An assessment of phosphorus limitations to soil nitrogen availability across forest ecosystems of north coastal British Columbia

J.M. Kranabetter, A. Banner, and A. de Groot

Abstract: The wet, slow-growing forests of western redcedar (*Thuja plicata* Donn ex D. Don) and salal (*Gaultheria shallon* Pursh) on the north coast of British Columbia are characteristically low in available phosphorus (P) compared with more productive forest ecosystems. It has been suggested that declining P availability can eventually limit soil biological activity and restrict nitrogen (N) cycling. We investigated this potential link between P availability and N cycling for three forest types (cedar–salal, hemlock – lanky moss and spruce – sword fern) covering a wide gradient in site productivity. Forest floors (upper 20 cm) and mineral soils (20 cm depth) were collected from five replicate sites of each forest type and incubated for 20 weeks at field moisture content with and without an amendment of NaH_2PO_4. We found that organic P concentrations of both forest floors and mineral soils were positively correlated to extractable inorganic N concentrations (unamended soils over 20 weeks). The addition of P to the low-productivity cedar–salal soils led to significant increases in extractable inorganic N in the forest floors and mineral soils. P amendments led to either a smaller or nonsignificant increase in extractable N for moderately and highly productive soils. Soil respiration of CO_2 and respiration quotients were substantially reduced in forest floors with a P amendment, suggesting N mineralization was governed by exoenzyme allocation rather than decomposition rates. These results demonstrate a possible enhancement in N supplies with an application of P to low-productivity cedar–salal forests.

Résumé : Comparativement aux écosystèmes forestiers plus productifs, les forêts humides à croissance lente de thuya géant (*Thuja plicata* Donn ex D. Don) et de gaulthérie shallon (*Gaultheria shallon* Pursh) de la côte nord de la Colombie-Britannique sont caractérisées par une faible disponibilité en phosphore (P). La diminution de la disponibilité en phosphore pourrait éventuellement limiter l'activité biologique du sol et restreindre le recyclage de l'azote (N). Les auteurs ont examiné ce lien potentiel entre la disponibilité de P et le recyclage de N pour trois types forestiers (cèdre–gaulthérie, pruche – rhytidiadelphe lanière et épinette – fougère épée) qui couvrent un large gradient de potentiel de station. La couverture morte (les 20 cm supérieurs) et le sol minéral (20 cm de profondeur) ont été récoltés dans cinq stations de chaque type forestier et incubés pendant 20 semaines à la teneur en humidité au champ avec ou sans amendement de NaH_2PO_4. Ils ont observé que la concentration de P organique de la couverture morte et du sol minéral était positivement corrélée à la concentration de N inorganique extractible (sols non amendés pendant 20 semaines). L'ajout de P aux sols à faible productivité du type forestier cèdre-gaulthérie s'est traduit par un accroissement significatif de N inorganique extractible dans la couverture morte et le sol minéral. Les amendements phosphatés se sont traduits par un accroissement, soit plus faible, soit non significatif de N extractible pour les sols modérément à fortement productifs. La respiration de CO_2 du sol et les quotients de respiration étaient substantiellement réduits dans la couverture morte amendée avec P, indiquant que la minéralisation était contrôlée par l'allocation d'exoenzymes plutôt que par le taux de décomposition. Ces résultats démontrent qu'une application de P peut augmenter les apports de N dans les forêts à faible productivité de cèdre et de gaulthérie.

[Traduit par la Rédaction]

Introduction

The low-productivity forests of western redcedar (*Thuja plicata* Donn ex D. Don), yellow cedar (*Chamaecyparis nootkatensis* (D. Don) Spach.), and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) on the north coast of British Columbia occur on gentle slopes, usually with deep accumulations of surface organic matter (often 50 cm or more) and imperfectly drained soils. These "cedar–salal" (*Gaultheria shallon* Pursh) forests have demonstrated significant deficiencies in soil and foliar nutrition, especially nitrogen (N) and phosphorus (P), and relatively poor rates of conifer growth (Messier 1993; Prescott et al. 1996; Kranabetter et al. 2003). For this reason the British Columbia Ministry of Forests is examining site treatments that may alleviate nutritional deficiencies and enhance plantation productivity on cedar–salal sites (http://www.for.gov.bc.ca/rni/Research/HyP3/hyp3-pg1.htm).

P is derived from the weathering of primary minerals, with limited inputs from soluble forms or atmospheric deposition (Walker and Syers 1976; Gressel and McColl 1997). P defi-

Received 31 May 2004. Accepted 22 October 2004. Published on the NRC Research Press Web site at http://cjfr.nrc.ca on 16 March 2005.

J.M. Kranabetter.[1] British Columbia Ministry of Forests, Bag 6000, Smithers, BC V0J 2N0, Canada.
A. Banner. British Columbia Ministry of Forests, Bag 6000, Smithers, BC V0J 2N0, Canada.
A. de Groot. Drosera Ecological Consulting, 8612 Horlings Road, Smithers, BC V0J 2N2, Canada.

[1]Corresponding author (e-mail: Marty.Kranabetter@gems5.gov.bc.ca).

 doi: 10.1139/X04-192

ciencies in cedar–salal forests likely arise because of relatively limited rooting through deep, poorly drained organic layers into mineral soils, thereby restricting plant uptake and cycling of primary P sources. In addition, glacial till deposits on the north coast are quite localized, and forest soils derived from parent materials such as granitic bedrock are relatively low in P (along with Mg and K) compared with metamorphic bedrock (Heilman and Gass 1974; Kranabetter and Banner 2000). Soils in the hypermaritime climate also undergo high rates of weathering and leaching, and more productive forests are positively influenced by disturbances, such as blowdown or mass wasting, which bring mineral subsoils to the surface (Bormann et al. 1995). Western redcedar – salal plantations from the south coast of British Columbia have generally responded to N and P fertilization, providing further evidence that limited P availability is characteristic of these lower productivity coastal forests (Weetman et al. 1989*a*, 1989*b*; Prescott et al. 1993).

The low availability of P in soils would be a direct stress on tree growth, but, in addition, might also affect soil N cycles and biological N fixation (Cole and Heil 1981; Tate and Salcedo 1988; Vitousek and Howarth 1991). Some evidence for this influence has been provided by the correlation of N and carbon (C) mineralization with the P content of litter and soils (Pastor et al. 1984; DeBusk and Reddy 1998; Carlyle and Nambiar 2001). The addition of P fertilizers has also been reported to affect N and C mineralization in some upland soils (Munevar and Wollum 197; Nommik 1978; Haynes and Swift 1988; Cleveland et al. 2002) and organic soils (Amador and Jones 1993; White and Reddy 2000). A suggested general pattern in ecosystem development is for P availability to decline over time and to eventually supersede N as the "master regulator" of biological activity (Chadwick et al. 1999; Wardle et al. 2004). Perhaps a similar restriction may be acting on N cycles in these low-productivity coastal forests, where P availability is limited by the aforementioned combination of soil processes.

In this study, we examined soils from three forest types on the north coast of British Columbia that span a wide gradient in site productivity for evidence of a relationship between N and P availability. We then tested the influence of a P amendment on extractable inorganic N and microbial activity for these soils in a laboratory incubation (for up to 20 weeks). We hypothesized that P amendments would have a larger effect on the more unproductive forest soils because of the limitations in microbial activity caused by low P availability. The results of the experiment will provide evidence for a link between P and N availability in these coastal soils and demonstrate the potential benefits of P amendments to cedar–salal forests relative to more productive ecosystems of the north coast.

Materials and methods

Site selection

The Coastal Western Hemlock zone (CWH) occurs at low to middle elevations mostly west of the coastal mountains, along the entire British Columbia coast, and on into Alaska, Washington, and Oregon (Meidinger and Pojar 1991). The CWH has a temperate, rainy climate, corresponding to Köppens's Cfb climatic regime (Krajina 1969). Low-productivity cedar–salal forests are typical of the very wet hypermaritime subzone of the Coastal Western Hemlock zone (CWHvh2), found on the outer coast of British Columbia, extending from northern Vancouver Island to the British Columbia – Alaska border. The CWHvh2 ranges in elevation from 0 to 600 m and has a cool, mild climate (mean annual temperature 7 °C), with little snow but foggy and rain year round (approx. 3000 mm/year) (Banner et al. 1993).

We chose plot locations based on site series (plant communities and associated site and soil factors), interpreted through the edatopic grid of the British Columbia biogeoclimatic ecosystem classification system (Pojar et al. 1987; Banner et al. 1993). The sites were located in unmanaged old-growth forests around Prince Rupert, British Columbia (54°19′, 130°19′). Three distinct site series ("forest type") of the CWHvh2 were sampled to provide a wide range in soil characteristics and site productivity: the low-productivity western redcedar – western hemlock – salal (site series 01 Cw–salal; mesic to subhygric moisture regime; poor to medium nutrient regime); the medium-productivity western hemlock – Sitka spruce (*Picea sitchensis* (Bong.) Carr.) – lanky moss (*Rhytiadelphus loreus* (Hedw.) Warnst.) (site series 04 Hw – lanky moss; submesic moisture regime and poor to medium nutrient regime); and the high-productivity western redcedar – Sitka spruce – sword fern (*Polystichum munitum* (Kaulf.) K.B. Presl) (site series 05 Ss – swordfern; submesic moisture regime and rich to very rich nutrient regime; Banner et al. 1993; Kranabetter et al. 2003). Site indices (metres, at 50 years) for western redcedar, western hemlock, and Sitka spruce in second-growth stands have been estimated as 15–18 for Cw–salal sites, 24–27 for Hw – lanky moss sites, and 30–33 for Ss – sword fern sites (A. Banner, unpublished data).

In the first week of July 2003, we located five replicates of each forest type for a total of 15 plots for the experiment. Our search for the appropriate forest type was aided by our field experience in this area, and we were able to locate replicates that were at least a few kilometres apart and across different parent materials. At each plot (20 m × 20 m), we collected soils from five random points and bulked these into one mineral soil or forest floor sample per plot. Forest floors (F and H layers only; litter layers were excluded) were sampled down to 20 cm, the general depth of the rooting zone, or sometimes less where organic accumulations were thinner. Mineral soils were sampled down to 20 cm, or occasionally shallower on thin soils, using a stony soil auger (4 cm wide). On deeper organic soils we continued to auger through the forest floor until we made contact with the surface of the mineral soil.

The Cw–salal sites had a characteristic plant community of salal, false azalea (*Menziesia ferruginea* Sm.), Alaskan blueberry (*Vaccinium alaskaense* Howell), deer fern (*Blechnum spicant* (L.) Roth), and scattered skunk cabbage (*Lysichiton americanum* Hult. & St. John). These gentler, more imperfectly drained sites had an average slope of 25%, with approximately 50 cm of forest floor. Forest floors were typically Resimors, dominated by an Hr horizon (Green et al. 1993) and deep enough to categorize as Humic Folisols (Soil Classification Working Group 1998). Mineral soils were derived from saprolitic granodiorite, gneissic diorite, and schist parent materials (Kranabetter and Banner 2000). Crown closure averaged 43% and comprised 24% Cw, 13% Hw, 5% Yc (yellow cedar), and 1% Ss.

Table 1. Average soil chemical properties (forest floors and mineral soils) of the Cw–salal, Hw – lanky moss, and Ss – sword fern sites.

	LOI (%)	Total C (g/kg)	Total N (g/kg)	C:N ratio	Extract. P (mg/kg)	Total P_o (mg/kg)	C:P_o ratio
Forest floor							
Cw–salal	86 (6)	510 (31)	12.6 (0.6)	40a (1.5)	16.1 (2.5)	592 (22)	867a (64)
Hw – lanky moss	89 (2)	528 (11)	13.4 (0.8)	40a (2.4)	20.9 (5.3)	679 (72)	807ab (70)
Ss – sword fern	83 (2)	470 (23)	14.6 (1.1)	33b (1.3)	20.6 (3.6)	754 (41)	630b (40)
$p > F$	0.541	0.267	0.322	0.012	0.666	0.077	0.039
Mineral soil							
Cw–salal	8.8 (0.9)	47 (2.6)	1.42 (0.07)	33 (1.2)	23.7 (11)	189 (21)	259 (26)
Hw – lanky moss	11.9 (2.0)	66 (9.1)	1.99 (0.32)	33 (1.7)	14.9 (7)	252 (25)	275 (52)
Ss – sword fern	9.4 (1.0)	51 (6.0)	1.69 (0.20)	31 (1.7)	4.5 (1)	266 (30)	284 (82)
$p > F$	0.275	0.546	0.163	0.361	0.123	0.111	0.951

Note: Values are means with standard errors in parentheses. LOI, loss-on-ignition; extract., extractable; exch., exchangeable; P_o, organic phosphorus.

The Hw – lanky moss sites were dominated by shrubs such as *Vaccinum alaskaense* and *Vaccinum ovalifolium* (Sm.). Sites were typically steeper (slopes of 40%–70%) and better drained, with approximately 20 cm of forest floor accumulation. Crown closure averaged 57% and comprised 20% Cw, 27% Hw, 1% Yc, 2% Ss, and 7% Aa (*Abies amabilis* (Dougl. ex Loud.) Dougl. ex Forbes). Forest floors of the Hw – lanky moss sites were classified as Resimors, and mineral soils were Orthic Humo-Ferric or Orthic Ferro-Humic Podzols. Mineral soils were derived from saprolitic granodiorite or colluvial gneissic diorite parent materials.

The Ss – sword fern sites were indicated by a near continuous cover of sword fern and were found only on schist parent materials with relatively active colluvial slopes. Sites were also steep and well drained, with approximately 15 cm of forest floor. Crown closure averaged 62% and comprised 2% Cw, 15% Hw, 38% Ss, and 7% Aa. Forest floors of the Ss – sword fern sites were classified as Resimors, and mineral soils were Orthic Humo-Ferric or Orthic Ferro-Humic Podzols.

Laboratory incubation

The fresh soil samples (both forest floor and mineral soils) were run through a coarse 12-mm sieve to remove large roots, stones, conifer cones, pieces of wood, etc., and any soil macrofauna (e.g., millipedes) were removed. A subsample was taken of the sieved soil to determine gravimetric field moisture content (105 °C for 24 h). A second subsample was frozen for a measurement of inorganic N (time 0). A third subsample was refrigerated and shipped immediately for a determination of microbial biomass. The equivalent dry mass of 100 g mineral soil or 25 g forest floor were put into 1-L Mason jars. Soil samples from each plot were put into two jars, one to serve as a control, while the other was amended with P. The P amendment was 0.6 g of NaH_2PO_4, equivalent to almost 150 mg P/jar. This amount represents an application rate equivalent to 150 kg P/ha. Sodium was chosen over Ca, K, or Mg to better isolate the effect of P, as these latter cations can have stronger effects on soils (Agarwal et al. 1971). The NaH_2PO_4 crystals were added to the soil and dissolved by stirring, while the control soils were stirred with no amendment. The remaining soils not used in the incubation were air-dried for chemical analysis. The dried soils were ground and sieved (2 mm) to correct for the gravel content of the incubated soils (12 mm). These saprolitic and colluvial soils (Kranabetter and Banner 2000) had almost no coarse fragments between 2 and 12 mm in size, however, so no correction factor was required for the comparison of soil properties.

The jars were incubated at 22 °C for up to 20 weeks, and lids were removed once a week to replenish the air. The mass of the jar plus moist soil was noted at the beginning of the experiment, and distilled water was added every 2 to 3 weeks to maintain the field moisture content. The incubation experiment was replicated to allow an analysis of soil respiration and N mineralization after 4, 12, and 20 weeks (a total of 180 jars).

Soil respiration was measured with a static laboratory method. We used a tripod and plunger apparatus to sample gas from the respiration jars, rather than a septum and syringe technique (Zibilske 1994), to avoid possible leakages when transporting gas samples to the analytical laboratory (Kranabetter and Banner 2000). At each sample date we removed the lids for 1 h, to ensure an ambient concentration of CO_2, and then sealed the jars and collected gas samples over a 24-h period. The concentration of CO_2 was almost always <2%, so aeration of the sample during the 24-h incubation was unnecessary (Zilbilske 1994). Six ambient air samples (from empty jars) were included as controls at each sample period. After each respiration measurement, we divided the soil into two subsamples, one of which was frozen for inorganic N, while the other was air-dried for extractable inorganic P. The exception was at week 20, where the sample was divided into three, with the third portion of soil undergoing a determination of microbial biomass.

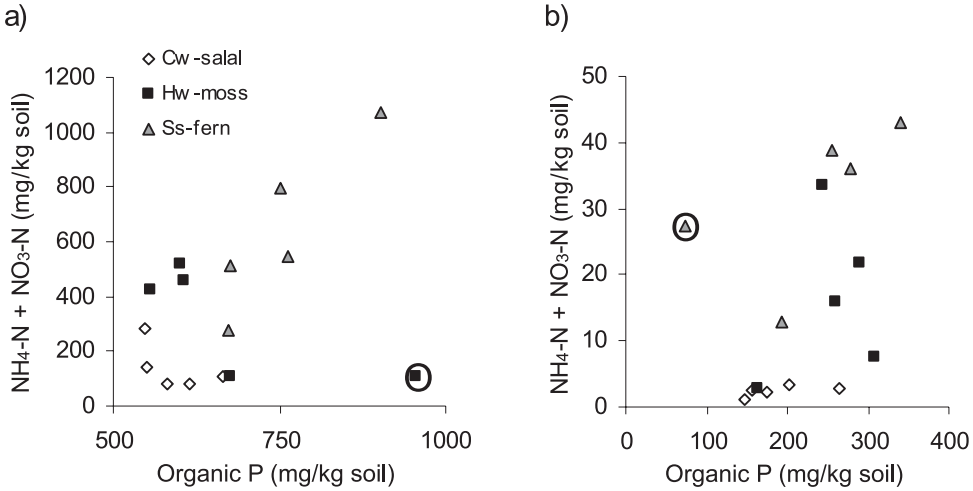
Laboratory methods

Mineral soil and forest floor samples collected for chemical analysis were air-dried, ground, and sieved (100 mesh). Total organic matter was determined by loss-on-ignition (450 °C for 20 h). Total C and N were measured using combustion elemental analysis and total sulphur by LECO S Analyzer (LECO Corp., St. Joseph, Michigan). Total organic P (P_o) of the mineral soil and forest floor were determined indirectly with a digestion method using sulfuric acid and a UV – visible spectrophotometer (O'Halloran 1993). Extractable inorganic P was determined by the Bray P1-method. Exchangeable cations and cation exchange capacity (CEC) were determined by the neutral ammonium acetate method. Soil pH in H_2O

N:P_o ratio	Total S (g/kg)	Exch. Ca (cmol/kg)	Exch. K (cmol/kg)	Exch. Mg (cmol/kg)	Exch. Na (cmol/kg)	pH (H_2O)
21.4 (1.0)	1.40 (0.1)	21.6 (3.4)	1.31a (0.13)	5.07 (0.7)	0.36 (0.03)	3.83 (0.06)
20.4 (2.1)	1.52 (0.1)	17.0 (3.0)	1.13ab (0.10)	6.26 (0.7)	0.48 (0.07)	3.65 (0.06)
19.4 (1.3)	1.81 (0.2)	17.0 (3.2)	0.86b (0.09)	5.89 (0.7)	0.49 (0.10)	3.80 (0.10)
0.661	0.157	0.567	0.022	0.433	0.396	0.196
7.8 (0.9)	0.25 (0.03)	0.46 (0.07)	0.016a (0.01)	0.14a (0.02)	0.039 (0.002)	4.58 (0.08)
8.2 (1.5)	0.34 (0.08)	0.43 (0.10)	0.052b (0.01)	0.19ab (0.03)	0.051 (0.009)	4.39 (0.03)
9.3 (2.7)	0.37 (0.12)	0.85 (0.34)	0.064b (0.01)	0.28b (0.05)	0.057 (0.012)	4.48 (0.15)
0.963	0.597	0.546	0.002	0.056	0.371	0.410

Treatment means followed by the same letter are not significantly different by forest type; forest floors and mineral soils were tested separately.

Fig. 1. Relationship between organic P concentrations and extractable inorganic N (week 20) for unamended (*a*) forest floors and (*b*) mineral soils. The outlier points removed from the linear regression are circled.



was determined with a 1:2 soil to solution ratio using an electronic pH meter (all analytical methods are found in Kalra and Maynard 1991 or Carter 1993).

Extractable inorganic N (NH_4-N + NO_3-N) was determined using a KCl extraction of a 5-g and 2-g dry-soil equivalent of mineral soils and forest floors, respectively (Hart et al. 1994). The KCl extractions were clarified by centrifugation for 15 min at 1000*g*. The extract was pipetted from the clear supernatant into an autoanalyzer cup for analysis. The extracts were immediately frozen (–80 °C), allowing all preincubation and postincubation samples to be analyzed together. The NH_4 and NO_3-N in the extracts were measured colorimetrically using an Alpkem Flow System IV analyzer (OI Analytical, College Station, Texas).

The gas samples were analyzed for CO_2 (*%v/v*) with a Perkin-Elmer Autosytem II gas chromatograph (Perkin-Elmer Corp., Boston, Massachusetts). The gas sample was transferred from the autosampler into the GC injection port via a 0.53-mm ID fused silica capillary column. Standards are prepared by purging the headspace vial for 1 min with gas standard prior to crimping. A duplicate set of standards was run before and after every 20 samples to permit bracket calibration. The respiration results were converted to micrograms of CO_2-C per gram soil (Zilbilske 1994).

Microbial biomass was determined by the chloroform fumigation–extraction method (Voroney et al. 1993). A 10-g and 2.5-g dry-soil equivalent of mineral soils and forest floors, respectively, were used to determine microbial C. The unfumigated and fumigated extracts (0.5 mol/L K_2SO_4) were analyzed for total organic carbon using an automatic TOC analyzer (Astro model 2002 system 2). Microbial C was determined by the change in organic C between the fumigated and unfumigated extracts, and the results were converted to microbial biomass (micrograms per gram soil) using a k_{EC} efficiency of 0.25 (a standard extraction of microbial C; Voroney et al. 1993). Respiration quotient (qCO_2 was determined as the amount of CO_2-C produced (per hour) per unit microbial biomass C (Anderson and Domsch 1990). The quotient was determined with the microbial biomass and soil respiration data collected at week 20 of the incubation.

Statistics

The experiment was a completely randomized design with repeated measures, with forest type as the main plot factor and P amendment as a split plot. The results were tested by ANOVA using repeated measures under Proc Mixed (SAS Institute Inc. 1988). Forest types were tested separately where significant interactions of type × treatment × time were found. Differences in initial soil properties amongst forest types

Fig. 2. Extractable inorganic P (Bray-1 extraction) in (*a*) forest floors and (*b*) mineral soils across forest types at weeks 0, 4, 12, and 20 for unamended soils (SE shown by error bars).

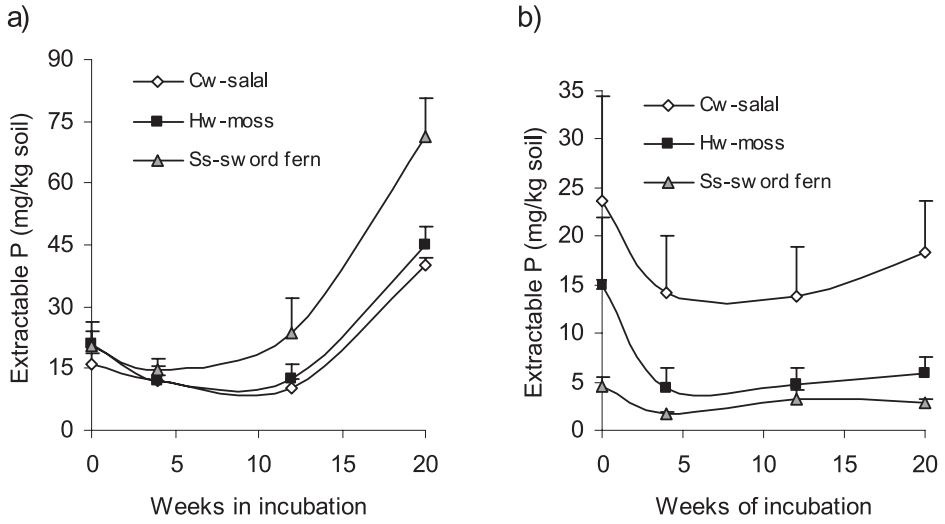


Table 2. ANOVA results ($p > F$) for P amendment effects on extractable inorganic N (NH_4-N + NO_3-N), soil respiration, microbial biomass, and respiration quotient (week 20) of forest floors and mineral soils.

Source	df	Extractable NH_4+NO_3	Soil respiration	Microbial biomass	Respiration quotient
Forest floor					
Forest type	2	0.001	0.232	0.005	0.579
Treatment	1	0.001	0.001	0.001	0.001
Type × treatment	2	0.139	0.130	0.004	0.789
Time	2	0.001	0.001	0.193	na
Type × time	4	0.591	0.098	0.101	
Treatment × time	2	0.239	0.001	0.001	
Type × treatment × time	4	0.033	0.025	0.004	
Mineral soil					
Forest type	2	0.001	0.540	0.186	0.194
Treatment	1	0.016	0.034	0.876	0.366
Type × treatment	2	0.253	0.029	0.060	0.224
Time	2	0.001	0.001	0.001	na
Type × time	4	0.008	0.271	0.247	
Treatment × time	2	0.189	0.001	0.876	
Type × treatment × time	4	0.026	0.007	0.060	

Note: na, not applicable.

were compared by general linear models (SAS Institute Inc. 1988). Soil chemical properties, extractable inorganic N, and soil respiration were log transformed for the statistical analysis. The relationship between soil properties and extractable inorganic N (week 20) was tested directly by multiple linear regression. Stepwise elimination of variables from regressions was used to determine the "best" (highest adj. R^2 with the least number of variables) relationship.

Results

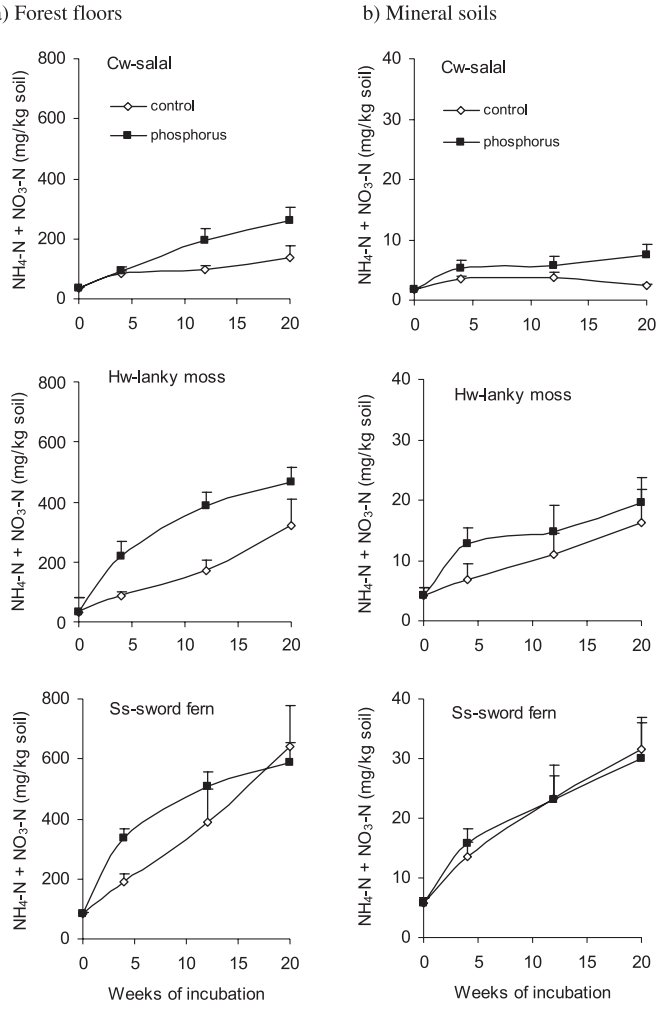
Soil properties among forest types

Forest floors of Ss – sword fern sites had higher concentrations of total organic P and lower C/P_o ratios than Cw–salal sites, but no differences in extractable inorganic P concentrations (Table 1). Many forest floor soil properties were quite consistent across forest types, with the exception of higher exchangeable K concentrations and wider C:N ratios on Cw–salal sites. The trends in organic P for mineral soils were similar to that for forest floors, but with no significant differences in C/P_o ratios (Table 1). Exchangeable K and Mg also increased in concentration from Cw–salal to Ss – sword fern sites.

The imperfectly drained Cw–salal sites had significantly wetter forest floors (average of 584% *m*/*m*) at the time of sampling compared with both Hw – lanky moss (468%) and Ss – sword fern (402%) sites ($p = 0.001$). There were no differences in mineral soil moisture content detected between forest types at the time of sampling (average of 80%) ($p = 0.495$).

Extractable inorganic N of the unamended soils after a 20-week incubation period showed a positive relationship with organic P concentrations for both forest floors and mineral

Fig. 3. Extractable inorganic N (NH_4-N + NO_3-N) in (*a*) forest floors and (*b*) mineral soils across forest types at weeks 4, 12, and 20, with and without a P amendment (SE shown by error bars).



soils, albeit after the removal of one outlier in each case (Fig. 1*a* and 1*b*) (p = 0.003, adj. R^2 = 0.49 and p = 0.009, adj. R^2 = 0.40 for forest floors and mineral soils, respectively, with n = 14 for both substrates).

Extractable inorganic P concentrations of the forest floors (unamended only) increased during the incubation period and were significantly higher for Ss – sword fern soils than for either Cw–salal or Hw–moss soils by week 20 (p = 0.006) (Fig. 2*a*). In contrast, extractable inorganic P of the mineral soils initially dropped and then remained relatively constant during the incubation and was significantly higher for Cw–salal soils (week 20, p = 0.011) (Fig. 2*b*). As expected, the P amendment substantially increased the availability of inorganic P compared with control soils, with Bray-P1 extractions of approximately 3400 mg/kg for forest floors and 440 mg/kg for mineral soils.

The effects of P amendments on extractable inorganic N

P amendments to forest floors caused significantly different patterns in extractable inorganic N over time among forest types (Table 2, Fig. 3*a*). Cw–salal forest floors showed no effect of the P additions at week 4, followed by larger increases in inorganic N by weeks 12 and 20, with no evidence yet of a convergence in treatments over time (Table 3). The Hw – lanky moss forest floors had large increases in extractable N from P additions in weeks 4 and 12, but the differences narrowed somewhat by week 20. The Ss – sword fern forest floors also showed large P addition effects early, but extractable N had converged by week 20, and no significant differences in inorganic N were detected (Table 3). The amendment of P led to a doubling in extractable N concentrations for the Cw–salal forest floors, which represented about 40% of the extractable N found on Ss – sword fern forest floors.

Similar interactions for extractable N were found in mineral soils, with large differences between forest types and varying responses over time (Table 2, Fig. 3*b*). We were unable to detect a significant effect of the P amendment on extractable inorganic N for either the Hw – lanky moss or Ss – sword fern soils (Table 3). Concentrations of extractable N on Cw–salal soils began to diverge by week 20 ($p < 0.10$), resulting in a relatively substantial (9.5× greater) difference in N availability. With this increase, however, the amended Cw–salal soils had only about 20% of the extractable N concentrations found on Ss – sword fern mineral soils.

Almost all of the extractable N in forest floors was extracted as NH_4 for the Cw–salal and Hw – lanky moss soils, but by week 20 some of the Ss – sword fern forest floors had accumulated considerable amounts of NO_3 (Fig. 4*a*) The number of plots with undetectable NO_3 concentrations precluded a statistical analysis, but the trend was for reduced concentrations of NO_3 with P amendments. Only small amounts of NO_3 were detected in Cw–salal mineral soils, and concentrations progressively increased across Hw – lanky moss and Ss – sword fern soils (Fig. 4*b*). Similar to forest floors, the P-amended soils had lower concentrations of NO_3 for those soils wherever nitrification had occurred.

The effects of P amendments on microbial activity

P amendments to soils caused significantly different patterns in respiration over time among forest types (Table 2, Fig. 5). In contrast to extractable N, the P amendment caused a substantial decrease (approx. 50%) in respiration of forest floors across all three forest types (Fig. 5*a*). The decrease in respiration was consistent for Ss – sword fern forest floors, but differences became larger for the Cw–salal and Hw–moss forest floors over time (Table 3). Respiration rates for the control and P-amended mineral soils fluctuated over time for Cw–salal and Hw – lanky moss sites as well, in contrast to a 30% increase in respiration for Ss – sword fern soils (Table 2 and 3, Fig. 5*b*).

Microbial biomass of the fresh forest floors had changed slightly by week 20, but biomass more than doubled for the mineral soils during the incubation period (Fig. 6*a* and 6*b*). Both forest floors and mineral soils had significant forest type × treatment × time interactions for microbial biomass (Table 2). In forest floors, microbial biomass was reduced by the P amendment for Hw – lanky moss sites only (Table 3). For mineral soils, microbial biomass increased after the P amendment for Ss – sword fern sites only (Table 3).

Table 3. ANOVA results ($p > F$) by forest type for P amendment effects on extractable inorganic N (NH_4-N + NO_3-N), soil respiration, and microbial biomass for forest floor (FF) and mineral soil (mineral).

	NH_4+NO_3			Soil respiration			Microbial biomass		
Source	df	FF	Mineral	df	FF	Mineral	df	FF	Mineral
Cw–salal									
Treatment	1	0.054	0.092	1	0.002	0.314	1	0.261	0.222
Time	2	0.002	0.508	2	0.001	0.001	1	0.446	0.001
Treatment × time	2	0.070	0.065	2	0.010	0.022	1	0.261	0.222
Hw – lanky moss									
Treatment	1	0.022	0.297	1	0.001	0.705	1	0.001	0.510
Time	2	0.001	0.004	2	0.002	0.001	1	0.335	0.005
Treatment × time	2	0.164	0.749	2	0.003	0.003	1	0.001	0.510
Ss – sword fern									
Treatment	1	0.285	0.946	1	0.004	0.001	1	0.274	0.013
Time	2	0.001	0.001	2	0.002	0.001	1	0.006	0.001
Treatment × time	2	0.044	0.253	2	0.558	0.400	1	0.177	0.013

Fig. 4. Nitrate concentrations in (*a*) forest floors and (*b*) mineral soils across forest types at weeks 4, 12, and 20, with and without a P amendment (SE shown by error bars).

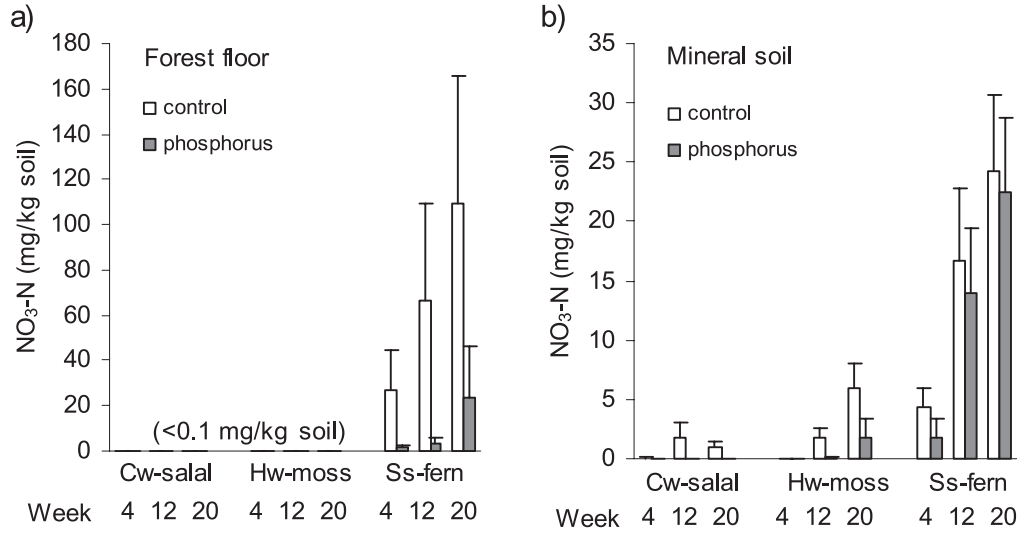


Fig. 5. Soil respiration in (*a*) forest floors and (*b*) mineral soils across forest types at weeks 4, 12, and 20, with and without a P amendment (SE shown by error bars).

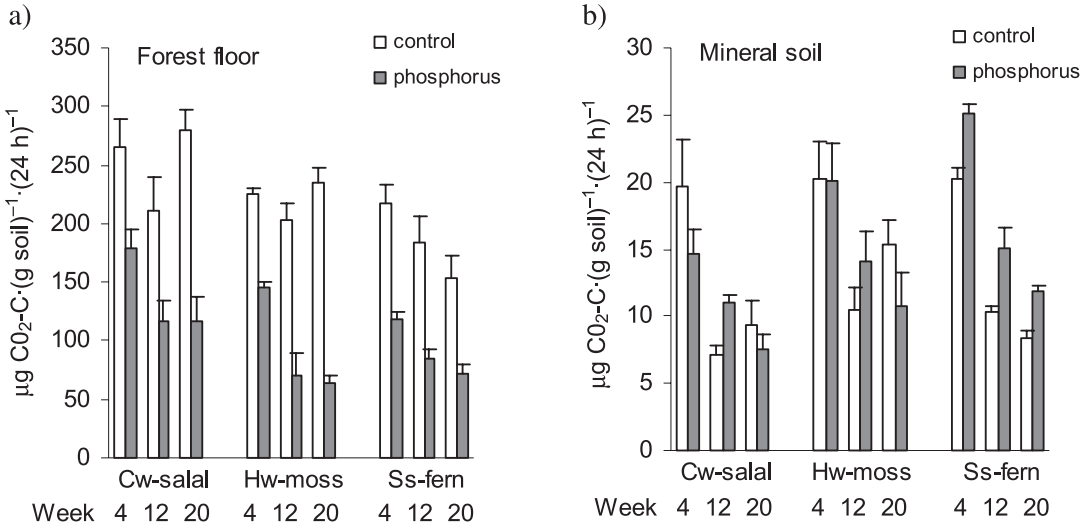


Fig. 6. Microbial biomass of fresh soils and incubated soils at week 20 across forest types with and without a P amendment for (*a*) forest floors and (*b*) mineral soils (SE shown by error bars).

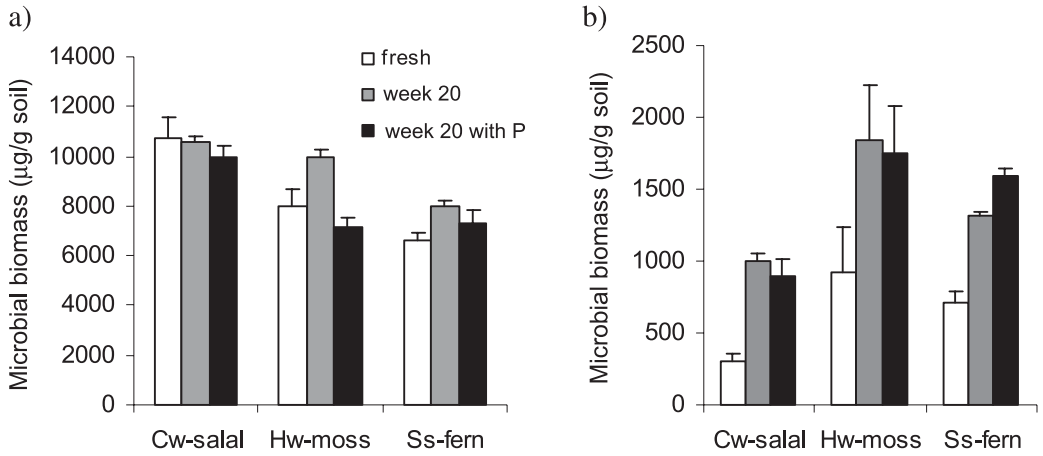
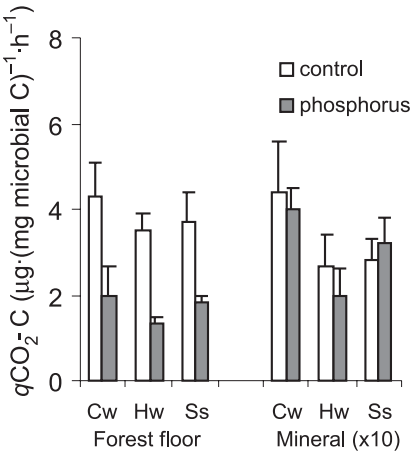


Fig. 7. Respiration quotient (qCO_2) across forest types for forest floors and mineral soils (×10) at week 20, with and without a P amendment (SE shown by error bars). Forest types: Cw, Cw–salal; Hw, Hw – lanky moss; Ss, Ss – sword fern.



The respiration quotient, an estimate of microbial specific activity, was significantly lower (approx. 55%) with a P amendment for forest floors across all forest types at week 20, with no treatment interactions (Fig. 7, Table 2). There was, however, no change in respiration quotients for mineral soils across forest types, nor with a P amendment (Fig. 7, Table 2). Minerals soils, in addition, had a qCO_2 approximately 10 times as high as that of forest floors.

Discussion

The changes in extractable N, NO_3 concentrations, soil respiration, and microbial biomass demonstrated a high sensitivity of these coastal forest soils to an input of NaH_2PO_4. Overall, the effects of the amendment on N availability matched our hypothesis: the low-productivity Cw–salal sites had increases in inorganic N for both forest floors and mineral soils; the moderately productive Hw – lanky moss sites had a more intermediate response, limited to forest floors; and the highly productive Ss – sword fern sites had no increases in inorganic N concentrations by the end of the incubation period. Part of the treatment responses may have been caused by Na with the amendment, however, and a salt effect (generally a reduction in soil pH; Fisher and Binkley 2000) might explain, for example, the initial flush of inorganic N on Ss – sword fern forest floors or reduced nitrification rates (Agarwal et al. 1971; Broadbent and Nakashima 1971; Heilman 1975; Nommik 1978). The initial pH of the soils was consistent between forest types, so the strong treatment × forest type interactions for many of the soil properties, along with significant differences over time, would suggest a larger effect from P inputs.

We found organic P was the soil property to best correlate with extractable inorganic N, which supported the hypothesis of a link between P and N availability across these ecosystems. Carlyle and Nambiar (2001) found $N:P_o$ ratios to be a good predictor of N availability in mineral soils, but we found relatively narrow ratios for mineral soils ($N:P_o < 10$) and no differences among forest types. Extractable inorganic P concentrations in the mineral soils of the more productive Hw – lanky moss and Ss – sword fern forests were relatively low (<10 mg/kg), but this is consistent with podzolic soils under high precipitation, where organic P forms predominate (McGill and Cole 1981; Preston and Trofymow 2000; Cade-Menum et al. 2000). The production of inorganic P in mineral soils over the incubation period was the inverse of what we might expect, however, which illustrates some of the gaps in our understanding of P cycles. We presume organic P concentrations of forest floors reflected differences in P uptake from mineral soils, although canopy species composition, such as the amount of western redcedar versus Sitka spruce, likely contributed to forest floor properties as well (Keenan et al. 1995).

The simplest explanation for positive P effects on N mineralization would be from increases in organic matter decomposition through greater microbial activity or growth in microbial biomass. These were the types of microbial responses to P described for some tropical soils and coastal wetlands (Munevar and Wollum 1977; White and Reddy 2000; Cleveland et al. 2002; Sundareshwar et al. 2003). On our Cw–salal incubated forest floors, however, the increase in inorganic N was accompanied by a reduction in soil respiration and no change in microbial biomass. More emphasis was given by Schimel and Bennett (2004) to depolymerization of soil organic matter through exoenzymes as the "bottleneck" in N cycling. Perhaps the P amendment affected the produc-

tion or activity of protease (or related enzymes), which then accelerated the breakdown of organic matter and reduced respiration quotients through a more efficient utilization of soil carbon (e.g., Thirukkumaran and Parkinson 2002; Schimel and Weintraub 2003).

We were unable to find evidence in the literature for a stimulatory influence of P on protease enzyme activity, although it is possible for the general synthesis of proteins by microbes to be restricted by low P availability (VanBogelen et al. 1996). Alternatively, the readily available PO_4 in the amended soils might reduce the need for phosphatase production (Spiers and McGill 1978) and allow microbes to optimize resource allocation to N- or C-acquiring exoenzymes (Sinsabaugh and Moorhead 1994, 1997). Haynes and Swift (1988) and Wright and Reddy (2001) found that the abundance of phosphatase decreased with P loading in soils, but no differences in other enzyme types, so as yet there is no clear evidence of an enzyme mechanism to link P availability with N cycles. Perhaps no single mechanism would explain P effects on mineral soil and forest floors, however, since large differences in microbial responses, such as respiration quotient, suggest further investigation is needed on, for example, fungi/bacteria ratios (Sakamoto and Oba 1994; Chang and Trofymow 1996; Forge and Simard 2001).

P amendments did not completely alleviate the differences in N mineralization rates between forest types, perhaps because of further limitations in organic matter quality (as indicated by C:N ratios), moisture regimes, or other nutrient deficiencies such as Mg and K. An increase in N availability through a P amendment might, over time, encourage a positive feedback between nutrient uptake and litter quality and further reduce the limitations in N cycling on these poorer forest floors (Berg et al. 2001; Prescott 2002). It was apparent that the rates of N mineralization during the incubation were changing and possibly converging over time, however, so P effects on soils cannot be extrapolated as yet to long-term trends in field settings. In addition, the increase in microbial biomass across mineral soils during the incubation likely represented an artefact of the experiment (i.e., high temperatures), so some soil responses to added P might differ under field conditions. Nevertheless, these preliminary results demonstrate that an application of P could enhance N supplies and promote forest productivity (i.e., Bradley et al. 2000; Turner et al. 2002). Further field trials on Cw–salal sites with P-only fertilizer will continue to explore the long-term effects of P amendments on N availability, organic matter dynamics, and tree nutrition.

Acknowledgements

We would like to thank Marcel Lavigne and Teresa White for their help in the laboratory incubation and sample processing. Clive Dawson and Dave Dunn, from the Ministry of Forests Analytical Lab, undertook the chemical analysis, and Monica Molina, from the University of Alberta, undertook the microbial biomass determination. Peter Ott, from the Ministry of Forests Research Branch, was consulted on the statistical analysis. Sara Leckie and Gordon Weetman provided useful feedback on an earlier draft of the manuscript. In 2003–2004, funds for the HYP^3 (Pattern, Process and Productivity in Hypermaritime Forests) project were provided by Forest Investment Account of British Columbia.

References

Agarwal, A.S., Singh, B.R., and Kanehiro, Y. 1971. Ionic effect of salts on mineral nitrogen release in an allophanic soil. Soil Sci. Soc. Am. Proc. **35**: 454–457.

Amador, J.A., and Jones, R.D. 1993. Nutrient limitations on microbial respiration in peat soils with different total phosphorus content. Soil Biol. Biochem. **25**: 793–801.

Anderson, J.P.E., and Domsch, K.H. 1990. Application of ecophysiological quotients (qCO_2 and qD) on microbial biomasses from soils of different cropping histories. Soil Biol. Biochem. **22**: 251–255.

Banner, A., MacKenzie, W., Haeussler, S., Thomson, S., Pojar, J., and Trowbridge, R. 1993. A field guide to site identification and interpretation for the Prince Rupert Forest Region. Ministry of Forests Field Handbook 26. Crown Publications, Victoria, B.C.

Berg, B., McClaugherty, C., Virzo de Santo, A., and Johnson, D. 2001. Humus buildup in boreal forests: effects of litter fall and its N concentration. Can. J. For. Res. **31**: 988–998.

Bormann, B.T., Spaltenstein, H., McClellan, M.H., Ugolini, F.C., Cromack, K., Jr., and Nay, S.M. 1995. Rapid soil development after windrow disturbance in pristine forests. J. Ecol. **83**: 747–757.

Bradley, R.L., Titus, B.D., Preston, C.M., and Bennett, J. 2000. Improvement of nutritional site quality 13 years after single application of fertiliser N and P on regenerating cedar-hemlock cutovers on northern Vancouver Island, B.C. Plant Soil, **223**: 195–206.

Broadbent, F.E., and Nakashima, T. 1971. Effect of added salts on nitrogen mineralization in three California soils. Soil Sci. Soc. Am. Proc. **35**: 457–460.

Cade-Menun, B.J., Berch, S.M., Preston, C.M., and Lavkulich, L.M. 2000. Phosphorus forms and related soil chemistry of Podzolic soils on northern Vancouver Island. I. A comparison of two forest types. Can. J. For. Res. **30**: 1714–1725.

Carlyle, J.C., and Nambiar, E.K.S. 2001. Relationships between net nitrogen mineralization, properties of the forest floor and mineral soil, and wood production in *Pinus radiata* plantations. Can. J. For. Res. **31**: 889–898.

Carter, M.R. (*Editor*). 1993. Soil sampling and methods of analysis. Lewis Publishers, Boca Raton, Fla.

Chadwick, O.A., Derry, L.A., Vitousek, P.M., Huebert, B.J., and Hedin, L.O. 1999. Changing sources of nutrients during four million years of ecosystem development. Nature (Lond.), **397**: 491–497.

Chang, S.X., and Trofymow, J.A. 1996. Microbial respiration and biomass (substrate-induced respiration) in soils of old-growth and regenerating forests on northern Vancouver Island, British Columbia. Biol. Fertil. Soils, **23**: 145–152.

Cleveland, C.C., Townsend, A.R., and Schmidt, S.K. 2002. Phosphorus limitation of microbial processes in moist tropical forests. Ecosystems, **5**: 680–691.

Cole, C.V. and Heil, R.D. 1981. Phosphorus effects on terrestrial nitrogen cycling. *In* Nitrogen cycling in terrestrial ecosystems: processes, ecosystem strategies, and management implications. *Edited by* F.E. Clark and T.H. Rosswell. Ecol. Bull. 33, Swedish Natural Science Research Council, Stockholm. pp. 363–374.

DeBusk, W.F., and Reddy, K.R. 1998. Turnover of detrital organic carbon in a nutrient-impacted Everglades marsh. Soil Sci. Soc. Am. J. **62**: 1460–1468.

Forge, T.A. and Simard, S.W. 2001. Short-term effects of nitrogen and phosphorus fertilizers on nitrogen mineralization and trophic structure of the soil ecosystem in forest clearcuts in the southern interior of British Columbia. Can. J. Soil Sci. **81**: 11–20.

Fisher, R.F., and Binkley, D. Ecology and management of forest soils. 3rd ed. John Wiley & Sons, New York.

Green, R.N., Trowbridge, R.L., and Klinka, K. 1993. Towards a taxonomic classification of humus forms. For. Sci. Monogr. **29**: 1–48.

Gressel, N., and McColl, J.G. 1997. Phosphorus mineralization and organic matter decomposition: a critical review. *In* Driven by nature: plant litter quality and decomposition. *Edited by* G. Cadisch and K.E. Giller. CAB International, Wallingford, UK. pp. 297–309.

Hart, S.C., Stark, J.M., Davidson, E.A., and Firestone, M.K. 1994. Nitrogen mineralization, immobilization, and nitrification. *In* Methods of soil analysis. Part 2. Microbiological and biochemical properties. *Edited by* R.V. Weaver, S. Angle, P. Bottomley, D. Bezdicek, S. Smith, A. Tabatabai, and A. Wollum. Soil Science Society of America, Madison, Wis. SSSA Book Series, 5. pp. 985–1018.

Haynes, R.J., and Swift, R.S. 1988. Effects of lime and phosphate additions on changes in enzyme activities, microbial biomass and levels of extractable nitrogen, sulphur and phosphorus in an acid soil. Biol. Fertil. Soils, **6**: 153–158.

Heilman, P. 1975. Effect of added salts on nitrogen release and nitrate levels in forest soils of the Washington coastal area. Soil Sci. Am. Proc. **39**: 778–782.

Heilman, P.E., and Gass, C.R. 1974. Parent materials and chemical properties of mineral soils in southeast Alaska. Soil Sci. **117**: 21–27.

Kalra, Y.P., and Maynard, D.G. 1991. Methods manual for forest soil and plant analysis. Can. For. Serv. North. For. Res. Cent. Inf. Rep. NOR-X-319.

Keenan, R.J., Prescott, C.E., and Kimmins, J.P. 1995. Litter production and nutrient resorption in western redcedar and western hemlock forests on northern Vancouver Island, British Columbia. Can. J. For. Res. **25**: 1850–1857.

Krajina, V. 1969. Ecology of forest trees in B.C. Ecology of Western North America, **1**: 1–147.

Kranabetter, J.M. and Banner, A. 2000. Selected biological and chemical properties of forest floors across bedrock types on the north coast of British Columbia. Can. J. For. Res. **30**: 971–981.

Kranabetter, J.M., Banner, A., and Shaw, J. 2003. Growth and nutrition of three conifer species across site gradients of north coastal British Columbia. Can. J. For. Res. **33**: 313–324.

McGill, W.B., and Cole, C.V. 1981. Comparative aspects of cycling of organic C, N, S and P through soil organic matter. Geoderma, **26**: 267–286.

Meidenger, D., and Pojar, J. 1991. Ecosystems of British Columbia. Crown Publications, Victoria B.C.

Messier, C. 1993. Factors limiting early growth of western redcedar, western hemlock and Sitka spruce seedlings on ericaceous-dominated clearcut sites in coastal British Columbia. For. Ecol. Manage. **60**: 181–206.

Munevar, F., and Wollum, A.G. 1977. Effects of the addition of phosphorus and inorganic nitrogen on carbon and nitrogen mineralization in Andepts from Colombia. Soil Sci. Soc. Am. J. **41**: 540–545.

Nommik, H. 1978. Mineralization of carbon and nitrogen in forest humus as influenced by additions of phosphate and lime. Acta Agric. Scand. **28**: 221–230.

O'Halloran, I.P. 1993. Total and organic phosphorus. *In* Soil sampling and methods of analysis. *Edited by* M. Carter. Lewis Publishers, Boca Raton, Fla. pp. 213–229.

Pastor, J., Aber, D., McClaugherty, A., and Melillo, J.M. 1984. Aboveground production and N and P cycling along a nitrogen mineralization gradient on Blackhawk Island, Wisconsin. Ecology, **65**: 256–268.

Pojar, J., Klinka, K., and Meidinger, D.V. 1987. Biogeoclimatic ecosystem classification in British Columbia. For. Ecol. Manage. **22**: 119–154.

Prescott, C.E. 2002. The influence of the forest canopy on nutrient cycling. Tree Physiol. **22**: 1193–1200.

Prescott, C.E., McDonald, M.A., and Weetman, G.F. 1993. Availability of N and P in the forest floors of adjacent stands of western redcedar – western hemlock and western hemlock – amabilis fir on northern Vancouver Island. Can. J. For. Res. **23**: 605–610.

Prescott, C.E., Weetman, G.F., and Barker, J.E. 1996. Causes and amelioration of nutrient deficiencies in cutovers of cedar-hemlock forests in coastal British Columbia. For. Chron. **72**: 293–302.

Preston, C.M., and Trofymow, J.A. 2000. Characterization of soil P in coastal forest chronosequences of southern Vancouver Island: effects of climate and harvesting disturbances. Can. J. Soil Sci. **80**: 633–647.

Sakamoto, K. and Obo, Y. 1994. Effect of fungal to bacterial biomass ratio on the relationship between CO_2 evolution and total soil microbial biomass. Biol. Fertil. Soils, **17**: 39–44.

SAS Institute Inc. 1988. SAS/STAT user's guide, release 6.03 [computer manual]. SAS Institute Inc., Cary, N.C.

Schimel, J.P., and Weintraub, M.N. 2003. The implications of exoenzyme activity on microbial carbon and nitrogen limitation in soil: a theoretical model. Soil Biol. Biochem. **35**: 549–563.

Schimel, J.P., and Bennett, J. 2004. Nitrogen mineralization: challenges of a changing paradigm. Ecology, **85**: 591–602.

Sinsabaugh, R.L., and Moorhead, D.L. 1994. Resource allocation to extracellular enzyme production: a model for nitrogen and phosphorus control of litter decomposition. Soil Biol. Biochem. **26**: 1305–1311.

Sinsabaugh, R.L., and Moorhead, D.L. 1997. Synthesis of litter quality and enzymic approaches to decomposition modelling. *In* Driven by nature: plant litter quality and decomposition. *Edited by* G. Cadisch and K.E. Giller. CAB International, Wallingford, UK. pp. 363–375.

Soil Classification Working Group. 1998. The Canadian system of soil classification. 3rd ed. Agriculture and Agri-Food Canada Publication 1646, Ottawa.

Spiers, G.A., and McGill, W.B. 1978. Effects of phosphorus addition and energy supply on acid phosphatase production and activity in soils. Soil Biol. Biochem. **11**: 3–8.

Sundareshwar, P.V., Morris, J.T., Koepfler, E.K., and Fornwalt, B. 2003. Phosphorus limitation of coastal ecosystem processes. Science (Washington, D.C.), **299**: 563–565.

Tate, K.R., and Salcedo, I. 1988. Phosphorus control of soil organic matter accumulation and cycling. Biogeochemistry, **5**: 99–107.

Thirukkumaran, C.M., and Parkinson, D. 2002. Microbial activity, nutrient dynamics and litter decomposition in a Canadian Rocky Mountain pine forest as affected by N and P fertilizers. For. Ecol. Manage. **159**: 187–201.

Turner, J., Lambert, M.J., and Humphreys, F.R. 2002. Continuing growth response to phosphate fertilizers by a *Pinus radiata* plantation over fifty years. For. Sci. **48**: 556–568.

VanBogolen, R.A., Olson, E.R., Wanner, B.L., and Neidhardt, F.C. 1996. Global analysis of proteins synthesized during phosphorus restriction in *Escherichia coli*. J. Bacteriol. **178**: 4344–4366.

Vitousek, P.M., and Howarth, R.W. 1991. Nitrogen limitation on land and in the sea: How can it occur? Biogeochemistry, **13**: 87–115.

Voroney, R.P., Winter, J.P., and Beyaert, R.P. 1993. Soil microbial biomass C and N. *In* Soil sampling and methods of analysis. *Edited by* M.R. Carter. Lewis Publishers, Boca Raton, Fla.

Walker, T.W., and Syers, J.K. 1976. The fate of phosphorus during pedogenesis. Geoderma, **15**: 1–19.

Wardle, D.A., Walker, L.R., and Bardgett, R.D. 2004. Ecosystem properties and forest decline in contrasting long-term chronosequences. Science (Washington, D.C.), **305**: 509–513.

Weetman, G.F., Fournier, R., Barker, J., Schnorbus-Panozzo, E., and Germain, A. 1989*a*. Foliar analysis and response of fertilized chlorotic Sitka spruce plantations on salal-dominated cedar–hemlock cutovers on Vancouver Island. Can. J. For. Res. **19**: 1501–1511.

Weetman, G.F., Fournier, R., Barker, J., and Schnorbus-Panozzo, E. 1989*b*. Foliar analysis and response of fertilized chlorotic western hemlock and western redcedar reproduction on salal-dominated cutovers on Vancouver Island. Can. J. For. Res. **19**: 1512–1520.

White, J.R., and Reddy, K.R. 2000. Influence of phosphorus loading on organic nitrogen mineralization of Everglades soils. Soil Sci. Soc. Am. J. **64**: 1525–1534.

Wright, A.L., and Reddy, K.R. 2001. Phosphorus loading effects on extracellular enzyme activity in Everglades wetland soils. Soil Sci. Soc. Am. J. **65**: 588–595.

Zibilske, L.M. 1994. Carbon mineralization. *In* Methods of soil analysis. Part 2. Microbiological and biochemical properties. *Edited by* R.V. Weaver, S. Angle, P. Bottomley, D. Bezdicek, S. Smith, A. Tabatabai, and A. Wollum. Soil Science Society of America, Madison, Wis. SSSA Book Series, 5. pp. 835–859.