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The impact of vine maple on site fertility of coastal temperate forests

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Abstract

Vine maple (*Acer circinatum* Pursh) has often been viewed as a competitor with conifers in coastal forests of the Pacific Northwest. Few researchers have examined vine maple's ecological role in forest ecosystems with much of the literature focusing on its role as a weed species. We studied vine maple to determine if it enhanced site fertility in mature coastal forests and whether the nutrient status of adjacent Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) was improved by the presence of vine maple. Site fertility was assessed by analyzing litterfall, forest floor and Douglas-fir foliage using plots where vine maple was present or absent. Paired plots were established in a 75-year-old and a 130-year-old stand in southwestern British Columbia, Canada. At both stands, total autumn litterfall collected from vine maple plots had significantly higher N content than litterfall from conifer plots. Both stands had autumn, needle litterfall from vine maple plots with significantly higher N concentrations relative to needle litterfall from conifer plots. At the 130-year-old stand, N concentration in Douglas-fir foliage had a weak tendency to be higher for vine maple plots compared to conifer plots, with Douglas-fir adjacent to vine maple having larger boles. At both stands, total B concentrations and contents in the forest floor were higher in vine maple compared to conifer plots. At the 75-year-old stand, Douglas-fir adjacent to vine maple had foliage with greater B concentrations and contents which appeared to alleviate a B deficiency. Vine maple may be desirable in managed stands of temperate coastal forests due to the positive impact on site fertility and the potential to influence Douglas-fir growth. © 2001 Elsevier Science B.V. All rights reserved.

Keywords: Litterfall; Forest floor; Foliage; Nutrient status; Douglas-fir; *Pseudotsuga menziesii*; Vine maple; *Acer circinatum*

1. Introduction

Although broad-leaved trees have traditionally been viewed as weed trees in conifer-dominated forests of the Pacific Northwest (Haeussler et al., 1990), recent research on broad-leaved species has reported that they may improve stand productivity. Bormann et al. (1994) and Puettmann and Hibbs (1996) showed that red alder (*Alnus rubra* Bong.) promotes productivity and long-term sustainability through its high litter nutrient concentrations and accelerated nutrient cycling. Simard (1996) concluded that mutualistic relationships existed between Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and paper birch (*Betula papyrifera* Marsh.). Douglas-fir and paper birch had increased growth when grown together rather than in stands of either species.

Not only do broad-leaved species promote stand growth, but they also contribute to biodiversity, wildlife habitat, and landscape aesthetics. In addition, they

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act as nurse crops for conifers (Perry et al., 1987; Comeau, 1996), aid in ameliorating the risk of forest health problems, and diversify forest end products (Tappeiner and Zasada, 1993; Simard, 1996). Potentially commercial, broad-leaved trees, such as red alder and paper birch, have received most research attention, unlike vine maple (*Acer circinatum* Pursh), a common species in coastal temperate forests.

Vine maple is a small tree ranging in size from 1 to 15 m in height and consists of a series of small stems emanating from a root ball (Haeussler et al., 1990). Vine maple has often been viewed negatively by forest managers due to its ability to quickly colonize logged areas thus competing with conifers (O'Dea et al., 1995). Vine maple growth has been noted to be most rapid in the first 50 years of the stand initiation phase in Douglas-fir dominated forests (O'Dea et al., 1995). The rapid initiation of vine maple is due to its ability to develop adventitious roots after a disturbance making it an aggressive competitor with conifers (Walstad et al., 1987). Additional research has found that vine maple leaves may be allelopathic to Douglas-fir seedlings which may inhibit conifer establishment in the vicinity of vine maple (Tinnin and Kirkpatrick, 1985).

As vine maple is a non-commercial tree species and competes with conifers for resources, most research has focused on ways to remove or control its growth in managed stands (Haeussler et al., 1990). However, some research has addressed the potential positive affects of vine maple on site fertility and productivity of coastal forests. Ogden and Schmidt (1997) found that vine maple litterfall was rich in N, P, K, Ca, Mg and Zn and that vine maple litter decomposed faster than conifer litter. Ogden and Schmidt (1997) stressed that further research was warranted with a larger sample size and additional measurements since their data reported trends that indicated vine maple may lead to improved site fertility. Wardman and Schmidt (1998) examined site productivity in the same stand that Ogden and Schmidt (1997) investigated. They found that site index and tree heights of Douglas-fir adjacent to vine maple plots were significantly higher compared to those within conifer plots, which may suggest that vine maple improves site fertility.

The goal of our research was to provide further insight into the influence of vine maple on site fertility by assessing nutrient concentrations and contents of litterfall, forest floor and Douglas-fir foliage. This study advances previous work by providing information on an increased number of nutrient properties, using a larger sample size and adding another study location to observe if vine maple's influence was similar in two stands.

2. Methodology

2.1. Study sites and experimental design

Our research was conducted in two stands: a 75-year-old stand located in Seymour Demonstration Forest near Vancouver, BC, Canada; and a 130-year-old stand at Malcolm Knapp Research Forest, 60 km east of Vancouver. Both stands are located within the Coastal Western Hemlock Biogeoclimatic Zone, which is characterized by moist and cool climatic conditions with a mean annual precipitation of 2088 mm (Meidinger and Pojar, 1991) and a mean annual temperature of 7.5°C (Klinka et al., 1979).

The study stands are dominated by coastal Douglas-fir and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), and have a small component of western red cedar (*Thuja plicata* Donn.). Vine maple occurs in clumps within the understory of the stands. The 75-year-old stand regenerated naturally after logging in the early to mid-1920s and has a canopy height ranging from 37.5 to 46.4 m (Wardman and Schmidt, 1998). The 130-year-old stand originated after a wildfire in 1868 (Sanders, 1981) and has attained a canopy height that ranges from 46.5 to 55.8 m.

The soils at the 75-year-old stand are sandy loam Duric Humo–Ferric Podzols (Agriculture Canada Expert Committee on Soil Survey, 1987) which are derived from ablation till and colluvium that is mantled by bouldery gravel (Armstrong and Hicock, 1976). Mor (Green et al., 1993) is the dominant humus form. Soils at the 130-year-old stand are derived from morainal and colluvial parent materials and are sandy loam Gleyed Dystric Brunisols (Agriculture Canada Expert Committee on Soil Survey, 1987). Mor and mull humus forms are present in this stand (Green et al., 1993).

Plots containing vine maple were paired with plots that did not contain vine maple, identified as conifer plots. Vine maple plots were established first, followed by conifer plots.

Seasonal litterfall, forest floor and current-year Douglas-fir foliage were collected from each plot. The area of the plots for litterfall and forest floor sampling was defined by the canopy limits of a single, healthy and well-established vine maple clump during the growing season and Douglas-fir adjacent to the vine maple were included in the plot for foliar sampling. Vine maple plots varied from approximately 50–190 m^2 in area and each conifer plot was equivalent in area to that of its vine maple plot counterpart.

Prior to plot selection, several criteria were established to define the sample population. Forest stands with patches of healthy, well-established vine maples were visually identified in each study area. Disturbed sites were avoided due to the risk of the disturbance masking the effect of vine maple. Sites were excluded if either bigleaf maple or red alder stems were less than 15 m away from sample plots or if evidence of their litter was observed in the plot.

A total of 15 paired plots were established in each stand, although three plots were later excluded in the 130-year-old stand due to the presence of red alder, thus reducing the sample size to 12 paired plots. Plots were paired by geographic proximity where site factors such as slope, aspect and elevation were similar, to reduce the variation within pairs. Plot selection was based on transects that were 200 or 250 m in length running through the study stands. All vine maple meeting the plot selection criteria and less than 50 m from the transects were selected as vine maple plots. Conifer plots were situated more than 15 m away from vine maple plots. Conifer plot selection was conducted by traveling south of a vine maple plot by 30 m, and if no suitable sites were found, site selection was then 30 m to the north of the vine maple plot. If still no sites were located, then a west direction was taken, followed by east if necessary.

McGhee (1996) studied the demography and persistence of vine maple in the 75-year-old stand used in our study and found evidence for the long-term persistence of vine maple. It is thus likely that vine maples were present on the vine maple plots at least since the time of stand establishment, and thus the vine maple influence is probably quite long-term. Conifer plots were selected such that there was no evidence of vine maple (dead or alive) within 15 m of their centers, thus it is likely that the conifer plots had not been influenced by vine maple at least since the time of stand establishment.

We have assumed in this study that the distribution of vine maple is not influenced by inherent soil fertility within the study stands. Previous research suggests that the distribution of vine maple is not influenced by inherent soil properties. McGhee (1996) found an equivalent number of large stumps in vine maple plots compared to the surrounding forest, indicating that the vine maple sites are equally suitable for the growth of conifers. Ogden (1996) found no significant differences in soil moisture, texture, gravel content, and pH of the parent materials (measured at 50 and 100 cm depths) between vine maple and conifer plots.

2.2. Litterfall, forest floor and foliage collection

Litterfall samples were collected from September 1996 to September 1997 once in each of the four seasons using five 0.125 m^2 plastic greenhouse trays in each plot. The autumn collection occurred after the autumnal equinox and when the majority of the vine maple leaves had senesced. The autumn, winter, spring and summer collections began on 31 October 1996, 20 March 1997, 22 June 1997 and 22 September 1997, respectively. To reduce variability, any branches greater than 2 mm in diameter and bark greater than 2 cm were removed from the sample. Litterfall samples were oven-dried overnight at 70°C and weighed (Kalra and Maynard, 1991). The mass of litterfall samples were averaged per plot, and an estimation of seasonal and annual litter input relative to each plot type was determined. Autumn litterfall was sorted into three categories: vine maple, Douglas-fir/western hemlock and western red cedar. Cones, seeds, bark, twigs, moss, lichen and unrecognizable material were placed in a category termed "other". The vine maple, fir/hemlock and cedar components were ground and composited on a plot basis for nutrient analysis.

Three forest floor samples were collected from each plot using systematic random sampling (Tashe, 1998). A 324 cm^2 template was used to cut out each forest floor sample. Decaying wood, coarse fragments and roots greater than 1 cm in diameter were not included in the sample. All forest floor samples were oven-dried for 24 h at 105°C, (Kalra and Maynard, 1991), their mass measured and were composited on a plot basis.

Due to the high cost of collecting the foliage, a subset of eight paired plots per stand were randomly selected for foliar analysis (Tashe, 1998). Plots selected for foliar analysis were required to have two or more dominant and healthy Douglas-fir adjacent to the plots. For each selected plot, current year's Douglas-fir needles were collected from 2 to 3 mature, disease-free, dominant Douglas-fir trees in the autumn of 1997 following a method outlined by Radwan et al. (1991). One vigorous branch from the upper third of the crown was removed from each tree (Radwan et al., 1991). The samples were oven-dried at 70°C overnight (Kalra and Maynard, 1991), composited on a plot basis and dry mass calculated from the average of three replicates of 100 whole needles from each plot.

2.3. Litterfall, forest floor and foliar analysis

Each composited litterfall, forest floor and Douglas-fir foliage sample underwent a Parkinson and Allen (1975) wet digest for nutrient analysis. In addition, a portion of each forest floor sample underwent a semi-micro Kjeldahl digestion followed by colorimetric analysis on a Technicon Autoanalyzer to measure total N (Black et al., 1965). Each litterfall and foliage sample had total N measured on a La Chat Autoanalyzer (Parkinson and Allen, 1975). Total concentrations of P, Ca, Mg, Mn, Fe, Cu, Zn and B in litterfall, forest floor and Douglas-fir foliage samples were measured on a Thermo-Jarrel Ash Atom Comp Series 11 inductively coupled plasma–atomic emission spectrometer (ICP). Potassium concentration was read on a Thermo-Jarrel Ash Video 22 Atomic Absorption Spectrophotometer (AAS). Foliar nutrient concentrations were used to diagnose the nutrient status of Douglas-fir located in vine maple and conifer plots following a method outlined by Ballard and Carter (1986).

2.4. Douglas-fir growth measurements

Measurements of tree diameter, height, age, and site index were made for the two to three (co)-dominant Douglas-fir trees on each of the eight paired plots which were selected for foliar analysis in the 130-year-old stand. Cores were extracted at breast height (1.3 m), tree rings were counted to determine age and tree heights were calculated using percent angles to the top and base of the tree. Site indices represent the height of (co)-dominant trees at age 50 and were calculated with the aid of "Freddie", a computer program designed for site index estimation (Polsson, 1993). Measurements of Douglas-fir tree diameter, height, age, site index, are available for the 75-year-old stand from research carried out by Wardman and Schmidt (1998).

2.5. Statistical analysis

Data were statistically analyzed using SYSTAT 7 (1997) software with a significance level (α) of 0.05. Significance levels ranging from 0.05 to <0.1 were reported as weak tendencies for the data. The calculated mean values for measured variables for each plot were used to test for the effect of vine maple on site fertility. Locations were analyzed separately to observe if the two sites responded differently to the presence of vine maple.

Paired *t*-tests were used to test for statistically significant differences between vine maple and conifer plots. Certain variables did not conform to the underlying assumptions and were transformed to achieve normality. When the underlying assumptions of the *t*-test were violated and could not be corrected through transformations, the Wilcoxon signed rank test (*Z*-statistic) was used.

One-way analysis of variance (ANOVA) tests were performed on autumn litterfall data to determine if statistical differences existed between litter type of vine maple, fir/hemlock, and cedar litterfall within vine maple plots. Significant differences between litterfall types were analyzed using the Tukey multiple comparison test to determine which of the specific litter type population means were significantly different from the others. Any variables not conforming to the underlying assumption of equality of variance (Sit, 1995) were transformed. To determine the risk of making a Type II error, or falsely accepting H_0, Power analysis was performed for all statistical data that did not reject the null hypothesis (H_0). Power ($1-\beta$) was computed by a program developed by Borenstein and Cohen (1988).

3. Results

3.1. Litterfall

No statistical differences were observed in total litterfall amounts between vine maple and conifer plots for the winter, spring and summer periods, but a weak tendency existed for greater autumn litterfall amounts for vine maple plots relative to conifer plots at the 75-year-old stand (Fig. 1). For the autumn litterfall, fir and hemlock needles contributed the most mass per unit area to both plot types, followed by vine maple litter for vine maple plots, and then cedar litter (Fig. 2). Vine maple litter made up of 18 and 20% of the autumn litterfall from vine maple plots at the 75- and 130-year-old stands, respectively.

Vine maple litter had significantly greater concentrations of all nutrients relative to both fir/hemlock

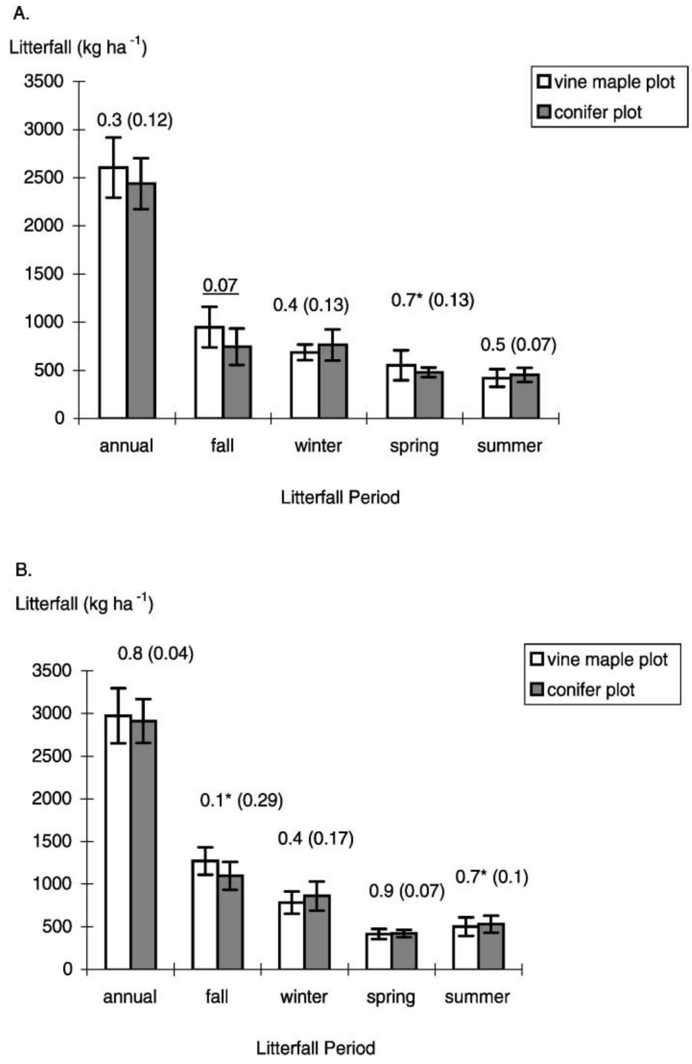


Fig. 1. Mean annual and seasonal litterfall amounts for vine maple and conifer plots at (A) the 75-year-old stand (mean of 15 replicates) and (B) the 130-year-old stand (mean of 12 replicates). Error bars represent one standard deviation from the mean. Probability values (*t*-test) are shown above the error bars. (*) Litterfall data that was log-transformed to meet underlying statistical assumptions. Significance level was set at $P<0.05$. Values in parentheses represent Power $(1-\beta)$.

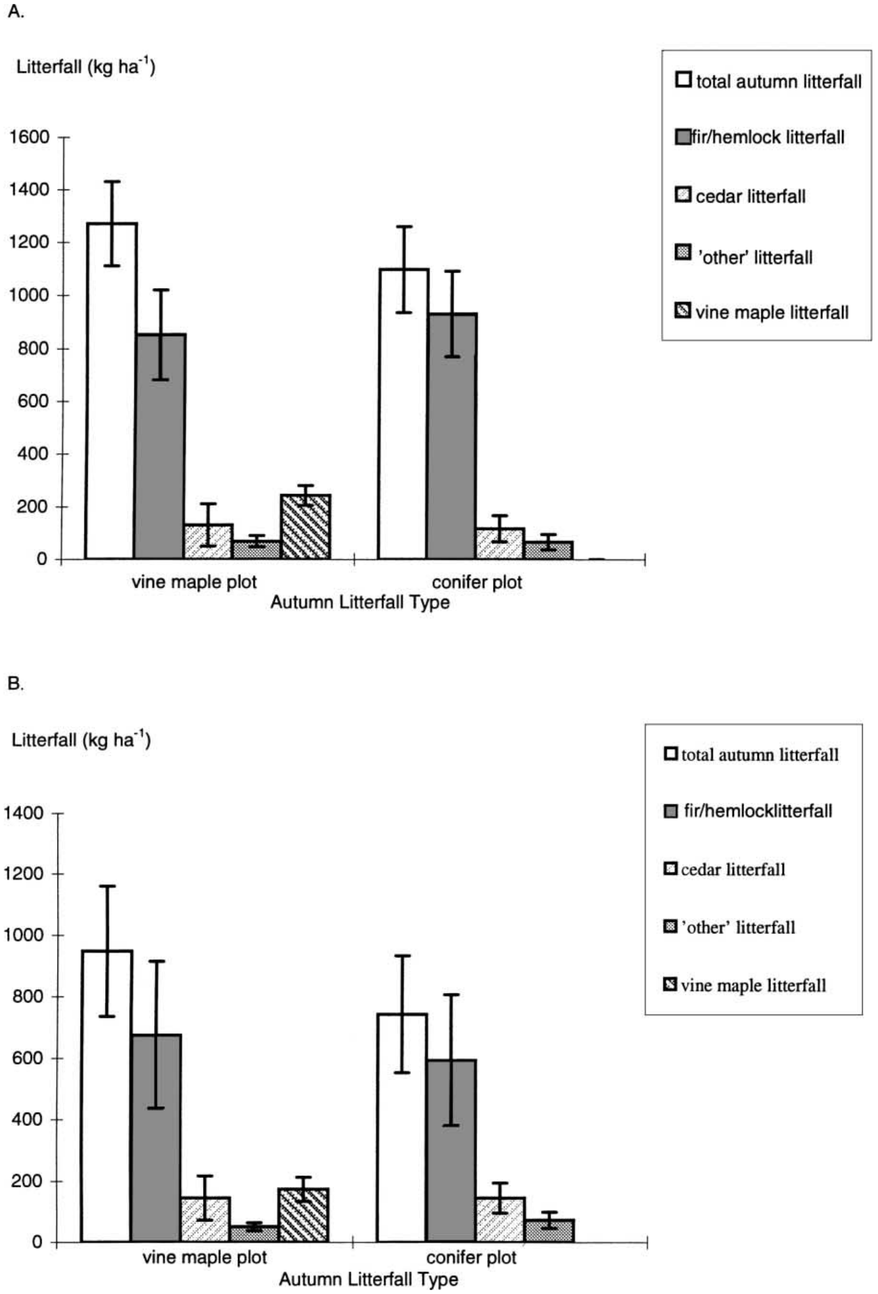


Fig. 2. Autumn litterfall amounts showing proportions of component contributions at (A) the 75-year-old stand (mean of 15 replicates) and (B) the 130-year-old stand (mean of 12 replicates). Error bars represent one standard deviation from the mean.

and cedar litter collected within vine maple plots at both study stands, with the exception of Ca (Tables 1 and 2). Calcium concentration was statistically greater for vine maple compared to fir/hemlock litter at the 130-year-old stand, and had a weak tendency to be higher for cedar compared to vine maple litter at both stands. Contents of N, P, Ca and Mg of fir/hemlock litterfall were significantly greater than vine

Table 1
Mass, nutrient concentration and content of vine maple (n=15), Douglas-fir/western hemlock (n=15) and western red cedar litterfall (n=10) collected during autumn within vine maple plots at the 75-year-old stand

	Vine maple litter[a] (vm)	Fir/hemlock litter[a] (*n*)	Red cedar litter[a] (*c*)	Anova *P* (*F*-statistic)	Tukey multiple comparison test		
					P (vm−*n*)	*P* (vm−*c*)	*P* (*n*−*c*)
Mass (kg ha^{-1})	174 (80)	675 (478)	144 (146)	0.003[*,b]	0.000[*]	0.3[b]	0.000[*,b]
Concentrations (μg g^{-1})							
N	10960 (2060)	7370 (830)	4810 (790)	0.000[*,b]	0.053[**]	0.036[*,b]	0.000[*,b]
P	717 (178)	366 (50)	324 (66)	0.000[*]	0.000[*]	0.000[*]	0.6
K	2193 (435)	646 (286)	777 (117)	0.000[*]	0.000[*]	0.000[*]	0.6
Ca	12658 (2239)	10785 (3415)	15121 (1825)	0.001[*]	0.14	0.062[**]	0.001[*]
Mg	801 (163)	405 (98)	430 (64)	0.000[*]	0.000[*]	0.000[*]	0.9
Mn	575 (252)	384 (125)	172 (51)	0.000[*,b]	0.018[*,b]	0.000[*,b]	0.000[*,b]
B	51 (8)	13 (4)	13 (4)	0.000[*]	0.000[*]	0.000[*]	0.9
Zn	201 (58)	45 (10)	26 (7)	0.000[*]	0.000[*]	0.000[*]	0.4
Contents (kg ha^{-1})							
N	1.96 (1.11)	4.94 (3.47)	1.01 (0.86)	0.000[*,b]	0.016[*,b]	0.127[b]	0.000[*,b]
P	0.13 (0.07)	0.27 (0.21)	0.07 (0.07)	0.002[*,b]	0.003[*,b]	0.5[b]	0.003[*,b]
K	0.38 (0.16)	0.36 (0.21)	0.16 (0.13)	0.007[*]	0.97	0.010[*]	0.016[*]
Ca	2.19 (1.00)	7.84 (6.19)	3.05 (2.38)	0.017[*,b]	0.017[*,b]	0.9[b]	0.11[b]
Mg	0.14 (0.07)	0.28 (0.22)	0.09 (0.07)	0.004[*]	0.026[*]	0.6	0.005[*]
Mn	0.10 (0.07)	0.22 (0.19)	0.04 (0.03)	0.000[*]	0.009[*]	0.4	0.001[*]
B	0.009 (0.005)	0.008 (0.006)	0.003 (0.002)	0.007[*]	0.8	0.007[*]	0.025[*]
Zn	0.033 (0.015)	0.029 (0.021)	0.005 (0.004)	0.000[*]	0.7	0.000[*]	0.002[*]

[*] Significant differences at $P<0.05$.
[**] Significant differences at $P<0.1$.
[a] Values in parentheses represent standard deviations.
[b] Data were log-transformed to meet underlying statistical assumptions.

maple litterfall within vine maple plots at both study stands (Tables 1 and 2). In the vine maple plots at both study stands, more than 25% of inputs from each measured nutrient, with the exception of Ca at the 75-year-old stand, came from vine maple litter.

Between plot comparisons showed that the concentrations of N in fir/hemlock litter were significantly greater for vine maple plots relative to conifer plots at both stands (Table 3). Concentrations of P and Zn were significantly greater for vine maple compared to conifer plots for the 130-year-old stand. At both stands no significant differences in needle litterfall amounts were found between plot types. Total autumn litterfall from vine maple plots compared to conifer plots had statistically greater N, P, K, Mg, Mn and Zn contents at both stands (Table 4). Calcium and B contents in autumn litterfall were statistically greater for vine maple compared to conifer plots at the 75-year-old stand and had a weak tendency to be greater for vine maple relative to conifer plots at the 130-year-old stand.

3.2. Forest floor

Zinc concentrations were significantly greater in the forest floor of vine maple plots relative to conifer plots at both stands (Table 5). At the 75-year-old stand, B concentration and B and Mn contents were significantly greater and Mn concentration had a weak tendency to be greater in the forest floor of vine maple relative to conifer plots. At the 130-year-old stand, Mg and K concentrations were significantly greater and P and B concentrations and B content had a weak tendency to be greater in the forest floor of vine maple relative to conifer plots.

Table 2
Mass, nutrient concentration and content of vine maple ($n=12$), Douglas-fir/western hemlock ($n=12$) and western red cedar litterfall ($n=9$) collected during autumn within vine maple plots at the 130-year-old stand

	Vine maple litter[a] (vm)	Fir/hemlock litter[a] (*n*)	Red cedar litter (*c*)	Anova *P* (*F*-statistic)	Tukey multiple comparison test		
					P (vm−*n*)	*P* (vm−*c*)	*P* (*n*−*c*)
Mass (kg ha^{-1})	244 (154)	852 (338)	131 (161)	0.000[*]	0.000[*,b]	0.085[*,b]	0.000[*,b]
Concentrations (μg g^{-1})							
N	10840 (1850)	7140 (880)	5710 (910)	0.000[*]	0.000[*]	0.000[*]	0.079[**]
P	802 (159)	478 (77)	418 (60)	0.000[*]	0.000[*]	0.000[*]	0.5
K	2344 (696)	793 (123)	865 (114)	0.000[*,c]	0.000[*,c]	0.000[*,c]	0.4[c]
Ca	12850 (1916)	9691 (1603)	14705 (2373)	0.000[*]	0.001[*]	0.055[**]	0.000[*]
Mg	1259 (245)	649 (78)	618 (81)	0.000[*,c]	0.000[*,c]	0.000[*,c]	0.9[c]
Mn	702 (210)	297 (54)	246 (64)	0.000[*]	0.000[*]	0.000[*]	0.6
B	46 (17)	19 (6)	26 (8)	0.000[*]	0.000[*]	0.000[*]	0.5
Zn	118 (36)	35 (5)	31 (8)	0.000[*]	0.000[*]	0.000[*]	0.95
Contents (kg ha^{-1})							
N	2.56 (1.61)	6.19 (2.71)	0.96 (0.87)	0.000[*,c]	0.002[*,c]	0.001[*,c]	0.000[*,c]
P	0.19 (0.13)	0.39 (0.14)	0.08 (0.08)	0.000[*]	0.001[*]	0.07[**]	0.000[*]
K	0.57 (0.39)	0.68 (0.28)	0.16 (0.16)	0.001[*]	0.6	0.01[*]	0.001[*]
Ca	3.11 (2.06)	8.60 (4.56)	2.44 (2.13)	0.000[*,c]	0.000[*,c]	0.5[c]	0.000[*,c]
Mg	0.32 (0.22)	0.56 (0.25)	0.11 (0.10)	0.000[*]	0.02[*]	0.07[**]	0.000[*]
Mn	0.18 (0.15)	0.25 (0.09)	0.045 (0.04)	0.001[*]	0.3	0.02[*]	0.000[*]
B	0.011 (0.007)	0.016 (0.016)	0.004 (0.004)	0.001[*]	0.14	0.04[*]	0.000[*]
Zn	0.03 (0.02)	0.030 (0.013)	0.005 (0.005)	0.000[*,c]	0.7[c]	0.000[*,c]	0.000[*,c]

[*] Significant differences at $P<0.05$.
[**] Significant differences at $P<0.1$.
[a] Values in parentheses represent standard deviations.
[b] Data were square root transformed to meet underlying statistical assumptions.
[c] Data were log-transformed to meet underlying statistical assumptions.

3.3. Douglas-fir foliage and growth measurements

Nitrogen concentration of Douglas-fir foliage had a weak tendency to be greater for vine maple relative to conifer plots at the 130-year-old stand (Table 6). Douglas-fir on both plot types at the 130-year-old stand was diagnosed as being severely deficient in N. At the 75-year-old stand we found statistically greater B concentration and B and Mn contents and a weak tendency for greater Mn concentration in Douglas-fir foliage from vine maple compared to conifer plots (Tables 6 and 7).

No statistical differences in Douglas-fir needle mass were found between vine maple and conifer plots at either study stand (Table 7). For the 130-year-old stand, Douglas-fir adjacent to vine maple had a weak tendency to have greater diameter at breast height than Douglas-fir in conifer plots (Table 8). No statistical differences were found between vine maple and conifer plots for tree heights, tree ages or site index.

4. Discussion

4.1. Litterfall amounts and nutrient inputs

Vine maple plots had a weak tendency ($P=0.07$, $n=15$) for greater amounts of total autumn litterfall relative to conifer plots at the 75-year-old stand. Although vine maple is small in stature relative to the surrounding trees it has significant leaf fall in autumn (Russel, 1973). Contrary to our findings, Ogden and Schmidt (1997) found a "weak tendency" ($P=0.12$, $n=6$) for smaller amounts of total litterfall beneath vine maple than beneath the conifer canopy in the autumn. The apparent discrepancy between the findings of Ogden and Schmidt (1997) and those of

Table 3
Nutrient concentrations and mass of Douglas-fir and western hemlock needle litterfall collected in autumn from vine maple and conifer plots at the 75-year-old stand (mean of 15 replicates) and the 130-year-old stand (mean of 12 replicates)

	Vine maple plots[a]	Conifer plots[a]	*P* (*t*-test)	*P* (*Z*-statistic)	Power $(1-\beta)$
75-*year-old stand*					
Mass (kg ha^{-1})	675 (478)	594 (429)	0.5		0.07
N (µg g^{-1})	7370 (830)	6790 (870)	0.015[*]		
P (µg g^{-1})	366 (50)	373 (36)	0.6		0.06
K (µg g^{-1})	646 (286)	542 (136)	0.2[b]		0.23
Ca (µg g^{-1})	10785 (3415)	9685 (1226)	0.2		0.20
Mg (µg g^{-1})	405 (98)	394 (49)	0.9[b]		0.05
Mn (µg g^{-1})	384 (125)	310 (55)	0.06[**]		
B (µg g^{-1})	13 (4)	10 (3)	0.1		0.40
Zn (µg g^{-1})	45 (10)	41 (11)		0.4	
130-*year-old stand*					
Mass (kg ha^{-1})	983 (262)	1047 (347)	0.6[b]		0.08
N (µg g^{-1})	7140 (880)	6600 (920)	0.016[*]		
P (µg g^{-1})	478 (77)	432 (89)		0.034[*]	
K (µg g^{-1})	793 (123)	810 (229)	0.8		0.04
Ca (µg g^{-1})	9691 (1603)	9826 (1631)	0.8		0.04
Mg (µg g^{-1})	649 (78)	616 (76)	0.4		0.17
Mn (µg g^{-1})	297 (54)	317 (89)	0.5[b]		0.09
B (µg g^{-1})	19 (6)	21 (7)	0.7		0.06
Zn (µg g^{-1})	35 (5)	38 (4)	0.007[*]		

[*] Significant differences at $P<0.05$.

[**] Significant differences at $P<0.1$.

[a] Values in parentheses represent standard deviations.

[b] Data was log-transformed to meet underlying statistical assumptions.

Table 4
Nutrient contents (kg ha^{-1}) of autumn litterfall from vine maple and conifer plots for the 75-year-old stand (mean of 15 replicates) and the 130-year-old stand (mean of 12 replicates)

	Vine maple plots[a]	Conifer plots[a]	*P* (*t*-test)	*P* (Z-statistic)
75-*year-old stand*				
N	7.54 (3.48)	4.58 (2.31)	0.004[*]	
P	0.44 (0.22)	0.29 (0.16)	0.009[*]	
K	0.84 (0.26)	0.41 (0.19)	0.000[*]	
Ca	12.0 (6.11)	8.10 (3.90)	0.018[*]	
Mg	0.48 (0.21)	0.31 (0.17)	0.01[*]	
Mn	0.37 (0.23)	0.21 (0.14)	0.009[*]	
B	0.019 (0.007)	0.008 (0.004)	0.000[*]	
Zn	0.065 (0.029)	0.025 (0.013)	0.000[*]	
130-*year-old stand*				
N	9.42 (2.67)	6.94 (2.74)	0.016[*]	
P	0.64 (0.20)	0.46 (020)	0.003[*]	
K	1.36 (0.50)	0.87 (0.40)	0.007[*]	
Ca	13.4 (4.32)	11.1 (4.44)		0.06[**]
Mg	0.95 (0.03)	0.66 (0.25)		0.03[*]
Mn	0.46 (0.18)	0.33 (0.15)		0.019[*]
B	0.029 (0.011)	0.022 (0.012)		0.1
Zn	0.060 (0.018)	0.040 (0.014)	0.001[*]	

[*] Significant differences at $P<0.05$.

[**] Significant differences at $P<0.1$.

[a] Values in parentheses represent standard deviations.

Table 5
Forest floor nutrient concentrations and contents for vine maple and conifer plots for the 75-year-old stand (mean of 15 replicates) and the 130-year-old stand (mean of 12 replicates)

	Vine maple plots[a]	Conifer plots[a]	P (t-test)	Power $(1-\beta)$
75-*year-old stand concentrations* (μg g^{-1})				
N	14300 (1740)	14700 (1320)	0.31	0.12
P	742 (82)	711 (94)	0.2	0.15
K	1292 (236)	1271 (353)	0.6[b]	0.04
Ca	6451 (1891)	5585 (1232)	0.1	0.30
Mg	439 (76)	417 (113)	0.6	0.09
Mn	551 (354)	350 (241)	0.08[**]	
B	5.5 (2.3)	2.3 (1.2)	0.000[*]	
Zn	62 (10)	54 (6)	0.009[*]	
75-*year-old stand contents* (kg ha^{-1})				
N	902 (695)	784 (339)	0.93[b]	0.08
P	45 (26)	37 (15)	0.4	0.14
K	77 (44)	65 (24)	0.6[b]	0.14
Ca	371 (198)	288 (116)	0.2	0.27
Mg	26 (13)	21 (9)	0.2	0.15
Mn	29 (21)	17 (13)	0.005[*,b]	
B	0.4 (0.3)	0.1 (0.1)	0.001[*,b]	
Zn	3.7 (2.2)	2.8 (1.0)	0.1	0.29
130-*year-old stand concentrations* (μg g^{-1})				
N	15100 (1610)	15700 (1730)	0.41	0.12
P	841 (84)	803 (112)	0.06[**]	
K	1114 (138)	1033 (133)	0.023[*]	
Ca	7603 (1496)	6862 (1727)	0.2	0.19
Mg	596 (138)	462 (90)	0.002[*]	
Mn	529 (225)	413 (199)	0.1	0.25
B	12 (12)	4 (3)	0.07[**,b]	
Zn	49 (9)	43 (10)	0.04[*]	
130-*year-old stand contents* (kg ha^{-1})				
N	347 (123)	475 (253)	0.1[b]	0.33
P	19 (6)	24 (11)	0.1	0.22
K	26 (9)	30 (12)	0.2	0.16
Ca	172 (49)	190 (70)	0.4	0.11
Mg	13 (4)	13 (6)	0.9	0.03
Mn	12 (6)	10 (3)	0.3	0.12
B	0.2 (0.2)	0.1 (0.1)	0.06[**]	
Zn	1.1 (0.4)	1.3 (0.7)	0.8[b]	0.11

[*] Significant differences at $P<0.05$

[**] Significant differences at $P<0.1$.

[a] Values in parentheses represent standard deviations.

[b] Data were log-transformed to meet underlying statistical assumptions.

our study may in part be due to differences in method of measurement, sample size, times of collection and inherent variability associated with litterfall. Our findings may be partially explained by Wardman and Schmidt (1998) who reported that Douglas-fir site basal area did not differ significantly between vine maple (70 m^2 ha^{-1}) and conifer (77 m^2 ha^{-1}) plots and that conifer crown expansion occurs over vine maple. Thus, in our study the amount of needle litterfall between plot types was not significantly different and the addition of vine maple litter increased total autumn litterfall.

Vine maple litter had significantly higher concentrations of all measured nutrients relative to both fir/

Table 6
Concentrations of nutrients (μg g^{-1}) from current year Douglas-fir foliage in vine maple and conifer plots for the 75-year-old and 130-year-old stands (mean of eight replicates per study stand) (nutrient status evaluation followed from Ballard and Carter (1986))

	Vine maple plots[a]		Conifer plots[a]		*P* (*t*-test)	*P* (*Z*-static)	Power $(1-\beta)$
75-*year-old stand*							
N	15200 (12700)	Adequate	14000 (2510)	Slight moderate deficiency	0.4		0.04
P	870 (55)	Moderate deficiency	842 (70)	Moderate deficiency	0.5		0.13
K	7824 (1860)	Possibly slight deficiency	7548 (1257)	Possibly slight deficiency		0.7	
Ca	2889 (779)	No deficiency	2649 (300)	No deficiency		0.7	
Mg	902 (79)	Possible slight moderate deficiency	918 (45)	Possible slight moderate deficiency	0.7		0.07
Mn	234 (32)	No deficiency	189 (54)	No deficiency	0.05**		
B	21 (7)	Probably no deficiency	14 (1)	Possibly deficient		0.012*	
Zn	22 (3)	No deficiency	19 (2)	No deficiency	0.3		0.29
130-*year-old stand*							
N	11200 (950)	Severely deficient	10900 (670)	Severely deficient	0.09**		
P	1034 (180)	Slightly deficient	1177 (361)	Slightly deficient	0.3		0.15
K	6493 (968)	Slight moderate deficiency	6728 (1249)	Slight moderate deficiency	0.7[b]		0.06
Ca	3088 (548)	No deficiency	3014 (534)	No deficiency		0.5	
Mg	1054 (175)	No deficiency	1042 (99)	No deficiency	0.8		0.04
Mn	203 (66)	No deficiency	220 (82)	No deficiency		0.7	
B	18 (8)	Probably not deficient	18 (8)	Probably not deficient	0.95[b]		0.03
Zn	15 (3)	No deficiency	16 (3)	No deficiency	0.4		0.10

* Significant differences at $P<0.05$.

** Significant differences at $P<0.1$.

[a] Values in parentheses represent standard deviations.

[b] Data were log-transformed to meet underlying statistical assumptions.

Table 7
Douglas-fir needle mass and nutrient contents (μg needle^{-1}) for vine maple and conifer plots for the 75-year-old and 130-year-old stands (mean of eight replicates per study area)

	Vine maple plots[a]	Conifer plots[a]	*P* (*t*-test)	Power $(1-\beta)$
75-*year-old stand*				
Needle mass (g)	0.27 (0.06)	0.24 (0.05)	0.23	0.17
N	3473 (1247)	3291 (596)	0.7	0.05
P	235 (61)	200 (28)	0.2	0.28
K	2111 (688)	1804 (452)	0.3	0.16
Ca	812 (405)	633 (141)	0.3	0.19
Mg	245 (70)	219 (41)	0.3	0.13
Mn	63 (15)	44 (9)	0.017	
B	5.5 (1.7)	3.2 (0.6)	0.002	
Zn	5.9 (2.1)	4.6 (0.8)	0.1	0.33
130-*year-old stand*				
Needle mass (g)	0.27 (0.04)	0.25 (0.05)	0.55	0.13
N	3270 (447)	2968 (636)	0.4	0.17
P	274 (65)	305 (150)	0.6	0.07
K	1692 (149)	1688 (460)	0.98	0.03
Ca	812 (162)	750 (195)	0.5	0.09
Mg	276 (38)	261 (61)	0.6	0.08
Mn	54 (19)	57 (32)	0.8	0.04
B	4.8 (2.5)	4.3 (1.5)	0.7[b]	0.07
Zn	4.0 (0.6)	4.1 (1.3)	0.9	0.04

[a] Values in parentheses represent standard deviations.
[b] Data were log-transformed to meet underlying statistical assumptions.

hemlock and cedar litterfall. The one exception was Ca concentration, which showed a weak tendency to be greater in cedar litter compared to vine maple litter, and was statistically greater in cedar litter relative to fir/hemlock litter. The high Ca concentrations in cedar litter are not unexpected since cedar tends to accumulate high concentrations of Ca in its foliage (Turner and Franz, 1985). The finding of greater concentrations of most nutrients in vine maple litter is consistent with those of Russel (1973), and Ogden and Schmidt (1997) who found vine maple to be rich in N, P, K, Ca and Mg.

We found that the autumn litterfall from vine maple plots had significantly higher nutrient contents relative to conifer plots. The higher nutrient contents in litterfall are attributed to the somewhat greater total litterfall inputs in vine maple compared with conifer plots and the significantly greater nutrient concentrations of vine maple litter compared to fir/hemlock litter. The greater nutrient input to sites with a component of vine maple suggest that over time vine maple may improve the nutritional status of these sites. This finding is further supported by our result of greater N concentration in fir/hemlock litterfall from vine maple plots

Table 8
Characteristics of Douglas-fir growing in vine maple and conifer plots at the 130-year-old stand (mean of eight replicates)

	Vine maple plots[a]	Conifer plots[a]	*P* (*t*-test)	Power $(1-\beta)$
Tree age at breast height (years)	110 (11.54)	105 (11.69)	0.12	0.12
Diameter at breast height (cm)	72.8 (11.08)	65.6 (8.32)	0.07*	
Tree height (m)	52.2 (6.05)	51.5 (5.13)	0.8	0.04
Site index	35.3 (3.18)	35.6 (2.96)	0.9	0.04

* Indicate significant differences at $P<0.1$.
[a] Values in parentheses represent standard deviations.

compared to conifer plots, which may suggest the foliage of conifers near vine maple contain more nutrients. Perry et al. (1987) also found conifers mixed with broad-leaved tree species returned more N in litterfall due to a greater N concentration in conifer litter relative to the litter of pure conifer stands. Our results are dissimilar from those of Ogden and Schmidt (1997) who found no significant difference in nutrient inputs in litterfall between vine maple and conifer plots. The lack of difference in nutrient inputs found by Ogden and Schmidt (1997) are most likely associated with their measurement of lower litterfall inputs for vine maple plots.

4.2. *Influence of vine maple on the forest floor*

With the exception of B and Zn, differences in nutrient concentrations in forest floors between vine maple and conifer plots were not consistent for the two stands, suggesting that vine maple had a variable influence on the two stands. Four and five of the eight measured nutrients were significantly greater or had a weak tendency to be greater for forest floors of vine maple compared to conifer plots for the 75- and 130-year-old study stands, respectively. The greater concentrations of nutrients in the litterfall of vine maple may partially account for the greater concentrations of those nutrients in the forest floor.

Though N concentrations were greater in the litterfall of vine maple compared to fir/hemlock, concentrations of N were not significantly different for forest floors beneath vine maple and conifer plots at both study stands. Similar results were found by Ogden and Schmidt (1997) who found no significant differences in N concentrations between forest floor of vine maple and conifer plots.

We found a weak tendency for greater concentration of Ca in the forest floor of vine maple compared to conifer plots at the 75-year-old stand and significantly greater concentrations of K and Mg in the forest floor of vine maple compared to conifer plots at the 130-year-old stand. We expected to find greater concentrations of K, Ca and Mg in forest floors of vine maple compared to conifer plots since vine maple litter was found to be rich in bases and since Ogden and Schmidt (1997) found greater concentrations of these nutrients in forest floors of vine maple compared to conifer plots. Klemmedson (1994) found the presence of New Mexican locust (*Robinia neomexicana* Gray), an understory tree species like vine maple, significantly increased concentrations of total K and Ca in the Oe and Oa (L, F, H) horizons in Ponderosa pine (*Pinus ponderosa* Laws) forests. Tree litter was found to be the most important source of Ca and Mg for the forest floor (51–69% of the total depending on the element) in a 30-year-old jack pine (*Pinus banksiana* Lamb) forest (Foster, 1974).

We found that B concentration in the forest floor was significantly greater at the 75-year-old stand and had a weak tendency to be greater at the 130-year-old stand for vine maple plots compared to conifer plots. Deficiencies of micronutrients, such as B, are most common on acid, highly leached sandy soils (Carter et al., 1984; Carter and Lowe, 1986), usually of igneous origin (Ballard and Carter, 1986). Boron deficiency also frequently occurs in forested sites experiencing a surplus of soil moisture during most of the growing season, followed by a short and potentially severe period of soil moisture deficit in the summer (Ballard and Carter, 1986). Both of these soil and climatic conditions occur in the 75-year-old stand which was diagnosed as possibly B deficient in conifer plots. Therefore, the greater B concentration in the forest floor under vine maple is nutritionally important to trees and may be partially attributed to nutrient inputs from vine maple litterfall.

4.3. *Douglas-fir foliar nutrient status*

Few significant differences were found in Douglas-fir foliar nutrient concentrations and contents between the two plot types in our study, however, the differences that were found are potentially important. The results suggest that the uptake of N, B and Mn may be enhanced by the presence of vine maple although the results were not consistent for the two study stands.

A weak tendency existed for greater N concentration in the foliage of Douglas-fir for vine maple compared to conifer plots at the 130-year-old stand. The higher N concentrations in foliage of Douglas-fir adjacent to vine maple may be related to significantly greater N contents in autumn litterfall on vine maple plots. The possibility that vine maple has enhanced the uptake of N is important since N is commonly limiting to Douglas-fir, which often readily responds to additions of N (Gessel et al., 1973). Nitrogen was assessed as being severely deficient at the 130-year-old stand and so any increase in N uptake could be very beneficial for the Douglas-fir on this site. No significant difference in foliar N concentration was found between the two plot types at the 75-year-old stand, but the N status at this stand was assessed as adequate to moderately deficient.

Foliar B concentration and content were significantly greater for Douglas-fir in the presence of vine maple at the 75-year-old stand, suggesting that a B deficiency may have been alleviated by the presence of vine maple. Boron deficiencies have been noted in coastal Douglas-fir located along coastal British Columbia (Carter et al., 1984). Boron deficiencies can lead to distorted growth and trees can experience retarded or stunted apical growth (Carter et al., 1984; Carter and Lowe, 1986), although these symptoms were not noted in our study stand.

4.4. Growth response of Douglas-fir

Wardman and Schmidt (1998) found significantly higher site index ($P=0.05$) for Douglas-fir adjacent to vine maple (42.6 m) compared to site index for Douglas-fir in conifer plots (40.2 m) at the 75-year-old stand. Wardman and Schmidt (1998) suggested that one potential reason for greater site index associated with vine maple plots might be greater concentrations of nutrients beneath vine maple. Our results indicate that the greater site index may be associated with greater content of nutrients in litterfall and greater concentration of some nutrients in the forest floor and Douglas-fir foliage. In particular, the apparently enhanced B nutrition of the site may have positively influenced the site quality at the 75-year-old stand.

Unlike the 75-year-old stand, no statistical difference was found in site index between vine maple (35.3 m) and conifer plots (35.6 m) at the 130-year-old stand. The apparently enhanced N nutrition associated with the presence of vine maple at the 130-year-old stand does not appear to have positively influenced Douglas-fir site index. The lower site index at the 130-year-old stand compared to the 75-year-old stand may be associated with the higher ground water table as indicated by the presence of mottles in soil pits.

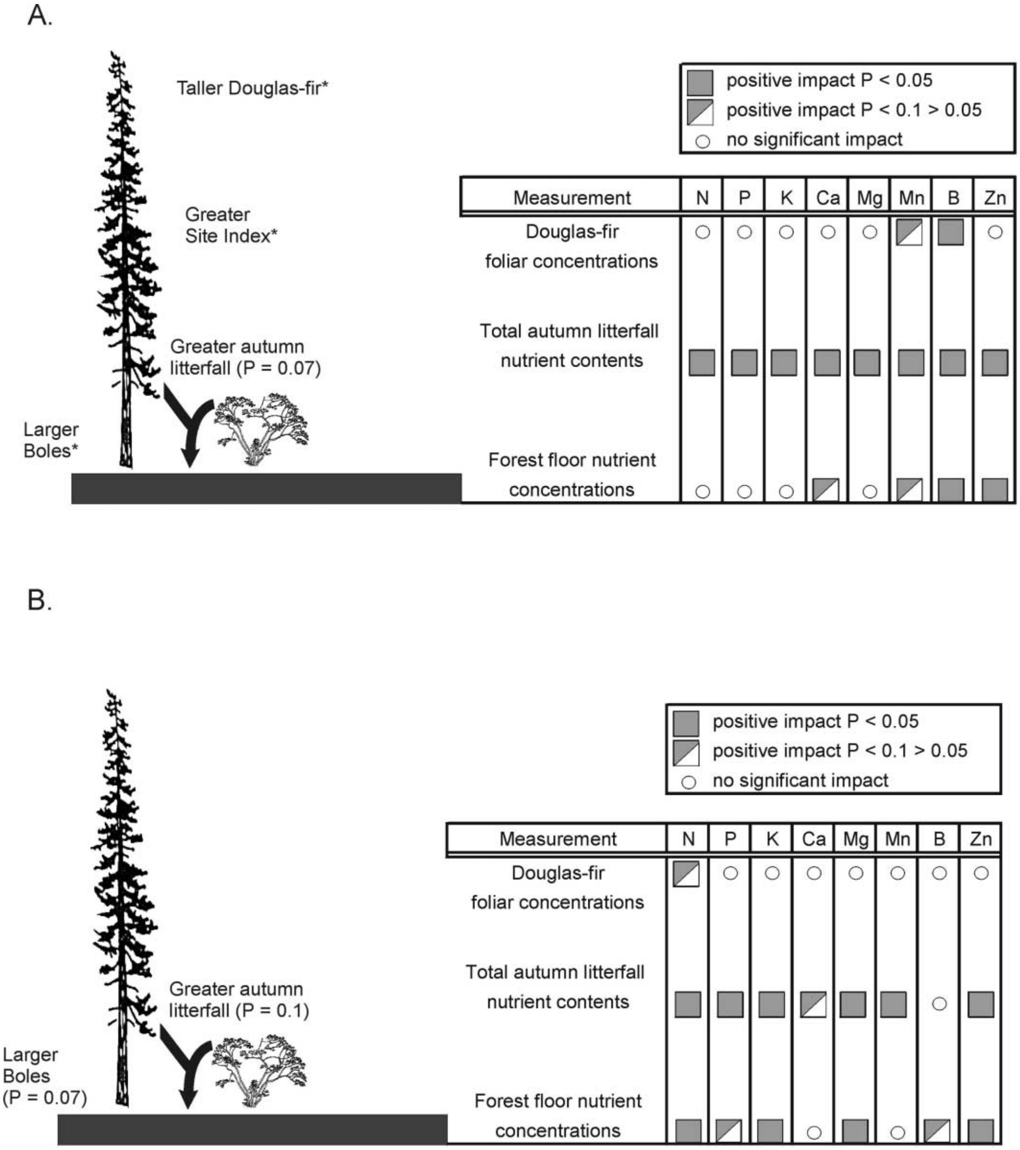
At the 75-year-old stand, Wardman and Schmidt (1998) reported significantly greater diameters at breast height for Douglas-fir adjacent to vine maple compared to conifer plots. Wardman and Schmidt (1998) had attributed the larger bole size to the presence of vine maple in the understory creating wider conifer spacing which allowed for increases in diameter. Our research suggests that the larger bole sizes could also be attributed to Douglas-fir investing available nutrients provided by vine maple to increases in girth. Older trees are known to allocate more growth to boles and stems rather than foliage (Kramer and Kozlowski, 1979). The significantly greater tree heights of Douglas-fir associated with vine maple could be attributed to the alleviation of B deficiency as leader development would be improved (Carter et al., 1984; Carter and Lowe, 1986).

The results for the 130-year-old stand were similar to those for the 75-year-old stand, with the diameter at breast height of Douglas-fir being greater for trees adjacent to vine maple compared to those in conifer plots. The larger bole sizes may be attributed to Douglas-fir investing available nutrients, in particular N, to increases in girth. Douglas-fir stands with low site index also experienced increases in girth in the presence of N-fixing red alder (Binkley, 1983). In our study, vine maple may have provided the additional N to Douglas-fir adjacent to vine maple since N is the major growth-limiting factor for trees, and N deficiencies are widespread in Pacific coastal forests (Edmonds et al., 1989).

5. Research implications

The differences in nutrient concentrations of litter between deciduous and coniferous trees are important as hardwoods tend to not use nutrients as efficiently, but release nutrients tied up in biomass through heavy annual litterfall and rapid decomposition (Massie et al., 1994). These differences between vine maple and conifers allow us to suggest that vine maple, through its nutrient-rich litterfall, was able to improve nutrient availability to the benefit of adjacent Douglas-fir in two coastal forest stands (Fig. 3).

Our study was successful in showing differences in nutrient concentrations between species and between plot types. The data presented represent two stands and results varied between them indicating that further replication is needed in other locations. For data that



A.

■ positive impact P < 0.05
◪ positive impact P < 0.1 > 0.05
○ no significant impact

Measurement	N	P	K	Ca	Mg	Mn	B	Zn
Douglas-fir foliar concentrations	○	○	○	○	○	◪	■	○
Total autumn litterfall nutrient contents	■	■	■	■	■	■	■	■
Forest floor nutrient concentrations	○	○	○	◪	○	◪	■	■

B.

■ positive impact P < 0.05
◪ positive impact P < 0.1 > 0.05
○ no significant impact

Measurement	N	P	K	Ca	Mg	Mn	B	Zn
Douglas-fir foliar concentrations	◪	○	○	○	○	○	○	○
Total autumn litterfall nutrient contents	■	■	■	◪	■	■	○	■
Forest floor nutrient concentrations	■	◪	■	○	■	○	◪	■

Fig. 3. Summary diagram illustrating the impact of vine maple on Douglas-fir growth, foliar concentrations, total autumn litterfall amounts and nutrient contents, and forest floor nutrient concentrations in relation to conifer-dominated areas at (A) the 75-year-old stand and (B) the 130-year-old stand. (*) Findings of Wardman and Schmidt (1998).

showed no significant differences low Power was encountered. Low Power indicates that vine maple and conifer plots may potentially show significant results if sample size was increased or variability reduced.

Management of mixed forests requires an ecological balancing act (Simard, 1996). Although maintaining broad-leaved species in conifer-dominated stands may be beneficial, forests must be managed in order to avoid potential problems such as resource competition, alteration of environmental conditions, and/or physical damage to crop trees (Simard, 1996). O'Dea et al. (1995) reported that Douglas-fir growth can be suppressed in managed stands by dense mats of vine maple. However, vine maple is a natural component in temperate coastal forests and contributes to biodiversity, wildlife food and habitat (Haeussler et al., 1990), and as our research suggests as an important source of nutrients to the site and surrounding Douglas-fir. The challenge that exists is finding a balance between vine maple's negative impact as a competitor with conifers and vine maple's positive influence on site fertility.

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