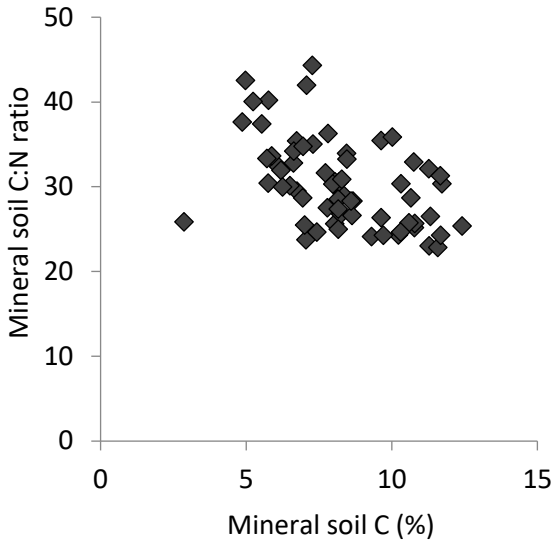
		No soil variable		Soil C:N		Soil C:P_o		Soil N:P_o	
	Df	F value	*p* value	F value	*p* value	F value	*p* value	F value	*p* value
Mineral soil									
Species	3	2.12	*0.110*	4.60	***0.007***	2.11	*0.113*	1.09	*0.363*
Spacing	2	7.12	***0.002***	11.94	***0.001***	10.06	***0.001***	7.88	***0.001***
Species × 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 ~~ratio~~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).

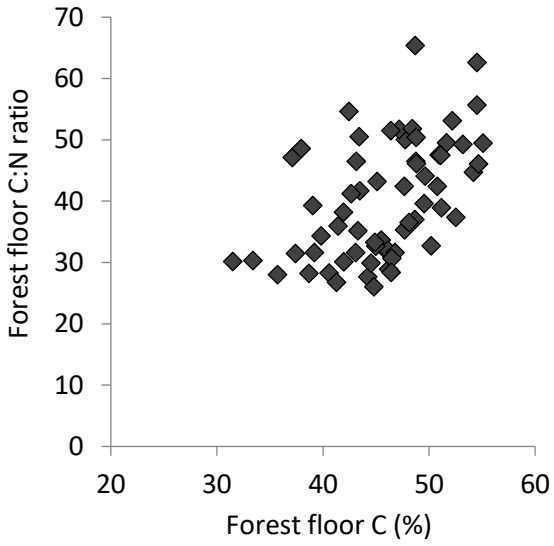
		Mineral soil		Forest floor	
	Df	F value	*p* value	F value	*p* value
Foliar N%					
Species	3	9.32	***< 0.001***	7.72	***0.001***
Spacing	2	0.39	*0.677*	0.97	*0.387*
Soil C:N	1	8.13	***0.006***	19.16	***< 0.001***
Foliar P%					
Species	3	12.56	***< 0.001***	11.94	***< 0.001***
Spacing	2	0.32	*0.729*	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
Nitrogen
Organic P
Soil N (%)
Soil organic P (mg kg-1)
0
5
10
15
Mineral soil C (%)

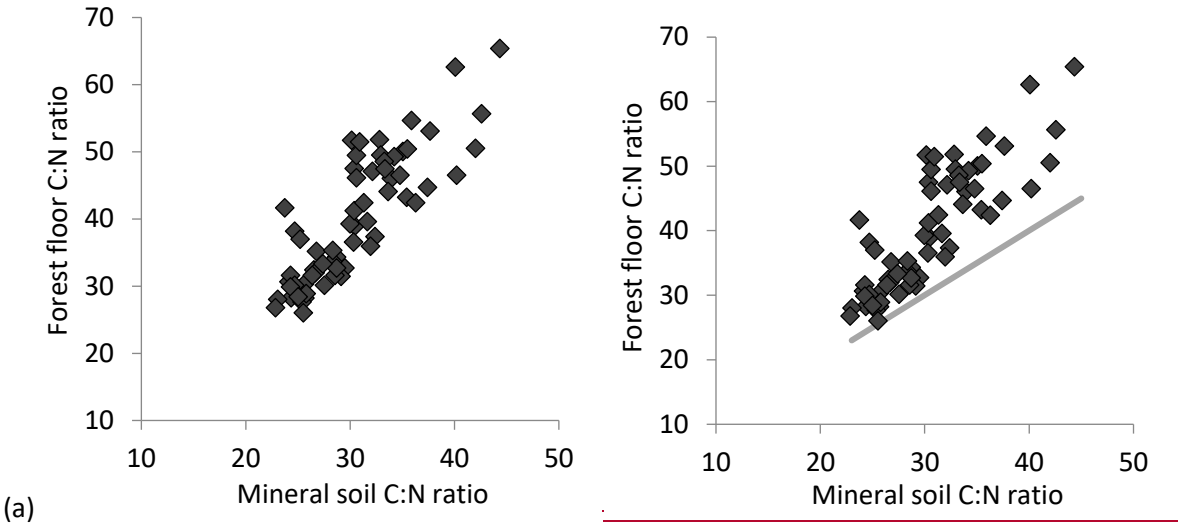

0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
1400
1200
1000
800
600
400
200
0
Nitrogen
Organic P
Mineral soil N (%)
Mineral soil organic P (mg kg-1)
0
5
10
15
Mineral soil C (%)


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

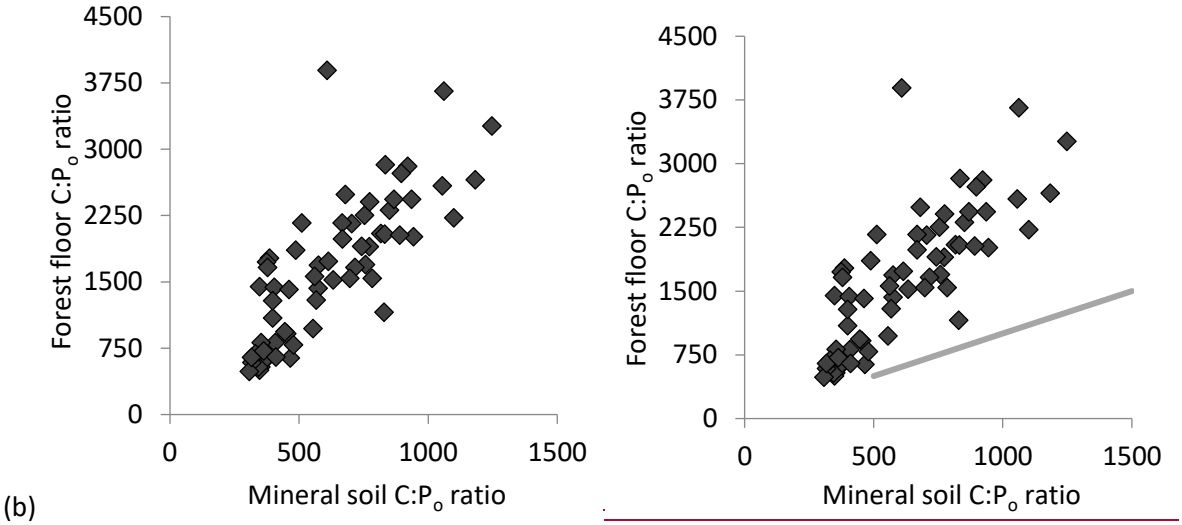
(a)


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

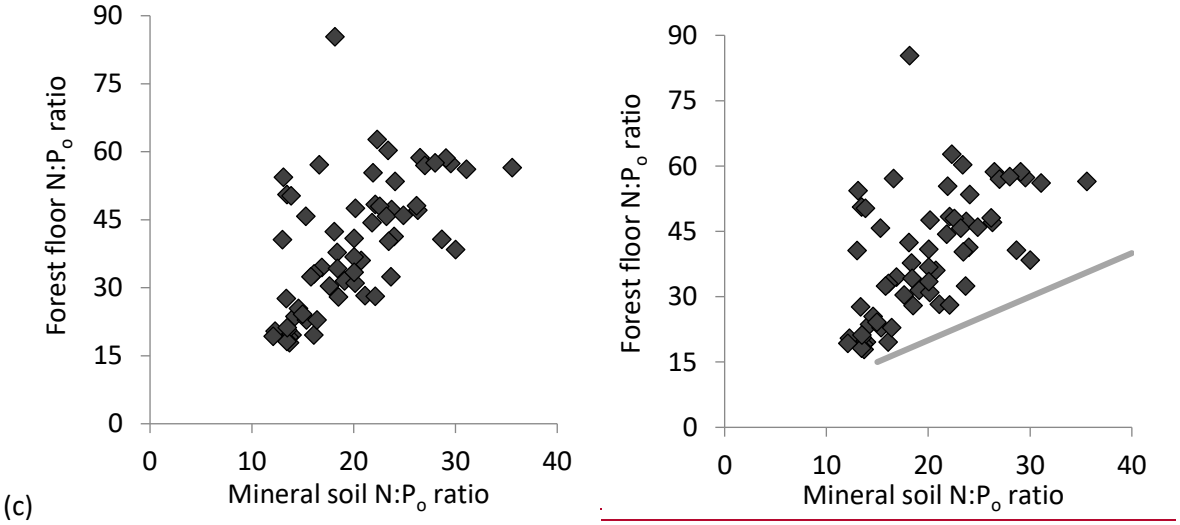
(b)


Forest floor C:N ratio
Mineral soil C:N ratio
10
20
30
40
50
60
70

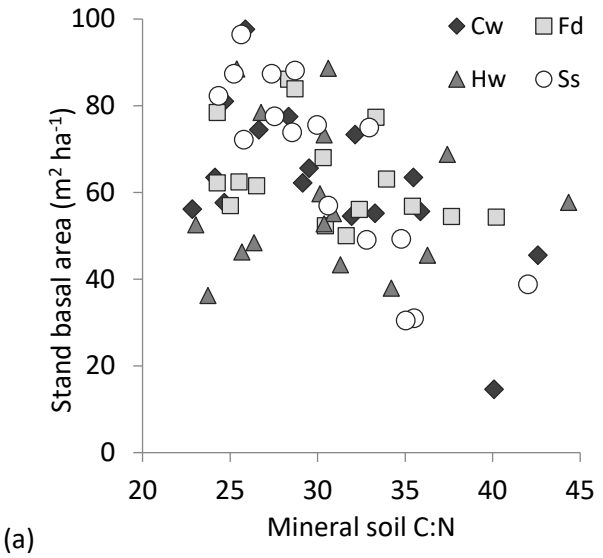
(a)


Forest floor C:P$_o$ ratio
Mineral soil C:P$_o$ ratio
0
750
1500
2250
3000
3750
4500
500
1000
1500

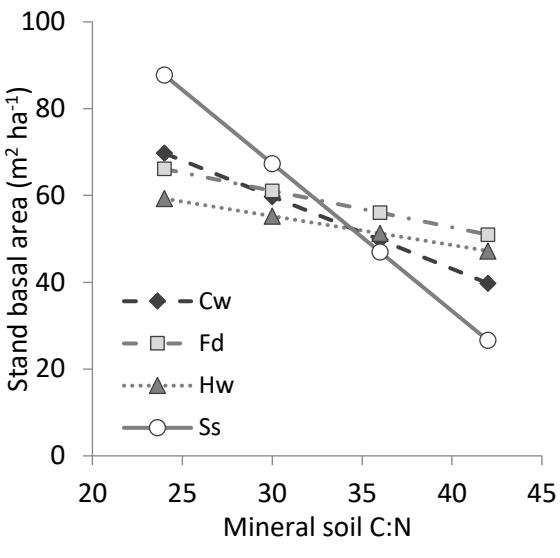
(b)


Forest floor N:P$_o$ ratio
Mineral soil N:P$_o$ ratio
0
15
30
45
60
75
90
10
20
30
40

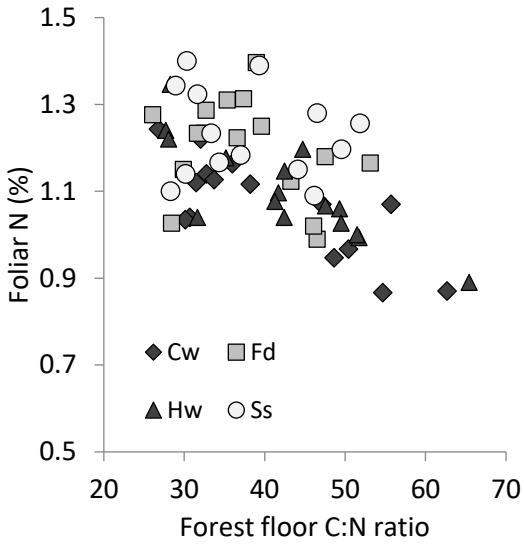
(c)


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) (b)