Plant and Soil **236:** 75–82, 2001.

Influence of broadleaf trees on soil chemical properties: A retrospective study in the Sub-Boreal Spruce Zone, British Columbia, Canada

Paul Sanborn
Ministry of Forests, 1011 – 4th Avenue, Prince George, British Columbia V2L 3H9, Canada

Received 29 November 1999. Accepted in revised form 10 July 2001

Key words: broadleaf, calcium, forest floor, lodgepole pine, nitrogen, paper birch

Abstract

A retrospective study examined the influence of broadleaf trees, principally paper birch (*Betula papyrifera* Marsh.), on soil properties under mixedwoods with lodgepole pine (*Pinus contorta* var. *latifolia* Dougl. ex Loud.) in the Sub-Boreal Spruce zone of central British Columbia, Canada. After 23 years, approximately 50% of the forest floor mass typical of mature forests in this zone had already accumulated on an initially denuded surface, but this new forest floor was poor in woody components. Correlation analysis found no relationship between the degree of broadleaf occupancy and total forest floor accumulation, but a significant qualitative influence on chemical properties of the non-woody forest floor components: higher pH, total N, available P, extractable Ca, Mg, and K, and lower C:N ratios. No such relationships existed for the surface (0–20 cm depth) mineral soils.

Introduction

Forest ecologists and managers increasingly recognize the ecological role performed by broadleaf trees growing in mixtures with conifers (Comeau and Thomas, 1996). Studies in temperate and boreal forests have documented differences in forest floor and/or mineral soil properties between broadleaf- and conifer-dominated stands (Brais et al., 1995; Paré et al., 1993; Perry et al., 1987; Vesterdal and Raulund-Rasmussen, 1998). Using either chronosequences or comparisons of adjacent monocultures, such case studies have often found soil nutrient enrichment under the broadleaf species. However, chronosequence studies can be confounded by site variability, and monocultures may not produce conditions typical of the multispecies stands which are much more common in both managed and natural forests. In a recent review, Binkley and Giardina (1998) observed that "the biogeochemistry of mixed-species forests ... remains largely uncharted territory'.

In addition, the presumed role of broadleaf trees in rebuilding forest floors after natural disturbances has led to the recommendation that these species be used in rehabilitating soils degraded by forest practices (Ministry of Forests, 1997; Peterson et al., 1997). Such suggestions apparently reflect a view that these species function as an ameliorating 'nutrient pump' and also rebuild soil organic matter capital by producing leaf litter. To determine the value of such recommendations, it would be useful to document the rate of forest floor accumulation, and the chemical characteristics of forest floors and mineral soils, associated with varying degrees of broadleaf influence. The data most relevant to rehabilitation practices would be those derived from severely disturbed sites where forest floors had been largely or entirely removed at a known time.

This study revisited a 23-year-old silvicultural research installation in the central interior of British Columbia, where a range of broadleaf-conifer mixtures has occupied a severely disturbed site. The objective was to examine whether the recovery in forest floor mass and the chemical properties of the forest floors and mineral soils had any relationship to the degree of broadleaf occupancy.

* FAX No: +250-565-66-71.
E-mail: Paul.Sanborn@gems9.gov.bc.ca

Materials and methods

Description and history of study area

The study site is located in the Willow variant of the Wet Cool subzone of the Sub-Boreal Spruce biogeoclimatic subzone (Delong, 1996) of central British Columbia (54° 8′ 30″ N; 121° 54′ 50″ W) at 680 m elevation. The predominantly Humo-Ferric Podzolic soils (USDA classification: Cryorthod) have formed on the glaciofluvial sands of a pitted outwash plain (Hortie et al., 1970), with local finer-textured veneers, possibly of glaciolacustrine origin. Long-term climatic averages for the nearest weather station (Aleza Lake Research Forest, 15 km to the southwest) are 930 mm annual precipitation and a mean annual temperature of 3 °C (Jull, 1992).

In 1971, a mechanical site preparation study (Project #72-F1) was initiated at this site by R. McMinn of the Canadian Forest Service (L. Bedford, pers. comm.). This project included a scalping treatment which used a crawler tractor to create 4-m-wide strips (20–40 m apart) from which the forest floor and some surface mineral soil were displaced. In 1995, these strips were still clearly bounded by low berms or ridges of displaced soil up to 30 cm high.

Portions of these 4-m-wide scalped strips, approximately 5 m long and 10–20 m apart, were designated as monitoring plots in the original study and were planted with 2-year-old bare-root lodgepole pine (*Pinus contorta* var. *latifolia* Dougl. ex Loud.) seedlings in June 1972 at a close initial spacing of approximately 1.0–1.5 m. Active maintenance of this installation ceased by the late 1970s, and no subsequent thinning of the pines was carried out. The exposure of mineral soil on the scalped strips allowed the establishment of broadleaf trees and shrubs, consisting primarily of paper birch (*Betula papyrifera* Marsh.) and black cottonwood (*Populus balsamifera* ssp. *trichocarpa* (T. & G.) Brayshaw), with lesser amounts of aspen (*Populus tremuloides* Michx.) and willow (*Salix* sp.). By 1995, the scalped strips were occupied by widely varying mixtures of pine and broadleaf trees. The areas between the scalped strips were generally poorly stocked with trees and were occupied by a vigorous understory of shrubs and herbs, dominated by thimbleberry (*Rubus parviflorus* Nutt. var. *parviflorus*). All plots were located on mid- or upper-slope positions, with well-drained conditions suggested by strongly oxidized colours and an absence of gleying in the mineral soils.

Sampling and analysis methods

Of the 56 original lodgepole pine monitoring plots on the scalped treatment, 31 were selected for study in 1995 based on sufficient stocking with pines and broadleaf trees to have suppressed the understory vegetation and provided a closed canopy over the scalped strip. Using the lateral berms bounding the scalped strips as a guide, a square (3 × 3 m) soil sampling plot was established within each of these selected original plots.

Forest floors were sampled in October 1995 using a 20 × 20 cm frame at 5 random locations in each sampling plot. Mineral soils (0–20 cm depth) were sampled at the same locations as the forest floors and usually consisted of B horizon materials. Eluvial mineral soil horizons were present at adjacent undisturbed locations at this site, but appeared to have been largely removed by the scarification treatment. Forest floors were sampled in their entirety because of the difficulty of having four operators make consistent separations between organic horizons (Federer, 1982). For the same reason, we did not attempt to classify individual samples according to the current British Columbia humus form classification (Green et al., 1993). Forest floor samples were air-dried, and any visible mineral contaminants were discarded. To reduce the variability of the forest floor chemical properties, we treated woody components separately, as recommended by Quesnel and Lavkulich (1981). All woody fragments with diameters greater than 5 mm were removed, weighed, and analyzed separately from the non-woody components of the forest floor.

Forest floor materials and mineral soils were analyzed for the following chemical properties: Total C and N (LECO CHN-600 elemental analyzer), total S (LECO SC-132 elemental analyzer), pH (H_2O and 0.01 M $CaCl_2$ in 1:2 and 1:4 soil: liquid ratios, respectively), mineralizable N (2-week anaerobic incubation at 30 °C), nitrate- and ammonium–N (Carter, 1993), available P (Bray P1 method; Kalra and Maynard, 1991), and extractable cations (Morgan's extractant; Klinka et al., 1980). Forest floor mass and chemical data are expressed on an oven-dry basis (105 °C, 24 h).

The total and relative basal areas of lodgepole pine and broadleaf trees were used to express stand species composition. To calculate total basal areas for trees potentially contributing each soil sampling plot, we measured stem diameter outside bark at 1.3 m height of all trees inside the sampling plots, as well as for those with crowns overhanging the plots. These measures of stand species composition were used in lieu of direct measurements of the species composition of fluxes such as litterfall. A lack of road access precluded any sampling programs that would have required multiple return visits to the site.

Mean values for forest floor mass and soil chemical properties were calculated for each soil sampling plot, and used in correlation analysis with the measures of stand composition using the SYSTAT 7.0 statistical software (SPSS Inc., 1997). Bonferroni adjusted probabilities, which provide protection for multiple tests, were used to identify significant Pearson correlation coefficients.

Results

Although, on average, lodgepole pine comprised more than 2/3 of the basal area of trees with crowns overhanging the sampling plots (Table 1), the stand compositions ranged from 1 to 86% broadleaf basal area. Paper birch was the most abundant broadleaf species, accounting for almost 2/3 of the average broadleaf basal area, and occurring within or adjacent to all but 2 of the 31 sampling plots. The sampling plots were heavily stocked, with an average total density exceeding 8000 stems per ha (Table 1).

Total forest floor accumulation since the scarification treatment averaged 30 290 kg ha^{-1} (Table 2). Based on the data in Table 2, the forest floors contained only 66 g kg^{-1} of woody components. Although the broadleaf trees would have begun producing leaf litter in their year of establishment, and in 1995 were usually taller and had wider crowns than the lodgepole pines, there were no significant correlations between the measures of stand composition and forest floor mass (Figure 1; Table 3).

The forest floors that have accumulated on this scalping treatment had wider C:N ratios than the underlying mineral soils. Although mineralizable N concentrations were higher in the non-woody forest floor components than in the mineral soil (Table 2), when expressed as a proportion of total N, this fraction was relatively more abundant in the mineral soil. Mineral nitrogen in the non-woody forest floor components consisted almost entirely of ammonium, with more than 2/3 of the samples having less than 1 mg $kg^{-1}NO_3{}^{-}$–N. Extractable cation concentrations were in the order of $Ca^{2+} >> K^{+} > Mg^{2+}$ for both non-woody forest floor and mineral soil, although mean values for K^{+} and Mg^{2+}were very close in the mineral soil. Compared to total N and available P, total S was more enriched in the non-woody forest floor components relative to the mineral soil. Although all pH values were in the acidic range, mineral soils were slightly more acidic than the forest floors.

Several chemical properties of the non-woody forest floor components were strongly correlated with stand composition (Figure 1; Table 4). Higher pH, higher concentrations of total N, available P and extractable Ca^{2+}, Mg^{2+}, and K^{+}, and lower C:N ratios were associated with an increasing basal area of broadleaf species. Although the relationship was not as strong, increasing broadleaf basal area was also positively correlated with mineralizable N concentration. Unlike for nutrient concentrations, forest floor nutrient mass data (kg ha^{-1}) were not significantly correlated with any of the measures of stand composition (data not shown). Similarly, mineral soil chemical properties (Tables 2 and 4) showed no significant correlations with stand basal area composition.

Discussion

Although the measured stand densities are well above current stocking standards for managed stands in this biogeoclimatic zone (Ministry of Forests, 1995), naturally-regenerated lodgepole pine stands often equal or exceed these densities (Johnstone, 1985). Thus, observations of soil properties at this site are relevant to conditions in which stand development and forest floor recovery have occurred after severe natural or human disturbance in this region.

Nutrient concentrations and pH values for this site are within the range observed for other forest soils in the Sub-Boreal Spruce zone of British Columbia (Arocena and Sanborn, 1999; Trowbridge et al., 1996). The low mineral soil S concentrations are consistent with a regional pattern found throughout the central and southern interior of the province (Arocena and Sanborn, 1999; Kishchuk, 1998).

A forest floor mass of approximately 55 000 kg/ha was estimated for a mature conifer stand on similar glaciofluvial sediments approximately 10 km to the northeast of the study site, based on data provided by Kimmins (1977). At 3 other sites in the Sub-Boreal Spruce zone, forest floor mass values under mature coniferous stands ranged from 41 000 to 78 000 kg/ha (Trowbridge et al., 1996). These comparative data suggest that approximately 50% of the forest floor mass

Table 1. Summary of stand composition (n = 31 plots)

Species	% of total basal area[a]		Stems / ha[b]		DBH[b,c] (cm)	
	Mean	*Std. Dev.*	Mean	*Std. Dev.*	Mean	*Std. Dev.*
Pinus contorta	69.00	*20.95*	4409	*1531*	14.1	*4.0*
Picea glauca × *engelmannii*	0.46	*0.96*	215	*446*	4.1	*1.5*
Abies lasiocarpa	0.12	*0.67*	72	*399*	5.7	*1.1*
Total coniferous	69.58	20.92	4696	*1641*		
Betula papyrifera	19.03	*21.12*	2151	*2450*	8.2	*4.1*
Populus balsamifera ssp. *trichocarpa*	7.18	*11.41*	717	*1268*	9.3	*5.9*
Salix sp.	3.99	*7.89*	645	*1339*	7.3	*2.5*
Populus tremuloides	0.21	*0.59*	143	*379*	5.1	*1.1*
Total broadleaf	30.42	20.92	3656	*3171*		

[a] For all trees with canopies overhanging sampling plots.
[b] Within sampling plots.
[c] Stem diameter outside bark at breast height (1.3 m).

typical of mature stands in this biogeoclimatic zone has accumulated under the mixedwoods at this site in slightly more than 20 years.

The proportion of woody materials in the young forest floors at this site is lower than in early successional stands after a natural disturbance or most forms of harvesting. Forest floors in the areas between the scalped strips contained a noticeably higher proportion of reddish decomposed woody material (L Bedford, pers. comm.). This contrast is consistent with the limited data available for other sites in the Sub-Boreal Spruce zone. For example, forest floors under two young lodgepole pine stands that were established after wildfire in 1961, and logging without subsequent prescribed fire in 1987, contained 144 and 154 g kg^{-1} woody material, respectively [1]. Elsewhere in northwestern North America, woody residues in forest soils have important roles in moisture retention and in providing microsites for nonsymbiotic N-fixation and occupancy by ectomycorrhizal roots (Harvey et al., 1987; Jurgensen et al., 1997). Revegetation and initial forest floor accumulation may not fully restore ecological functioning until woody residues are produced by stand self-thinning and branch litterfall.

Forest floor accumulation rates represent the balance between litterfall and decomposition, but without direct measurements of these processes, there are several possible explanations of the lack of significant correlations between forest floor mass and stand basal area species composition. For example, if litter production increased with the proportion of paper birch in a mixture with lodgepole pine, this might be offset by a higher litter decomposition rate for the broadleaf species. In an earlier study, MacLean and Wein (1978) found that mass loss of paper birch litter was much faster than for jack pine (*Pinus banksiana* Lamb.) – a species closely related to lodgepole pine. In the much simpler monocultures studied by Vesterdal and Raulund-Rasmussen (1998), forest floor C accumulation was significantly higher under lodgepole pine than for 6 other conifer and broadleaf species. The difficulty in rationalizing these disparate findings provides additional support for the comment by Binkley and Giardina (1998) that "mixtures of species produce litter that commingles, fosters novel soil communities, and generally complicates attempts to determine simple effects of the species".

Comparative data on forest floor accumulation rates under mixedwoods with a significant paper birch component are absent in the literature. For paper birch monocultures in southern B.C., the chronosequence study of Wang et al. (1998) showed no clear trend in forest floor mass with age in stands ranging from 2 to 75 years old. Differences in the type and degree of initial disturbance at these sites confound any attempt to infer rates of forest floor accumulation. Although France et al. (1989) compared 27-year-old monocultures established on agricultural soils in southern Ontario, and found forest floor mass under paper birch

* B.C. Ministry of Forests file data for Experimental Projects No.'s 660 and 1185.

Table 2. Summary of forest floor mass and chemical properties (n= 31 plots)

Property	Forest Floor Components: Non-Woody Mean	Non-Woody *Std. Dev.*	Woody Mean	Woody *Std. Dev.*	Mineral Soil Mean	Mineral Soil *Std. Dev.*
Mass (g m^{-2})	2828.1	*713.0*	200.9	*127.3*		
Total Carbon (g kg^{-1})	448.1	*53.0*	542.8	*16.8*	26.1	*14.9*
Total Nitrogen (g kg^{-1})	16.0	*2.4*	7.1	*1.8*	1.7	*0.96*
C:N ratio	28.4	*3.0*	78.3	*11.0*	15.1	*0.88*
Mineralizable N (mg kg^{-1})	599.8	*211.9*	n.d.[a]		95.2	*40.2*
Ammonium-N (mg kg^{-1})	135.2	*40.1*	n.d.		n.d.	
Nitrate-N (mg kg^{-1})	5.1	*16.3*	n.d.		n.d.	
Extractable Ca (mg kg^{-1})	6127.0	*1136.5*	n.d.		420.4	*233.6*
Extractable K (mg kg^{-1})	1673.7	*364.3*	n.d.		59.1	*23.7*
Extractable Mg (mg kg^{-1})	1184.0	*245.0*	n.d.		55.3	*30.1*
Available P (mg kg^{-1})	203.61	*35.16*	n.d.		47.8	*18.9*
Total Sulphur (g kg^{-1})	1.25	*0.26*	0.56	*0.17*	0.10	*0.06*
pH_{Water}	5.01	*0.21*	n.d.		4.83	*0.17*
pH_{CaCl_2}	4.70	*0.22*	n.d.		4.25	*0.14*

[a] n.d. = not determined.

Table 3. Pearson correlation coefficients: stand basal area (BA) composition vs. forest floor mass

Forest floor components:	Conifer BA[a]	Broadleaf BA[a]	Total BA[a]	Broadleaf BA (% of total)
Non-woody	0.178	0.004	0.229	−0.132
Woody	−0.369	0.333	−0.230	0.371
Total	0.110	0.061	0.184	−0.065

[a]Basal area of trees with crowns overhanging sampling plots.

was 60% lower than under white spruce (*Picea glauca* (Moench) Voss) , and 82% lower than under white pine (*Pinus strobus* L.), they did not indicate if stocking levels were similar for all species.

The increased concentrations of forest floor N, Ca, K and Mg with an increased proportion broadleaf occupancy are consistent with the view that these species, and particularly birch (Miles and Young, 1980), have fertility-enhancing effects on soil properties. However, the literature is not unanimous (Binkley and Valentine, 1991), and Miller's (1984) modelling study concluded that the nutrient cycling behaviour of birch did not differ greatly from other tree species with similar growth patterns and rates. Furthermore, in the monocultures studied by France et al. (1989) significantly lower forest floor pH values occurred under paper birch, compared with two conifer species. Forest floor chemical properties can also be influenced by tree species-related differences in litter acid-base status. For example, Côté and Fyles (1994) found that aqueous litter extracts of both paper birch and eastern cottonwood (*Populus deltoides* Marsh.) had higher pH and excess titratable bases than did eastern white pine.

As in the present study, France *et al.* (1989) found no between-species differences in mineral soil pH in their monoculture study. In both cases, this could reflect the young age of the stands, or the expression of vegetation influences in a shallower depth interval than was sampled. Similarly, a Finnish study of Scots pine, Norway spruce, and silver birch monocultures (Priha and Smolander, 1997) attributed the absence of species-related differences in chemical properties of the 0–10 cm depth mineral soil to too thick a sampling increment.

In conclusion, this retrospective study of mixed-woods established on a silvicultural scalping treatment has indicated substantial recovery of forest floor mass after 23 years. This organic material differs from older forest floors elsewhere in the Sub-Boreal Spruce zone in having a much smaller proportion of woody

Table 4. Pearson correlation coefficients: stand basal area (BA) composition vs. forest floor and mineral soil chemical properties[a]

	Conifer BA	Broadleaf BA	Broadleaf BA (% of total)
Non-woody components:			
Total Carbon (%)	0.353	−0.151	−0.291
Total Nitrogen (%)	−0.324	**0.650**	0.503
C:N ratio	**0.609**	**−0.787**	**−0.750**
Mineralizable N (ppm)	−0.124	0.502	0.291
Ammonium–N (ppm)	0.059	0.018	−0.001
Nitrate–N (ppm)	−0.024	0.250	0.147
Extractable Ca (ppm)	−0.442	**0.724**	**0.571**
Extractable K (ppm)	−0.480	**0.619**	**0.570**
Extractable Mg (ppm)	**−0.565**	**0.735**	**0.668**
Available P (ppm)	**−0.689**	0.503	**0.603**
Total Sulphur (%)	0.053	0.361	0.117
pH_{Water}	**−0.604**	**0.745**	**0.668**
pH_{CaCl_2}	**−0.613**	**0.759**	**0.671**
Woody components:			
Total Carbon (%)	−0.252	0.197	0.257
Total Nitrogen (%)	0.224	0.025	−0.039
C:N ratio	−0.239	−0.030	0.050
Total Sulphur (%)	0.092	0.094	0.022
Mineral soil:			
Total Carbon (%)	0.240	−0.078	−0.143
Total Nitrogen (%)	0.216	−0.042	−0.125
C:N ratio	0.103	−0.210	−0.045
Mineralizable N (ppm)	0.005	0.153	0.049
Extractable Ca (ppm)	0.082	0.124	0.010
Extractable K (ppm)	0.131	0.190	0.005
Extractable Mg (ppm)	−0.019	0.250	0.130
Available P (ppm)	0.175	−0.132	−0.176
Total Sulphur (%)	0.170	0.069	−0.056
pH_{Water}	−0.274	0.176	0.206
pH_{CaCl_2}	−0.084	0.146	0.105

[a]Underlined Pearson correlation coefficients are significant at $p > 0.05$ (Bonferroni adjusted probabilities).

materials. Unlike for forest floor mass, nutrient concentrations and pH in the forest floor were positively correlated with the degree of broadleaf occupancy. Other studies of birch, the dominant broadleaf genus at this site, do not indicate that this is a consistent pattern. Perhaps, as suggested by Perry et al. (1987), it is not possible to explain nutrient dynamics of mixed species communities as simply an additive function of the component species.

Acknowledgements

Marvin Grismer (Canadian Forest Service, retired) provided indispensable assistance during the field work. Lorne Bedford (B.C. Ministry of Forests) shared background information, arranged logistical assistance, and reviewed a draft version of this paper. Rhian Evans, Brenda Roosdahl, Marianne Johnson, and Angie Dale helped during field work, sample preparation and data analysis. Vera Sit (Ministry of Forests, Research Branch) advised on statistical matters. Laboratory analyses were performed by the Glyn Road Research Station, B.C. Ministry of Forests. Jim

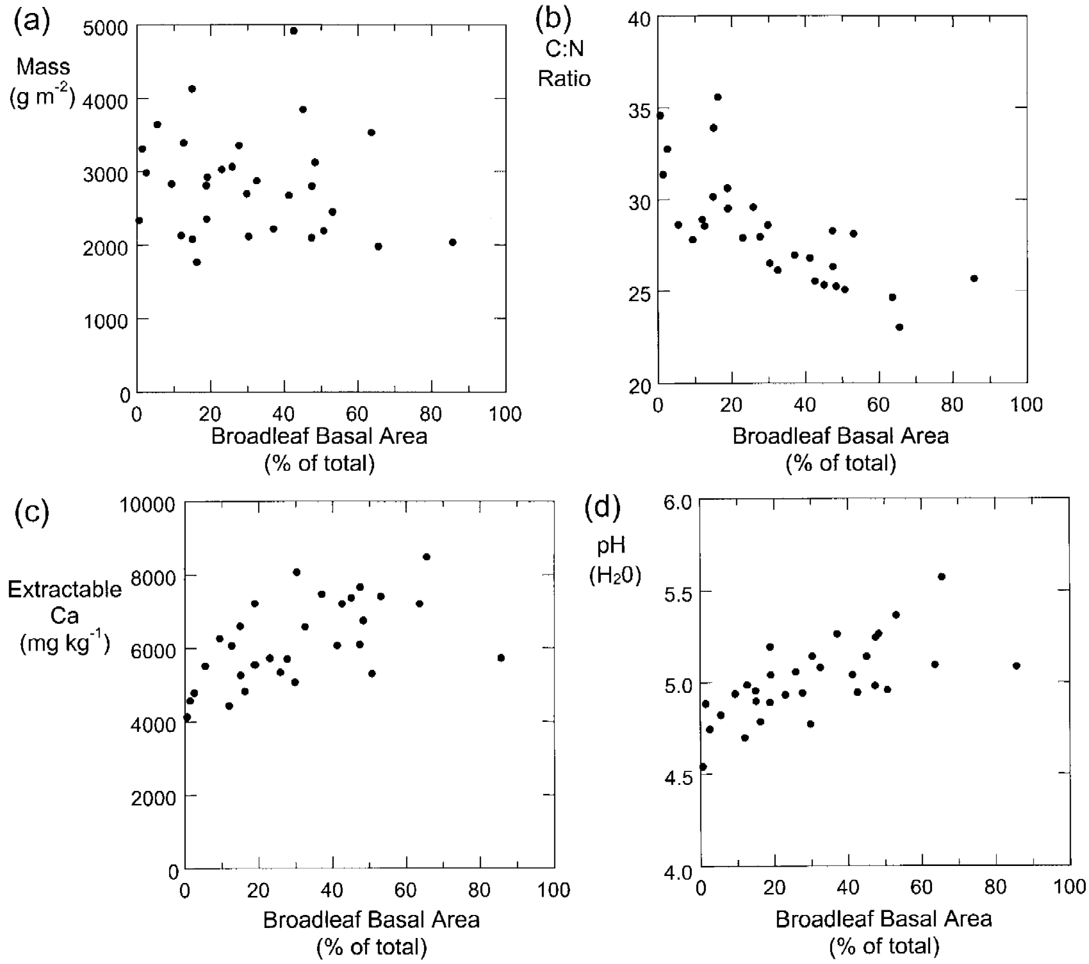

Figure 1. Scatter diagrams of relative broadleaf basal area vs. properties of non-woody forest floor components: (a) mass, (b) C:N ratio, (c) extractable Ca, and (d) pH.

Fyles (McGill Univ.) and Art Fredeen (Univ. Northern British Columbia) and Dave Coopersmith (B.C. Ministry of Forests) provided helpful reviews.

References

Arocena J and Sanborn P 1999 Mineralogy and genesis of selected soils and their implications for forest management in central and northeastern British Columbia. Can. J. Soil Sci. 79, 571–592.

Binkley D and Giardina C 1998 Why do tree species affect soils? The warp and woof of tree-soil interactions. Biogeochemistry 42, 89–106.

Binkley D and Valentine D 1991 Fifty-year biogeochemical effects of green ash, white pine, and Norway spruce in a replicated experiment. For. Ecol. Manag. 40, 13–25.

Brais S, Camiré C, Bergeron Y and Paré D 1995 Changes in nutrient availability and forest floor characteristics in relation to stand age and forest composition in the southern part of the boreal forest of northwestern Quebec. For. Ecol. Manag. 76, 181–189.

Carter M R 1993 Soil Sampling and Methods of Analysis. Lewis Publishers, Boca Raton, USA. 823 p.

Comeau P G and Thomas K D 1996 Silviculture of temperate and boreal broadleaf-conifer mixtures. Land Management Handbook 36. Ministry of Forests, Victoria, B.C., Canada. 163 p.

Côté B and Fyles J W 1994 Nutrient concentration and acid-base status of leaf litter of tree species characteristic of the hardwood forest of southern Quebec. Can. J. For. Res. 24, 192–196.

Delong S C 1996 Draft field guide insert for site identification and interpretation for the southeast portion of the Prince George Forest Region. Ministry of Forests, Prince George, B.C., Canada. 193 p.

Federer C A 1982 Subjectivity in the separation of organic horizons of the forest floor. Soil Sci. Soc. Am. J. 46, 1090–1093.

France E A, Binkley D and Valentine D 1989 Soil chemistry changes after 27 years under four tree species in southern Ontario. Can. J. For. Res. 19, 1648–1650.

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

Harvey A E, Jurgensen M F, Larsen M J and Graham R T 1987 Decaying organic materials and soil quality in the Inland Northwest:

a management opportunity. General Technical Report INT-255. U.S.D.A. Forest Service. 15 p.
Hortie H J, Green A J and Lord T M 1970 Soils of the upper part of the Fraser valley in the Rocky Mountain Trench of British Columbia. Report No. 10, B.C. Soil Survey. Research Branch, Canada Dept. of Agriculture, Ottawa, Canada. 55 p.
Johnstone W D 1985 Thinning lodgepole pine. *In* Lodgepole Pine: The Species and its Management. Eds. D M Baumgartner, R G Krebill, J T Arnott and G F Weetman. pp 253–262. Washington State University, Pullman.
Jull M 1992 Aleza Lake Research Forest: Management and Working Plan #1. Ministry of Forests, Prince George, B.C., Canada. 39 p.
Jurgensen M F, Harvey A E, Graham R T, Page-Dumroese D S, Tonn J R, Larsen M J and Jain T B 1997 Impacts of timber harvesting on soil organic matter, nitrogen, productivity, and health of Inland Northwest forests. For. Sci. 43, 234–251.
Kalra Y P and Maynard D G 1991 Methods manual for forest soil and plant analysis. Information Report NOR-X-319. Forestry Canada, Edmonton, Alberta, Canada. 116 p.
Kimmins J P 1977 Evaluation of the consequences for future tree productivity of the loss of nutrients in whole-tree harvesting. For. Ecol. Manag. 1, 169–183.
Kishchuk B 1998 Sulphur availability on interior lodgepole pine sites. Ph.D. dissertation. Univ. British Columbia, Vancouver, Canada.
Klinka K, Feller M C, Lavkulich L M and Kozak A 1980 Evaluation of methods of extracting soil cations for forest productivity studies in southwestern British Columbia. Can. J. Soil Sci. 60, 697–705.
MacLean D A and Wein R W 1978 Weight loss and nutrient changes in decomposing litter and forest floor material in New Brunswick forest stands. Can. J. Bot. 56, 2730–2749.
Miles J and Young W F 1980 The effects on heathland and moorland soils in Scotland and northern England following colonization by birch (*Betula* sp.). Bull. Ecol. 11, 233–242.
Miller H G 1984 Nutrient cycles in birchwoods. Proc. R. Soc. Edinb. 85B, 83–96.
Ministry of Forests 1995 Establishment to free growing guidebook: Prince George Forest Region. Forest Practices Code of British Columbia. 159 p.
Ministry of Forests 1997 Soil rehabilitation guidebook. Forest Practices Code of British Columbia. 77 p.
Paré D, Bergeron Y and Camiré C 1993 Changes in the forest floor of Canadian southern boreal forest after disturbance. J. Veg. Sci. 4, 811–818.
Perry D A, Choquette C and Schroeder P 1987 Nitrogen dynamics in conifer-dominated forests with and without hardwoods. Can. J. For. Res. 17, 1434–1441.
Peterson E B, Peterson N M, Simard S W and Wang J R 1997 Paper birch managers' handbook for British Columbia. Forestry Canada and B.C. Ministry of Forests, Victoria, B.C., Canada. 133 p.
Priha O and Smolander A 1997 Microbial biomass and activity in soil and litter under *Pinus sylvestris*, *Picea abies* and *Betula pendula* at originally similar field afforestation sites. Biol. Fertil. Soils 24, 45–51.
Quesnel H J and Lavkulich L M 1981 Comparison of the chemical properties of forest floors, decaying wood and fine roots in three ecosystems on Vancouver Island. Can. J. For. Res. 11, 215–217.
SPSS Inc. 1997 SYSTAT 7.0 for Windows.
Trowbridge R, Kranabetter M, Macadam A, Battigelli J, Berch S, Chapman W, Kabzems R, Osberg M and Sanborn P 1996 The effects of soil compaction and organic matter retention on long-term soil productivity in British Columbia (Experimental Project 1148): Establishment report. Ministry of Forests, Victoria, B.C., Canada. 95 p.
Vesterdal L and Raulund-Rasmussen 1998 Forest floor chemistry under seven tree species along a soil fertility gradient. Can. J. For. Res. 28, 1636–1647.
Wang J R, Zhong A L, Simard SW and Kimmins J P 1996 Above-ground biomass and nutrient accumulation in an age sequence of paper birch (*Betula papyrifera*) in the Interior Cedar Hemlock zone, British Columbia. For. Ecol. Manag. 83, 27–38

Section editor: S. Recous