

AN ABSTRACT OF THE THESIS OF

Jeremy Steven Fried for the degree of Master of Science in Forest Management presented on May 2, 1985.

Title: Two Studies of *Acer macrophyllum*: I. The Effects of Bigleaf Maple on Soils in Douglas-fir Forests. II. The Ecology of Bigleaf Maple Seedling Establishment and Early Growth in Douglas-fir Forests.

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Dr. John Tappeiner

Bigleaf maple (*Acer macrophyllum*) is a deciduous, persistent, sprouting species that frequently accounts for as much as 20% of the basal area in Douglas-fir forests. Because of the lack of knowledge of the role of bigleaf maple in Douglas-fir forest ecosystems and the problems that it poses as a vigorous competitor to commercial conifer seedlings, two studies were undertaken to determine its possible effects on forest soils, and to gain insight into the seedling establishment phase of its life cycle.

Soil chemical and physical properties and forest floor and litterfall weights, nutrient content and forest floor turnover rates under bigleaf maple and Douglas-fir

(*Pseudotsuga menziesii*) were compared on five sites on the eastern margin of the Oregon Coast Range. Litterfall weight and nutrient content were greater under maple on virtually every site for every macro and micro-nutrient. Forest floor biomass and nutrient content were extremely variable, much more so than litterfall, and there were no significant differences among the two species. However, turnover rates for forest floor biomass and nutrients were significantly faster under maple for every nutrient on every site. Bulk density of mineral soil was also highly variable with significant differences on only two sites.

Soil nitrogen was generally greater under maple and there was a trend towards greater potassium under maple also. Amounts of calcium, magnesium and phosphorous showed no consistent trends. Soil organic matter content under maple was significantly greater than under Douglas-fir on 4 of 5 sites. The greater soil nutrients and organic matter under maple may be attributed to the more rapid forest floor turnover in that system.

The establishment phase of bigleaf maple, a ubiquitous, deciduous hardwood in western Oregon's Douglas-fir forests, was studied in a variety of stands ranging from 1 to 150 years of age to identify those stages in Douglas-fir forest succession where bigleaf maple is most likely to become successfully established from seed. Germination rates of seed protected from rodents averaged from 30 to 40 % in all

environments but typically less than 2 % of the unprotected seed germinated, indicating that seed predators play an important role in regulating seedling establishment.

Seedling survival was highly dependent on light and mortality after one growing season was particularly high in stands with greater than 90 % overstory cover. At least half of the first year mortality was due to browsing by burrowing rodents and invertebrates, with dessication as the second greatest cause of mortality during the first year.

On plots that were monitored over two growing seasons, overwinter mortality was the second most frequent classification. Seedling survival was not related to soil moisture content or soil moisture tension. The highest survival rates (90 %) were in clearcuts and very open stands and the lowest (0 %) were in dense, young, conifer stands. Maple establishment in clearcuts will likely only be successful if seedlings escape shading by competing shrubs and herbs. Optimum long term survival is most likely in Douglas-fir stands over 40 years of age.

Two Studies of *Acer macrophyllum*:

I. The Effects of Bigleaf Maple on Soils
in Douglas-fir Forests.

II. The Ecology of Bigleaf Maple Seedling Establishment
and Early Growth
in Douglas-fir Forests.

by

Jeremy Steven Fried

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Two Studies of Acer macrophyllum I. The Effects
of Bigleaf Maple on Soils in Douglas-fir Forests.
II. The Ecology of Bigleaf Maple Seedling Establishment
and Early Growth in Douglas-fir Forests.

INTRODUCTION

Research on hardwoods and hardwood ecology in Oregon has yielded considerable information about red alder (*Alnus rubra*), and more recently, tanoak (*Lithocarpus densiflorus*) and madrone (*Arbutus menziesii*). There have been investigations of their ecology, water use, nutrient dynamics and sprouting potential, yet bigleaf maple (*Acer macrophyllum*), the state's second most abundant hardwood, has been virtually unstudied until now. Forest managers have long been concerned about the competitive potential of this species with young conifers because of its capacity for extremely rapid sprout growth in response to fire or cutting. Many now routinely spray maple with herbicides or use frill injection to kill the trees, or at least control their growth.

If maple control results in large scale removal of this species from Douglas-fir forest ecosystems, conceivable effects include changes in soil properties due to elimination of a significant component of the ecosystem. The first study was undertaken to determine what, if anything, bigleaf

maple contributes to the soil or the nutrient system that could be lost by removal of the species from conifer forests.

Because the control of tree-sized bigleaf maple can be a difficult and expensive proposition, it might be wise to seek the most vulnerable periods in its life cycle to either kill off the organism or, through silvicultural management, prevent its establishment. The purpose of the second study was to learn about maple's requirements for successful seedling establishment and to evaluate establishment success in a range of stands and successional environments.

THE EFFECTS OF BIGLEAF MAPLE ON SOILS IN DOUGLAS-FIR FORESTS

by

Jeremy S. Fried and James Boyle

ABSTRACT

Soil chemical and physical properties and forest floor and litterfall weights, nutrient content and forest floor turnover rates under bigleaf maple (*Acer macrophyllum*) and Douglas-fir (*Pseudotsuga menziesii*) were compared on five sites on the eastern margin of the Oregon Coast Range. Litterfall weight and nutrient content were significantly greater under maple on virtually every site for every macro- and micro-nutrient. Forest floor biomass and nutrient content were extremely variable, much more so than litterfall, and there were no significant differences among the two species. However, turnover rates for forest floor biomass and nutrients were significantly faster under maple for every nutrient on every site. Bulk density of mineral soil was also highly variable with significant differences on only two sites. Soil nitrogen was generally greater under maple and there was also a trend towards greater potassium under maple. There were no trends in amounts of calcium, magnesium and phosphorous. Soil organic matter content under maple was significantly greater than under Douglas-fir on 4 of 5 sites. The greater soil nutrients and organic matter under maple may be attributed to the more rapid forest floor turnover in that system.

THE EFFECTS OF BIGLEAF MAPLE ON SOILS IN DOUGLAS-FIR FORESTS

INTRODUCTION

Many scientists have sought to identify the effects of vegetation on soils (e.g. Crocker, 1959; Ovington, 1955). Some have established definite differences in soil chemical and physical properties between soils influenced by vegetation and soils devoid of vegetation (Doescher et al, 1984; Zinke, 1961; Zinke and Crocker, 1962) while others observed differences in mineral soil properties generated by different tree and understory species in forest stands (Alban, 1969; Challinor, 1968; Tappeiner and Alm, 1975; Tarrant and Miller, 1963). Still other investigations have focused on differences in the chemical composition of litter and forest floor under different species to gain a better understanding of varying nutrient cycling dynamics and the effects of succession (Gessel and Balci, 1965; Gessel and Turner, 1974; Grier and McColl, 1971; MacLean and Wein, 1978; Peterson and Rolfe 1982; Tarrant and Chandler, 1951). Many earlier studies of this type are summarized by Bray and Gorham (1964).

In some cases, a particular species may affect soil properties sufficiently to warrant special consideration in

developing forest management strategies, as in the case of the nitrogen-fixing red alder, which adds substantial quantities of nitrogen to the soil through nitrogen-fixing root nodules (Tarrant and Miller, 1963). Alder can even increase the growth rates of interplanted conifers compared to the growth rates of those conifers growing without the influence of red alder (Tarrant et al., 1961).

The objective of this study was to examine the effects of bigleaf maple (*Acer macrophyllum*), a deciduous, persistent hardwood species common in Douglas-fir (*Pseudotsuga menziesii*) stands in Western Oregon, on soil properties. Bigleaf maple's ability to grow rapidly (up to 2 m/year) from the sprouts of cut or burned stumps has prompted forest managers to undertake measures to control or eliminate this competitive species from conifer plantations. However, improvements in soil properties by bigleaf maple could conceivably offset the negative impacts of competition and justify the selective retention of bigleaf maple as a component of Douglas-fir stands. To explore this assumption we compared soil properties and litter and forest floor biomass and chemical composition under Douglas-fir and under bigleaf maple.

Jenny (1958) postulated a model of soil genesis with five independent variables: climate, organisms, relief, parent material and time. In this study, our approach was to hold four of these constant while choosing different

conditions of the organism variable by the selection of plots under bigleaf maple and under Douglas-fir trees.

STUDY SITES

The study was conducted on the MacDonald and Dunn Forests (T. 10 and 11 S, R. 5 W, Willamette meridian), which are maintained by the College of Forestry, Oregon State University in Benton County, western Oregon. The sites are at Lat. 44° 40' N., Long. 123° 20' in the foothills west of the Willamette Valley, on the eastern fringe of the Coast Range. Annual rainfall averages 130 cm, average annual air temperature is 9 to 12° C, and the frost free season is 165 to 200 days (Knezevich 1975). A complete description of the vegetation in this area is given by Hall and Alaback (1982). Elevation of the sites ranges from 175 to 400 m. The soils are silty clay loams derived principally from fractured or weathered basalt, range from 75 to 152 cm in depth and are typical of commercial Douglas-fir/bigleaf maple stands found on the eastern margin of the Coast Range (Table 1).

The study sites were located in five Douglas-fir stands from 35 to 60 years of age, each with scattered bigleaf maple trees or groups comprising less than 20 % of the total basal area. Within each stand, litterfall and soil properties were sampled on a pair of plots spaced 5 to 35 m apart, one each under maple and Douglas-fir, with comparable slope position and aspect. The undergrowth layer, which ranged from a sparse cover, < 5%, of moss to a 15 to 50 % cover of

Table 1. Description of location and soils for study sites.

SITE	SLOPE	ASPECT	SOIL SERIES	SOIL SUBGROUP	DEPTH TO ROCK	SOIL TEXTURE	PARENT MATERIAL
1	35%	N	DIXONVILLE	Pachic Ultic Argixerolls	94 cm	silty clay loam	weathered basalt bedrock
2	25%	N	DIXONVILLE	Pachic Ultic Argixerolls	94 cm	silty clay loam	weathered basalt bedrock
3	20%	NW	PRICE	Dystric Xerochrepts	127 cm	silty clay loam	ptly weath. basalt bedrock
4	5%	-	JORY	Xeric Haplohumults	152 cm	silty clay loam	sed./basic igneous colluvium
5	55%	SE	RITNER	Dystric Xerochrepts	75 cm	gravelly, si cl lo	fractured basalt bedrock

swordfern (*Polistichum munitum*), was similar under both Douglas-fir and big-leaf maple (Table 2). Douglas-fir resulted from natural regeneration following fire or harvest of the previous stand. Bigleaf maple usually originated from stump sprouts of trees in the previous stand; because of their sprouting ability following fire or cutting, it is likely that they were present in several previous Douglas-fir stands.

Table 2. Description of overstory and understory vegetation for study sites.

SITE	PLOT	AGE (yrs)	TREES/HA.			BA(m ² /ha)			oth.	UNDERSTORY COMPOSITION/COVER %						OTHERS @ <5%
			DF	MA	hdwd	DF	MA	hdwd		SP.1	%COVER	SP.2	%COVER	SP.3	%COVER	
1	DF	52	420	90	--	62.5	1.6	--	moss	>50	rusp	<5	pomu	<5		
	MA	61	100	460	--	53.1	30.3	--	moss	15-50	drar	5-15	pomu	<5		
2	DF	57	410	40	110	88.0	1.5	0.9	moss	>50	pomu	<5	CoCo	<5	rusp , grass	
	MA	34	180	80	130	63.1	5.9	2.9	moss	15-50	pomu	5-15	rusp	5-15	CoCo , syal	
3	DF	49	710	60	--	66.6	4.0	--	moss	>50	pomu	15-50	rusp	<5		
	MA	40	380	110	90	47.3	11.3	2.2	moss	15-50	pomu	5-15				
4	DF	34	1580	60	--	63.9	0.3	--	pomu	<5						
	MA	49	470	50	--	30.9	16.6	--	pomu	5-15	moss	<5	grass	<5		
5	DF	56	170	20	--	44.9	7.3	--	pomu	<5	moss	<5	grass	<5	rogy	
	MA	50	240	70	--	6.4	22.3	--	{none}							
<div> <div>CoCo = <u>Corylus Cornuta</u></div> <div>drar = <u>Dryoptera arguta</u></div> </div> <div> <div>pomu = <u>Polystichum munitum</u></div> <div>syal = <u>Symphoricarpos albus</u></div> </div> <div> <div>rogy = <u>Rosa gymnocarpa</u></div> <div>rusp = <u>Rubus</u> spp</div> </div>																

METHODS

Plot Layout and Sampling

In summer 1983, we located one five meter radius circular plot each under Douglas-fir and maple overstory at each of the five sites. Each plot was divided into four equal quadrants. Within each quadrant, sampling points were selected randomly, given these constraints:

- * for litterfall and forest floor - two randomly selected points per quad, one at 2 m and one at 3.5 m from plot center; 8 per plot.
- * for soil chemical properties - two points 2 m from the center and three points 3.5 m from the center; 20 per plot.
- * for bulk density - three undisturbed points in each quadrant; 12 per plot.

Sample Collection

Mineral soil, forest floor and bulk density samples were collected and litter traps erected during the second week in September 1983, just prior to the onset of leaf fall and presumably at the time when the biomass and nutrient

content of the forest floor would approach an annual minimum. The forest floor samples were obtained by pressing a square, 1000 cm², sheet steel sampling frame into the forest floor and collecting all organic material above mineral soil. One litter trap (1 X 1 m) consisting of nylon mesh on a wooden frame was installed horizontally 10 cm above each forest floor sampling point.

Litterfall collections were carried out in 3 periods: two collections in period I, between September 8 and October 28, a time of heavy bigleaf maple litter fall and no rain; four collections at six week intervals in period II, a rainy period from October 28 to April 30 which included the remaining interval of bigleaf maple litterfall which ended about December 10; and one collection at the end of Period III consisting of litterfall between April 30 and September 4, 1984, which was entirely devoid of maple leaf litter.

Each litter and forest floor sample was separated by hand into leaf and twig components, and any woody material > 2 cm in diameter (generally insignificant) was discarded before weighing and analysis. All litter and forest floor samples were dried at 70° C for 48 hours and weighed to +/- 0.1 g. The forest floor and litterfall leaf and twig samples were first ground in a hammermill-type pulverizer and then in a Wiley mill to pass a 1 mm screen.

The five 125 cm³ soil samples collected in each quadrant from the 0-10 cm depth were bulked to yield a total of

4 samples per plot for nutrient analysis. A 100 gram subsample of soil was separated from each bulked quadrant sample, sealed in an air-tight soil can and refrigerated at 2° C for determination of mineralizable nitrogen.

Bulk density measurements of the mineral soil were taken with a 10 X 4 cm cylinder (a bulb planter), oven-dried at 105° C for 24 hours and weighed to +/- 0.1 g. A *Soiltest Model 980 Volumeasure* was used in the sampling holes to determine the volumes of soil removed.

Chemical Analysis

For each litter trap, there were six nutrient analyses: one for twig and fine woody material and one for leaves from each of the three collection periods. Litter and forest floor chemical analysis was conducted at the Oregon State University Plant Analysis Lab. Total N was measured using the N-Micro-Kjeldahl technique outlined by Bremner (1965). In addition, concentrations of 16 cations, including all 12 essential macro- and micro-nutrients, were determined using a plasma emission spectrometer to process solutions of ashed samples as described by Jones (1977).

All four soil samples from each plot were analyzed in the Oregon State University Forest Science Department Soil Laboratory for chemical properties, including: total N using the micro-Kjeldahl method (Bremner, 1965), dilute acid-flouride method for extractable P (Bray 1945, Jackson

1958), extractable K, Ca and Mg via the ammonium acetate method (Peech et al. 1947), total carbon using a LECO 12 carbon analyzer, and cation exchange capacity using the ammonium acetate method (Schollenberger and Simon 1945). One moist, refrigerated composite soil sample from each plot was analyzed for mineralizable N using an incubation technique modified from Waring and Bremner (1964) by maintaining a temperature of 40° C for 1 week instead of 30° C for 2 weeks (Keeney and Bremner, 1966) and the steam distillation method (Bremner and Keeney, 1966) for determination of ammonium-nitrogen.

Data analyses consisted of performing t-tests to identify significant differences in the mean values of chemical and physical properties of the soil, forest floor and litter between maple and Douglas-fir plots on the same site. Comparisons of properties between Douglas-fir and maple plots on all sites examined together were conducted using analysis of variance with a blocked design in which the sites served as blocks. The data were analyzed and are presented separately for all five sites because important differences would be masked if the analysis were conducted only on the five sites combined.

RESULTS

Litterfall Weight and Composition

Annual litterfall weight was substantially greater under bigleaf maple on all 5 sites ($p < .05$), with values ranging from 385 to 532 g/m² under bigleaf maple and 256 to 407 g/m² under Douglas-fir (Table 3).

The composition of the litter was quite different for the different collection periods. The maple litter was evenly divided between autumn and winter (Periods I and II). Autumn litter samples were relatively pure maple or Douglas-fir but all winter samples contained litterfall from both species. In winter, all traps contained considerable Douglas-fir needle litter and 30 to 60 cm long green, non-nodal branches (Jensen, 1983) blown down by winter storms which also blew small amounts of maple litter into the traps on the Douglas-fir plots. We estimated that Douglas-fir needles and branches sometimes accounted for more than half the weight of litter removed from maple plot traps in the winter. In Period III, May through September, the traps contained mostly Douglas-fir needles and flower parts from both species.

Litterfall Nutrient Concentrations

Comparisons of concentrations of nutrients in leaf litter between the dry autumn period and the rainy winter

Table 3. Litter weights and element weights of leaves and twigs combined.

SITE	PLOT	WEIGHT	N	P	K	Ca	S	Mg	Mn	Fe	Cu	B	Zn	Mo	Co	Al	Na	Se	Cd
		G/M ²	G/M ²	G/M ²	G/M ²	G/M ²	G/M ²	G/M ²	G/M ²	G/M ²	MG/M ²	MG/M ²	MG/M ²	MG/M ²	MG/M ²	G/M ²	MG/M ²	MG/M ²	MG/M ²
1	DF	259. ** (15.40)	2.02 ** (0.117)	0.41 ** (0.026)	1.02 ** (0.080)	2.86 ** (0.210)	0.29 ** (0.019)	0.33 ** (0.021)	0.09 ** (0.010)	0.09 ** (0.004)	0.87 ** (0.074)	5.55 ** (0.276)	6.36 ** (0.451)	0.03 ** (0.003)	0.05 ** (0.003)	0.08 ** (0.003)	24.3 ** (1.800)	0.01 ** (0.000)	0.03 ** (0.001)
	NA	501. (31.72)	4.13 (0.203)	0.77 (0.042)	2.37 (0.103)	7.28 (0.950)	0.71 (0.046)	0.88 (0.060)	0.13 (0.007)	0.21 (0.014)	2.60 (0.221)	9.94 (0.480)	17.3 (2.067)	0.08 (0.007)	0.11 (0.009)	0.21 (0.028)	44.6 (2.693)	0.02 (0.002)	0.06 (0.003)
2	DF	313. ** (22.10)	2.39 ** (0.158)	0.52 ** (0.037)	1.19 ** (0.094)	3.57 ** (0.232)	0.34 ** (0.024)	0.38 ** (0.026)	0.12 ** (0.006)	0.12 (0.009)	1.14 ** (0.091)	5.68 ** (0.333)	8.47 ** (0.633)	0.02 ** (0.001)	0.07 (0.006)	0.10 (0.008)	26.9 ** (1.446)	0.01 ** (0.000)	0.02 (0.005)
	NA	425. (23.94)	3.55 (0.172)	0.83 (0.061)	2.28 (0.164)	6.60 (0.416)	0.80 (0.054)	0.73 (0.039)	0.17 (0.014)	0.14 (0.013)	1.82 (0.104)	7.90 (0.440)	16.9 (0.944)	0.04 (0.002)	0.07 (0.006)	0.12 (0.010)	39.3 (3.282)	0.02 (0.001)	0.02 (0.001)
3	DF	345. ** (8.523)	3.18 ** (0.092)	0.60 (0.022)	1.24 ** (0.041)	4.13 ** (0.153)	0.40 ** (0.014)	0.55 ** (0.017)	0.09 (0.005)	0.09 (0.006)	1.49 ** (0.054)	4.59 ** (0.171)	9.28 ** (0.324)	0.03 (0.002)	0.04 (0.003)	0.07 (0.007)	25.9 ** (0.822)	0.01 (0.000)	0.03 (0.003)
	NA	385. (8.006)	3.78 (0.128)	0.68 (0.062)	1.51 (0.088)	6.01 (0.350)	0.53 (0.040)	0.78 (0.082)	0.10 (0.006)	0.10 (0.006)	2.68 (0.542)	7.47 (0.963)	13.5 (1.326)	0.23 (0.180)	0.27 (0.217)	0.08 (0.006)	34.0 (2.601)	0.02 (0.010)	0.15 (0.124)
4	DF	407. ** (28.87)	3.18 ** (0.218)	0.59 ** (0.040)	1.25 ** (0.078)	3.99 ** (0.263)	0.44 ** (0.028)	0.43 ** (0.027)	0.14 ** (0.009)	0.10 * (0.007)	1.28 ** (0.089)	5.09 ** (0.345)	8.26 ** (0.628)	0.04 ** (0.002)	0.09 (0.006)	0.10 (0.007)	23.5 ** (1.660)	0.01 ** (0.001)	0.03 (0.004)
	NA	507. (32.88)	4.56 (0.296)	0.87 (0.045)	3.27 (0.313)	6.75 (0.664)	1.48 (0.137)	0.84 (0.069)	0.19 (0.011)	0.12 (0.008)	2.47 (0.232)	7.56 (0.526)	24.1 (2.842)	0.06 (0.006)	0.08 (0.003)	0.09 (0.004)	33.7 (2.847)	0.02 (0.001)	0.03 (0.002)
5	DF	256. ** (22.89)	1.82 ** (0.187)	0.47 ** (0.052)	0.84 ** (0.088)	2.62 ** (0.199)	0.26 ** (0.021)	0.36 ** (0.037)	0.06 ** (0.005)	0.06 ** (0.006)	0.92 ** (0.113)	4.11 ** (0.338)	5.48 ** (0.525)	0.02 ** (0.001)	0.02 ** (0.002)	0.05 * (0.004)	20.9 ** (2.081)	0.00 ** (0.000)	0.01 ** (0.001)
	NA	532. (31.66)	4.68 (0.309)	1.38 (0.071)	3.82 (0.267)	11.9 (0.931)	1.09 (0.068)	1.61 (0.085)	0.10 (0.006)	0.11 (0.018)	2.05 (0.185)	6.70 (0.497)	26.6 (1.766)	0.09 (0.005)	0.04 (0.004)	0.07 (0.012)	47.7 (2.817)	0.03 (0.002)	0.04 (0.006)
Grand Mean	DF	316. ** (28.25)	2.52 ** (0.285)	0.52 * (0.036)	1.11 ** (0.078)	3.43 ** (0.299)	0.35 * (0.033)	0.41 * (0.039)	0.10 (0.013)	0.09 (0.009)	1.14 ** (0.114)	5.01 ** (0.293)	7.57 ** (0.708)	0.03 (0.003)	0.05 (0.011)	0.08 (0.010)	24.3 ** (1.047)	0.01 ** (0.001)	0.02 (0.003)
Grand Mean	NA	470. (27.69)	4.14 (0.217)	0.91 (0.121)	2.65 (0.403)	7.72 (1.077)	0.92 (0.167)	0.97 (0.162)	0.14 (0.016)	0.14 (0.019)	2.32 (0.166)	7.92 (0.543)	19.7 (2.453)	0.10 (0.032)	0.11 (0.041)	0.12 (0.025)	39.9 (2.806)	0.02 (0.001)	0.06 (0.023)

Note: Averages with a "*" adjacent to them indicate that the difference between maple and Douglas-fir is significant at the p=.10 level for that nutrient on that site.
Averages with a "**" adjacent to them indicate that the difference between maple and Douglas-fir is significant at the p=.05 level for that nutrient on that site.
Numbers in parentheses are standard errors for the individual plots or for the whole study.

period, Periods I and II showed significant differences for many nutrients on most sites (Table 4), for both Douglas-fir and bigleaf maple plots. For example, on the 5 maple plots, nitrogen (N) ranged from .74 to .93% in the autumn and from 0.96 to 1.17% in the winter while the corresponding ranges for potassium (K) were 0.64 to 1.09% and .30 to .33% with differences significant for both nutrients on all 5 plots. The abundance of green, non-nodal Douglas-fir branches on these sites in the winter litterfall probably accounted for the greater concentration of N in those samples. The dramatic differences in concentrations of K and other mobile, water-soluble nutrients may be attributed to leaching by rain during the winter.

Due to the mixing of litter in the winter and lack of maple litter in the spring and summer, we made nutrient concentration comparisons between Douglas-fir and maple leaf litter for the fall collections only (Table 5). Concentrations of K, calcium (Ca), zinc (Zn) and molybdenum (Mo) in the maple litter were significantly ($p < .05$) greater than in the Douglas-fir litter at all five sites. Nitrogen concentration was significantly greater in maple litter on four sites and phosphorous (P) on two sites. Ranges of average nutrient concentrations for the five Douglas-fir plots were: N .56-.74%, P 0.21-0.32%, K 0.45-0.60%, Ca 1.16-1.76%, magnesium (Mg) 0.14-0.25% and Zn 13.6-27.7 ppm; for maple, the ranges were: N 0.74-0.93%, P 0.24-0.37%, K 0.64-1.09%, Ca

Table 4. Comparison of mean element concentrations in leaf component of litter between collections I and II.

		DOUGLAS-FIR PLOTS																
		N	P	K	Ca	S	Mg	Mn	Fe	Cu	B	Zn	Mo	Co	Al	Na	Se	Cd
		PERCENT	PERCENT	PERCENT	PERCENT	PERCENT	PERCENT	PPM	PPM	PPM	PPM	PPM	PPM	PPM	PPM	PPM	PPM	PPM
SITE	COLLECTION																	
1	#1	0.70 ** (0.020)	0.23 ** (0.008)	0.60 ** (0.021)	1.16 ** (0.049)	0.13 ** (0.006)	0.15 ** (0.006)	523. * (36.23)	320. ** (15.96)	3.12 (0.398)	26.7 ** (0.632)	20.2 (1.058)	0.14 * (0.009)	0.16 (0.014)	293. ** (21.08)	107. (11.09)	0.04 (0.001)	0.06 (0.007)
	#2	0.92 (0.044)	0.15 (0.007)	0.33 (0.017)	1.32 (0.043)	0.11 (0.004)	0.12 (0.003)	424. (39.71)	178. (13.86)	2.83 (0.306)	22.7 (0.956)	19.9 (1.179)	0.09 (0.024)	0.11 (0.031)	153. (12.27)	101. (6.632)	0.04 (0.001)	0.05 (0.016)
2	#1	0.68 ** (0.017)	0.27 ** (0.002)	0.59 ** (0.019)	1.32 * (0.029)	0.13 ** (0.002)	0.16 ** (0.003)	641. ** (21.86)	238. * (6.313)	2.12 ** (0.251)	21.7 (0.333)	18.3 * (2.693)	0.10 (0.008)	0.14 (0.009)	193. (4.588)	78.8 ** (2.755)	0.04 (0.000)	0.05 (0.005)
	#2	1.00 (0.020)	0.17 (0.008)	0.35 (0.009)	1.41 (0.032)	0.11 (0.003)	0.12 (0.003)	514. (11.23)	295. (29.73)	3.85 (0.205)	21.3 (0.453)	24.9 (0.673)	0.09 (0.012)	0.13 (0.019)	254. (34.65)	96.6 (4.970)	0.04 (0.001)	0.05 (0.007)
3	#1	0.74 ** (0.032)	0.24 ** (0.009)	0.54 ** (0.015)	1.52 ** (0.040)	0.13 ** (0.007)	0.23 ** (0.011)	360. * (24.10)	192. (6.416)	4.10 (0.433)	14.2 (0.780)	27.7 (1.715)	0.14 (0.009)	0.13 (0.014)	154. (8.856)	91.7 * (5.793)	0.05 ** (0.001)	0.05 (0.007)
	#2	1.14 (0.058)	0.14 (0.011)	0.26 (0.016)	1.24 (0.060)	0.10 (0.004)	0.13 (0.006)	269. (35.50)	224. (29.63)	4.44 (0.170)	13.7 (0.792)	24.0 (1.447)	0.11 (0.020)	0.14 (0.035)	204. (41.82)	73.1 (6.588)	0.04 (0.001)	0.07 (0.021)
4	#1	0.56 ** (0.014)	0.21 ** (0.008)	0.45 ** (0.013)	1.25 ** (0.024)	0.14 ** (0.004)	0.14 ** (0.005)	699. ** (34.87)	164. (17.58)	2.31 (0.341)	14.3 (0.470)	13.6 * (1.130)	0.10 * (0.012)	0.19 (0.018)	186. (21.10)	55.6 (3.448)	0.04 ** (0.001)	0.05 (0.008)
	#2	0.99 (0.014)	0.14 (0.007)	0.32 (0.005)	1.01 (0.019)	0.09 (0.002)	0.10 (0.002)	379. (12.67)	142. (6.281)	2.50 (0.039)	13.4 (0.657)	16.3 (0.777)	0.07 (0.014)	0.16 (0.013)	156. (6.525)	62.0 (2.943)	0.03 (0.000)	0.05 (0.022)
5	#1	0.56 ** (0.017)	0.32 ** (0.013)	0.49 ** (0.029)	1.76 ** (0.110)	0.20 ** (0.012)	0.25 ** (0.019)	428. ** (20.87)	317. (71.70)	3.43 (0.390)	19.0 (0.679)	23.6 (1.764)	0.16 ** (0.015)	0.12 (0.015)	210. (53.86)	70.8 ** (4.267)	0.05 (0.002)	0.10 (0.031)
	#2	0.77 (0.058)	0.16 (0.018)	0.30 (0.026)	1.10 (0.074)	0.09 (0.007)	0.12 (0.007)	275. (24.76)	213. (32.69)	3.06 (0.140)	18.7 (1.272)	21.7 (1.061)	0.11 (0.010)	0.12 (0.013)	181. (29.87)	111. (6.494)	0.04 (0.003)	0.08 (0.009)
		BIGLEAF MAPLE PLOTS																
1	#1	0.82 ** (0.009)	0.24 ** (0.006)	0.90 ** (0.029)	1.66 (0.053)	0.22 ** (0.009)	0.27 ** (0.010)	422. ** (17.94)	568. ** (96.87)	6.83 ** (0.681)	23.5 (0.723)	37.6 ** (1.812)	0.22 * (0.027)	0.25 (0.039)	570. (183.7)	123. ** (14.41)	0.06 (0.003)	0.09 (0.011)
	#2	0.98 (0.052)	0.14 (0.005)	0.33 (0.010)	1.62 (0.022)	0.12 (0.004)	0.16 (0.003)	310. (26.10)	260. (30.23)	4.81 (0.184)	22.5 (0.644)	29.2 (1.357)	0.14 (0.028)	0.18 (0.039)	257. (51.52)	82.5 (6.874)	0.05 (0.001)	0.07 (0.016)
2	#1	0.83 ** (0.035)	0.32 ** (0.016)	1.00 ** (0.022)	2.00 ** (0.020)	0.32 ** (0.014)	0.25 ** (0.006)	644. ** (43.02)	249. (11.06)	3.75 ** (0.254)	20.8 (0.793)	46.3 ** (1.246)	0.15 ** (0.008)	0.13 ** (0.009)	172. (10.18)	93.4 (6.601)	0.06 ** (0.000)	0.08 ** (0.006)
	#2	1.07 (0.023)	0.14 (0.005)	0.31 (0.006)	1.74 (0.036)	0.12 (0.003)	0.16 (0.003)	403. (26.24)	236. (22.04)	4.99 (0.293)	21.9 (0.411)	36.2 (1.138)	0.06 (0.014)	0.06 (0.019)	178. (20.19)	108. (7.243)	0.05 (0.002)	0.04 (0.014)
3	#1	0.74 ** (0.039)	0.24 ** (0.012)	0.64 ** (0.016)	1.69 (0.055)	0.15 (0.007)	0.28 * (0.011)	361. (17.92)	251. (12.38)	5.84 (0.328)	18.6 (0.919)	36.3 (1.425)	0.17 (0.007)	0.15 (0.012)	202. (13.54)	132. ** (11.76)	0.05 (0.001)	0.07 (0.008)
	#2	1.17 (0.033)	0.16 (0.024)	0.30 (0.027)	1.82 (0.133)	0.14 (0.017)	0.20 (0.034)	294. (34.06)	229. (25.72)	8.52 (2.848)	22.8 (4.973)	36.1 (6.566)	1.06 (0.961)	1.29 (1.160)	193. (25.11)	84.6 (8.164)	0.10 (0.055)	0.73 (0.664)
4	#1	0.93 * (0.028)	0.22 ** (0.007)	1.07 ** (0.038)	1.70 ** (0.045)	0.52 ** (0.017)	0.22 ** (0.005)	485. ** (33.55)	262. (15.70)	5.84 ** (0.201)	14.3 ** (0.194)	70.3 ** (2.774)	0.14 (0.010)	0.11 ** (0.009)	148. * (10.96)	78.3 (4.171)	0.05 ** (0.001)	0.07 (0.007)
	#2	1.08 (0.063)	0.13 (0.005)	0.31 (0.015)	1.04 (0.156)	0.11 (0.004)	0.13 (0.004)	343. (29.61)	313. (76.60)	4.63 (0.493)	19.2 (0.732)	33.1 (3.495)	0.11 (0.022)	0.17 (0.022)	288. (65.52)	69.1 (4.835)	0.04 (0.002)	0.05 (0.009)
5	#1	0.80 ** (0.014)	0.37 ** (0.017)	1.09 ** (0.057)	2.64 ** (0.168)	0.29 ** (0.012)	0.41 ** (0.024)	246. ** (12.49)	172. (12.92)	3.33 (0.205)	9.69 ** (0.592)	63.7 ** (3.186)	0.21 ** (0.014)	0.09 (0.005)	100. ** (12.22)	91.9 * (5.053)	0.06 ** (0.003)	0.09 (0.009)
	#2	0.96 (0.036)	0.13 (0.007)	0.30 (0.010)	1.79 (0.060)	0.11 (0.002)	0.19 (0.007)	194. (11.73)	187. (18.09)	3.72 (0.266)	17.7 (0.708)	35.0 (2.132)	0.13 (0.019)	0.09 (0.009)	147. (14.22)	104. (3.816)	0.05 (0.001)	0.06 (0.011)

Note: Averages with a "*" adjacent to them indicate that the difference between maple and Douglas-fir is significant at the p=.10 level for that nutrient on that site. Averages with a "**" adjacent to them indicate that the difference between maple and Douglas-fir is significant at the p=.05 level for that nutrient on that site. Numbers in parentheses are standard errors for the individual plots.

Table 5. Element concentration of leaf component of litter in period I.

		N	P	K	Ca	S	Hg	Mn	Fe	Cu	B	Zn	Mo	Co	Al	Na	Se	Cd
		PERCENT	PERCENT	PERCENT	PERCENT	PERCENT	PERCENT	PPM	PPM	PPM	PPM	PPM	PPM	PPM	PPM	PPM	PPM	PPM
SITE 1	PLOT																	
	DF	0.70 ** (0.020)	0.23 (0.008)	0.60 ** (0.021)	1.16 ** (0.049)	0.13 ** (0.006)	0.15 ** (0.006)	523. ** (36.23)	320. ** (15.96)	3.12 ** (0.398)	26.7 ** (0.632)	20.2 ** (1.058)	0.14 ** (0.009)	0.16 ** (0.014)	293. (21.08)	107. (11.09)	0.04 ** (0.001)	0.06 ** (0.007)
	MA	0.82 (0.009)	0.24 (0.006)	0.90 (0.029)	1.66 (0.053)	0.22 (0.009)	0.27 (0.010)	422. (17.94)	568. (96.87)	6.83 (0.681)	23.5 (0.723)	37.6 (1.812)	0.22 (0.027)	0.25 (0.039)	570. (183.7)	123. (14.41)	0.06 (0.003)	0.09 (0.011)
2	DF	0.68 ** (0.017)	0.27 ** (0.002)	0.59 ** (0.019)	1.32 ** (0.029)	0.13 ** (0.002)	0.16 ** (0.003)	641. (21.86)	238. (6.313)	2.12 ** (0.251)	21.7 (0.333)	18.3 ** (2.693)	0.10 ** (0.008)	0.14 (0.009)	193. * (4.588)	78.8 * (2.755)	0.04 ** (0.000)	0.05 ** (0.005)
	MA	0.83 (0.035)	0.32 (0.016)	1.00 (0.022)	2.00 (0.020)	0.32 (0.014)	0.25 (0.006)	644. (43.02)	249. (11.06)	3.75 (0.254)	20.8 (0.793)	46.3 (1.246)	0.15 (0.008)	0.13 (0.009)	172. (10.18)	93.4 (6.601)	0.06 (0.000)	0.08 (0.006)
3	DF	0.74 (0.032)	0.24 (0.009)	0.54 ** (0.015)	1.52 ** (0.040)	0.13 (0.007)	0.23 ** (0.011)	360. (24.10)	192. ** (6.416)	4.10 ** (0.433)	14.2 ** (0.780)	27.7 ** (1.715)	0.14 ** (0.009)	0.13 (0.014)	154. ** (8.856)	91.7 ** (5.793)	0.05 * (0.001)	0.05 (0.007)
	MA	0.74 (0.039)	0.24 (0.012)	0.64 (0.016)	1.69 (0.055)	0.15 (0.007)	0.28 (0.011)	361. (17.92)	251. (12.38)	5.84 (0.328)	18.6 (0.919)	36.3 (1.425)	0.17 (0.007)	0.15 (0.012)	202. (13.54)	132. (11.76)	0.05 (0.001)	0.07 (0.008)
4	DF	0.56 ** (0.014)	0.21 (0.008)	0.45 ** (0.013)	1.25 ** (0.024)	0.14 ** (0.004)	0.14 ** (0.005)	699. ** (34.87)	164. ** (17.58)	2.31 ** (0.341)	14.3 (0.470)	13.6 ** (1.130)	0.10 ** (0.012)	0.19 ** (0.018)	186. (21.10)	55.6 ** (3.448)	0.04 ** (0.001)	0.05 (0.008)
	MA	0.93 (0.028)	0.22 (0.007)	1.07 (0.038)	1.70 (0.045)	0.52 (0.017)	0.22 (0.005)	485. (33.55)	262. (15.70)	5.84 (0.201)	14.3 (0.194)	70.3 (2.774)	0.14 (0.010)	0.11 (0.009)	148. (10.96)	78.3 (4.171)	0.05 (0.001)	0.07 (0.007)
5	DF	0.56 ** (0.017)	0.32 ** (0.013)	0.49 ** (0.029)	1.76 ** (0.110)	0.20 ** (0.012)	0.25 ** (0.019)	428. ** (20.87)	317. * (71.70)	3.43 (0.390)	19.0 ** (0.679)	23.6 ** (1.764)	0.16 ** (0.015)	0.12 * (0.015)	210. * (53.86)	70.8 ** (4.267)	0.05 ** (0.002)	0.10 (0.031)
	MA	0.80 (0.014)	0.37 (0.017)	1.09 (0.057)	2.64 (0.168)	0.29 (0.012)	0.41 (0.024)	246. (12.49)	172. (12.92)	3.33 (0.205)	9.69 (0.592)	63.7 (3.186)	0.21 (0.014)	0.09 (0.005)	100. (12.22)	91.9 (5.053)	0.06 (0.003)	0.09 (0.009)
Grand Mean	DF	0.65 * (0.037)	0.25 (0.018)	0.53 ** (0.028)	1.40 (0.105)	0.15 (0.013)	0.19 (0.022)	530. (63.39)	246. (31.92)	3.02 (0.363)	19.2 (2.355)	20.7 ** (2.387)	0.13 * (0.010)	0.15 (0.011)	207. (23.30)	80.8 (8.791)	0.05 ** (0.000)	0.06 (0.009)
Grand Mean	MA	0.82 (0.031)	0.28 (0.029)	0.94 (0.082)	1.94 (0.187)	0.30 (0.063)	0.29 (0.033)	432. (66.22)	300. (68.72)	5.12 (0.673)	17.4 (2.445)	50.8 (6.897)	0.18 (0.015)	0.15 (0.028)	238. (84.49)	103. (10.29)	0.06 (0.001)	0.08 (0.005)

Notes: Averages with a "*" adjacent to them indicate that the difference between maple and Douglas-fir is significant at the p=0.10 level for that nutrient on that site. Averages with a "**" adjacent to them indicate that the difference between maple and Douglas-fir is significant at the p=0.05 level for that nutrient on that site. Numbers in parentheses are standard errors for the individual plots or for the whole study.

1.66-2.64%, Mg 0.22-0.41% and Zn 36.3-70.3 ppm. The ranges for K and Zn do not overlap. Only manganese (Mn) showed a trend, with greater concentrations in the Douglas-fir litter with significant differences at three sites.

Weights of Nutrients in Litterfall

Average annual litterfall biomass values were significantly greater ($p < .05$) under maple (385 to 532 g/m²) than under Douglas-fir (256 to 407 g/m²) on all five sites (Table 3). Nutrient weights were calculated as the sum of the products of nutrient concentrations of leaf and twig components and the corresponding leaf or twig weights for each period. Average total weights of N, K, Ca, Mg, copper (Cu), boron (B), Zn, sulfur (S), and sodium (Na) in litter were significantly ($p < .05$) greater on the maple plots on all five sites and greater than Douglas-fir for every element on every site, except Cobalt (Co) on one site. The smallest mean nutrient weights for maple from the five sites were greater than the greatest averages for Douglas-fir (Table 3).

Despite the substantial quantities of Douglas-fir litter present in the maple plot traps during autumn and winter and the green, non-nodal branches in the Douglas-fir traps in the autumn, weights of nitrogen were significantly ($p < .05$) greater in the litter under maple (3.55 to 4.68 g/m²) than in the litter under Douglas-fir (1.82 to 3.18 g/m²) on all five sites. Examples of ranges of nutrient

weights for Douglas-fir and maple plots respectively were: N 1.82-3.18 and 3.55-4.68, P 0.41-0.60 and 0.68-1.38, K 0.84-1.25 and 1.51-3.82, Ca 2.62-4.13 and 6.01-11.9, Mg 0.33-0.55 and 0.73-1.61 g/m². Total Mo was significantly ($p < .05$) greater in the litterfall under bigleaf maple on 4 of the 5 sites and the smallest means for those elements under maple were larger than the greatest means for litter under Douglas-fir.

Forest Floor: Weight and Composition

Differences in forest floor weights between Douglas-fir and maple plots were inconsistent and much more variable than were weights of litterfall. On site #4, forest floor weight was significantly ($p < .05$) greater under maple; on site #5, it was significantly ($p < .10$) greater under Douglas-fir, and on the other sites there were no significant differences (Table 6). Both plots on site 5 had substantially heavier forest floors compared to the other sites, probably a reflection of both the greater litter input and the slower rate of decomposition on this moisture-limited site. The forest floor samples consisted primarily of maple leaves and Douglas-fir needles with 20-35% woody material by weight.

Table 6. Forest floor weights and element weights of leaves and twigs combined.

SITE	PLOT	WEIGHT	N	P	K	Ca	S	Hg	Mn	Fe	Cu	B	Zn	Mo	Co	Al	Na	Se	Cd
		G/M ²	G/M ²	G/M ²	G/M ²	G/M ²	G/M ²	G/M ²	G/M ²	G/M ²	MG/M ²	MG/M ²	MG/M ²	MG/M ²	MG/M ²	G/M ²	MG/M ²	MG/M ²	MG/M ²
1	DF	1570	12.6	1.44	2.90	15.5	1.79	2.74	1.31	9.35	19.7	16.3	42.7	2.56	6.81 *	14.8	87.4	0.21	1.25
		(277.1)	(2.418)	(0.265)	(0.519)	(3.248)	(0.344)	(0.543)	(0.385)	(2.207)	(3.554)	(2.830)	(9.068)	(0.517)	(1.613)	(3.190)	(14.20)	(0.043)	(0.244)
	MA	1437	14.8	1.44	2.91	20.6	1.99	2.58	0.99	5.94	16.1	19.8	49.6	1.71	3.12	9.58	75.4	0.16	0.79
		(108.2)	(1.686)	(0.118)	(0.277)	(2.499)	(0.213)	(0.271)	(0.153)	(0.690)	(1.584)	(2.601)	(7.927)	(0.157)	(0.523)	(0.955)	(10.99)	(0.016)	(0.086)
2	DF	1487	11.2 *	1.56	3.15	15.4 **	1.67 **	2.56 **	1.92	11.4	26.6	16.8 **	45.6 **	3.15 *	10.1 **	16.0	80.4 *	0.24	1.44
		(117.4)	(1.418)	(0.144)	(0.184)	(1.274)	(0.137)	(0.178)	(0.276)	(1.555)	(2.208)	(1.426)	(4.195)	(0.281)	(1.375)	(1.579)	(8.105)	(0.021)	(0.149)
	MA	1845	18.8	1.88	3.93	31.6	2.92	3.61	1.71	10.0	26.7	25.2	76.0	2.45	6.19	12.7	116.	0.23	1.43
		(227.2)	(3.441)	(0.208)	(0.489)	(4.663)	(0.409)	(0.429)	(0.259)	(0.933)	(2.673)	(3.347)	(11.86)	(0.268)	(0.618)	(1.252)	(16.73)	(0.024)	(0.157)
3	DF	1473	14.3 **	1.55 *	2.78	15.7	1.81 *	2.38	0.97	8.39	34.3	14.8	47.8	1.75	4.56	7.81	66.0	0.15	0.97
		(130.8)	(1.258)	(0.155)	(0.205)	(1.361)	(0.139)	(0.241)	(0.195)	(1.572)	(6.736)	(1.563)	(6.661)	(0.237)	(0.657)	(1.208)	(7.139)	(0.021)	(0.154)
	MA	1208	9.85	1.12	2.32	12.8	1.38	1.97	0.78	7.80	33.2	12.9	38.9	1.60	3.80	8.06	50.4	0.14	0.83
		(142.9)	(1.435)	(0.159)	(0.289)	(1.217)	(0.190)	(0.300)	(0.157)	(1.762)	(7.141)	(1.899)	(5.048)	(0.412)	(0.863)	(1.989)	(14.65)	(0.028)	(0.190)
4	DF	1621 **	13.4	1.51	2.40	14.8	1.82	1.78	1.30 **	7.66 *	45.6 **	14.6	44.4	1.61 *	6.76 **	9.04	54.7 **	0.15	0.98
		(85.00)	(0.559)	(0.090)	(0.148)	(0.572)	(0.074)	(0.126)	(0.165)	(1.294)	(7.149)	(1.207)	(2.342)	(0.262)	(1.265)	(1.464)	(6.195)	(0.020)	(0.113)
	MA	1234	11.6	1.57	2.16	15.8	1.69	1.70	0.74	4.92	27.1	12.6	49.3	1.03	2.97	6.22	35.3	0.11	0.77
		(150.0)	(1.649)	(0.444)	(0.237)	(1.768)	(0.231)	(0.217)	(0.081)	(0.567)	(2.813)	(1.605)	(5.674)	(0.121)	(0.325)	(0.704)	(4.588)	(0.012)	(0.091)
5	DF	2653 *	26.8 **	2.50 **	4.74 **	33.0 **	3.65 **	4.41 **	1.40	15.9	66.4	31.8 **	90.6 **	2.67	5.55	11.8	152.	0.27 **	1.62
		(176.6)	(1.907)	(0.136)	(0.250)	(2.557)	(0.283)	(0.290)	(0.074)	(0.776)	(4.587)	(2.516)	(6.247)	(0.224)	(0.410)	(0.930)	(24.54)	(0.017)	(0.128)
	MA	3083	42.3	3.69	6.15	69.2	6.55	7.41	1.43	14.7	72.5	49.5	150.	2.58	5.20	10.9	162.	0.34	1.90
		(140.0)	(3.283)	(0.160)	(0.316)	(4.366)	(0.324)	(0.487)	(0.170)	(2.196)	(7.628)	(2.353)	(10.95)	(0.300)	(0.742)	(1.519)	(13.55)	(0.023)	(0.221)
Grand Mean	DF	1761	15.7	1.71	3.19	18.9	2.15	2.78	1.38	10.5	38.5	18.9	54.2	2.35	6.77	11.9	88.3	0.20	1.25
		(224.6)	(2.835)	(0.198)	(0.405)	(3.536)	(0.375)	(0.438)	(0.152)	(1.488)	(8.184)	(3.258)	(9.133)	(0.290)	(0.950)	(1.586)	(17.11)	(0.024)	(0.126)
Grand Mean	MA	1761	19.5	1.94	3.49	30.0	2.91	3.45	1.13	8.69	35.1	24.0	72.9	1.87	4.26	9.51	87.8	0.19	1.14
		(349.5)	(5.918)	(0.453)	(0.734)	(10.31)	(0.947)	(1.041)	(0.190)	(1.754)	(9.745)	(6.799)	(20.38)	(0.287)	(0.623)	(1.125)	(23.03)	(0.039)	(0.225)

Note: Averages with a "*" adjacent to them indicate that the difference between maple and Douglas-fir is significant at the p=.10 level for that nutrient on that site. Averages with a "**" adjacent to them indicate that the difference between maple and Douglas-fir is significant at the p=.05 level for that nutrient on that site. Numbers in parentheses are standard errors for the individual plots or for the whole study.

Forest Floor: Nutrient Concentrations and Weights

The forest floor nutrient concentrations were also quite variable (Table 7). Maple forest floor contained significantly ($p < .05$) greater concentrations of Ca, Mg, Zn and S on four sites. Despite the much greater annual input of N and K in the bigleaf maple litterfall, the concentrations in the forest floor were not consistently, significantly greater. Ranges of average nutrient concentrations of the leaf component of the forest floor for Douglas-fir and maple were : N .79 to 1.16 and 0.91 to 1.49%, K 0.15 to .23 and .18 to .22%, Ca .98 to 1.36 and 1.11 to 2.41 and Mg .13 to .20 and .15 to .26%.

There were few significant differences in weights of elements in the forest floors except for Mo and Co which were always greater under Douglas-fir. For other than these elements, there were no apparent trends towards differences in weights for any nutrient (Table 6). For example, N content ranged from 11.2 to 26.8 g/m² under Douglas-fir and 9.9 to 42.3 g/m² under maple while the corresponding values for P were 1.44 to 2.5 and 1.12 to 3.69 g/m².

The variability of the weights of elements in the forest floors was much greater than that in the litterfall samples. For example, the coefficients of variation of forest floor weight were 1.4 to 3.5 times greater than those for litterfall weight and the coefficients of variation for N in the forest floor were 1.6 to 5 times more variable than

Table 7. Forest floor element concentrations of leaf component.

		N	P	K	Ca	Mg	Mn	Fe	Cu	B	Zn	S	Al	Mo	Na	Se	Cd	Co
		PERCENT	PERCENT	PERCENT	PERCENT	PERCENT	PPM	PPM	PPM	PPM	PPM	PERCENT	PPM	PPM	PPM	PPM	PPM	PPM
SITE 1	DF	0.88 ** (0.057)	0.10 * (0.005)	0.20 ** (0.007)	1.00 ** (0.080)	0.19 (0.009)	938. (112.8)	7025 (797.7)	14.6 (1.216)	11.5 ** (0.518)	27.5 ** (1.010)	0.12 ** (0.009)	1140 (1259.)	1.98 * (0.193)	58.8 (6.418)	0.16 (0.011)	0.97 (0.145)	5.35 ** (0.910)
	MA	1.13 (0.057)	0.11 (0.003)	0.22 (0.005)	1.48 (0.047)	0.20 (0.005)	918. (106.7)	5520 (378.2)	13.3 (0.484)	14.9 (0.690)	35.1 (2.957)	0.15 (0.007)	9017 (553.4)	1.59 (0.086)	53.6 (5.590)	0.14 (0.006)	0.72 (0.061)	3.00 (0.502)
2	DF	0.79 (0.077)	0.11 (0.005)	0.23 (0.011)	1.02 ** (0.054)	0.19 ** (0.005)	1512 ** (108.9)	9132 ** (633.2)	20.8 ** (0.845)	12.3 * (0.880)	31.6 ** (1.052)	0.12 ** (0.006)	1301 ** (733.8)	2.55 ** (0.137)	58.0 (6.979)	0.19 ** (0.008)	1.16 (0.104)	8.28 ** (0.796)
	MA	1.00 (0.140)	0.11 (0.003)	0.22 (0.005)	1.74 (0.103)	0.21 (0.006)	1092 (113.8)	6775 (593.7)	16.8 (1.089)	14.3 (0.476)	42.2 (3.297)	0.16 (0.008)	8787 (973.6)	1.68 (0.207)	67.5 (4.950)	0.14 (0.008)	0.95 (0.080)	4.24 (0.484)
3	DF	1.07 ** (0.034)	0.11 (0.003)	0.20 (0.010)	1.13 (0.039)	0.18 (0.005)	772. (80.90)	6673 * (584.3)	26.4 ** (2.553)	11.3 (0.551)	33.1 (1.917)	0.13 (0.004)	6399 ** (458.0)	1.46 (0.125)	47.7 (4.493)	0.11 ** (0.006)	0.75 * (0.063)	3.79 (0.323)
	MA	0.91 (0.056)	0.11 (0.006)	0.22 (0.012)	1.11 (0.038)	0.19 (0.007)	979. (127.0)	9384 (1194.)	38.4 (4.577)	11.8 (0.836)	37.4 (2.025)	0.12 (0.005)	9632 (1282.)	1.86 (0.221)	42.8 (6.869)	0.15 (0.014)	0.97 (0.082)	4.73 (0.623)
4	DF	1.01 (0.044)	0.11 (0.004)	0.15 ** (0.005)	0.98 ** (0.012)	0.13 ** (0.007)	1116 ** (91.43)	6768 (912.3)	39.4 (5.088)	10.1 * (0.538)	26.3 ** (1.043)	0.13 ** (0.003)	8086 (1064.)	1.43 (0.183)	33.1 (3.300)	0.12 (0.013)	0.87 (0.088)	5.96 * (0.873)
	MA	1.10 (0.036)	0.12 (0.015)	0.18 (0.007)	1.25 (0.030)	0.15 (0.002)	847. (39.60)	5879 (399.2)	31.4 (2.355)	11.3 (0.329)	42.0 (2.013)	0.15 (0.005)	7558 (515.8)	1.23 (0.077)	29.9 (1.310)	0.12 (0.005)	0.93 (0.041)	3.85 (0.517)
5	DF	1.16 ** (0.034)	0.11 ** (0.002)	0.19 (0.005)	1.36 ** (0.046)	0.20 ** (0.005)	717. * (53.67)	8212 ** (433.1)	33.1 (1.717)	13.4 ** (0.343)	37.8 ** (1.386)	0.15 ** (0.005)	6105 ** (383.4)	1.35 ** (0.083)	61.7 (7.644)	0.12 (0.006)	0.81 (0.038)	2.86 ** (0.139)
	MA	1.49 (0.078)	0.13 (0.005)	0.20 (0.004)	2.41 (0.088)	0.26 (0.008)	540. (64.48)	5600 (829.8)	26.9 (3.107)	17.1 (0.218)	52.4 (3.636)	0.23 (0.009)	4187 (618.7)	0.97 (0.121)	53.6 (3.253)	0.12 (0.008)	0.71 (0.080)	2.00 (0.296)
Grand Mean	DF	0.98 (0.066)	0.11 (0.002)	0.19 (0.011)	1.10 (0.071)	0.18 (0.012)	1011 (143.2)	7562 (479.4)	26.8 (4.374)	11.7 (0.554)	31.2 * (2.057)	0.13 (0.006)	9003 (1376.)	1.75 (0.228)	51.8 (5.244)	0.14 (0.013)	0.91 (0.071)	5.25 (0.936)
Grand Mean	MA	1.13 (0.099)	0.12 (0.003)	0.21 (0.007)	1.60 (0.229)	0.20 (0.017)	875. (92.91)	6632 (723.2)	25.4 (4.629)	13.9 (1.056)	41.8 (2.973)	0.16 (0.018)	7836 (972.5)	1.47 (0.160)	49.5 (6.269)	0.13 (0.006)	0.86 (0.057)	3.56 (0.483)

Note: Averages with a "*" adjacent to them indicate that the difference between maple and Douglas-fir is significant at the p=.10 level for that nutrient on that site. Averages with a "**" adjacent to them indicate that the difference between maple and Douglas-fir is significant at the p=.05 level for that nutrient on that site. Numbers in parentheses are standard errors for the individual plots or for the whole study.

Table 8. Coefficients of variation comparisons for biomass and macro-nutrients.

COMPONENT	Douglas-fir Plots		:	bigleaf maple plots	
	FOREST FLOOR	LITTER		FOREST FLOOR	LITTER
BIOMASS	.36	.25	:	.56	.16
N	.50	.31	:	.85	.15
P	.32	.19	:	.66	.38
K	.35	.20	:	.59	.43
Ca	.53	.25	:	.97	.37
Mg	.45	.27	:	.85	.47

in the litterfall samples (Table 8).

Forest Floor Biomass and Nutrient Turnover Rates

Calculated turnover time (Olsen, 1963) for the forest floor biomass was significantly ($p < .05$) longer for material from beneath Douglas-fir on 4 sites, ranging from 4.2 to 10.9 years, while for maple it was 2.5 to 5.9 years (Table 9). Turnover time is apparently slower under Douglas-fir for most nutrients on most sites and most differences are significant. Potassium, the nutrient with the most rapid cycling, apparently "recycles" in 2 to 6 years under Douglas-fir and in only 0.7 to 1.7 years under maple. Turnover rates for nitrogen, Ca and Mg generally paralleled rates for total biomass, while rates for P and K were more rapid.

Bulk Density

Bulk density of the mineral soil was lower under maple on every site; however, the differences were significant ($p < .05$) on only two sites because of high variability and the small magnitude of the differences. Much of the variability can be attributed to the activity of small rodents, probably gophers (*Thomomys* sp.) and voles (*Microtus* sp.) on many of the plots. The surface soil under both species was permeated by a network of tunnels and the resulting mixing in the upper layers made the soil very heterogeneous. While samples were taken with scrupulous care to avoid tunnels,

Table 9. Forest floor biomass and element turnover rate for leaf and twig components.

SITE	PLDT	WEIGHT	N	P	K	Ca	S	Mg	Mn	Fe	Cu	B	Zn	Mo	Co	Al	Na	Se	Cd
		YRS	YRS	YRS	YRS	YRS	YRS	YRS	YRS	YRS	YRS	YRS	YRS	YRS	YRS	YRS	YRS	YRS	YRS
1	DF	5.89 ** (0.851)	5.98 * (0.893)	3.38 ** (0.463)	2.81 ** (0.398)	5.16 * (0.849)	5.79 ** (0.826)	8.16 ** (1.356)	13.2 * (2.677)	101. ** (24.19)	23.1 ** (4.085)	2.88 (0.419)	6.45 ** (0.998)	75.0 ** (14.19)	131. ** (33.58)	169. ** (38.51)	3.49 ** (0.440)	19.6 ** (3.505)	41.4 ** (9.180)
	HA	3.02 (0.391)	3.75 (0.554)	1.95 (0.257)	1.27 (0.170)	3.15 (0.499)	2.96 (0.435)	3.10 (0.459)	7.67 (1.557)	28.1 (3.921)	6.65 (0.977)	2.08 (0.336)	3.18 (0.658)	22.2 (3.539)	29.9 (5.809)	46.2 (12.34)	1.73 (0.269)	6.89 (0.883)	13.2 (1.253)
2	DF	4.95 (0.638)	4.87 (0.748)	3.18 * (0.498)	2.78 ** (0.312)	4.45 (0.484)	5.04 * (0.646)	7.03 * (0.929)	16.7 (3.568)	96.9 (19.93)	24.4 ** (3.229)	3.04 (0.331)	5.68 (0.853)	113. ** (9.730)	152. ** (27.67)	155. * (23.79)	2.95 (0.195)	19.1 ** (2.659)	87.1 (14.43)
	HA	4.29 (0.477)	5.11 (0.885)	2.20 (0.158)	1.68 (0.152)	4.65 (0.624)	3.52 (0.403)	4.85 (0.474)	9.86 (1.088)	69.9 (8.093)	14.6 (1.388)	3.11 (0.354)	4.40 (0.606)	51.3 (4.496)	84.1 (7.524)	107. (12.34)	2.98 (0.460)	10.6 (1.088)	63.9 (9.925)
3	DF	4.24 * (0.317)	4.53 ** (0.408)	2.57 ** (0.252)	2.26 * (0.208)	3.81 ** (0.293)	4.45 ** (0.291)	4.29 ** (0.437)	10.3 (2.046)	88.1 (14.17)	23.7 (5.240)	3.20 ** (0.258)	5.19 ** (0.733)	48.3 (7.905)	100. * (14.88)	105. (16.78)	2.56 (0.293)	9.96 (1.185)	28.2 (4.881)
	HA	3.17 (0.428)	2.68 (0.484)	1.68 (0.284)	1.57 (0.253)	2.18 (0.263)	2.70 (0.469)	2.64 (0.501)	7.46 (1.658)	74.4 (17.94)	14.0 (3.753)	1.88 (0.383)	2.97 (0.442)	28.1 (8.967)	55.2 (15.25)	94.5 (23.59)	1.65 (0.634)	6.78 (1.827)	26.3 (7.720)
4	DF	4.18 ** (0.470)	4.35 ** (0.317)	2.62 (0.218)	1.99 ** (0.209)	3.85 ** (0.337)	4.22 ** (0.297)	4.18 ** (0.283)	9.07 ** (1.013)	72.6 ** (9.627)	34.6 ** (3.866)	2.92 ** (0.211)	5.58 ** (0.500)	33.5 ** (4.823)	70.5 ** (11.68)	81.3 (9.685)	2.47 ** (0.382)	9.35 ** (0.933)	29.4 (3.470)
	HA	2.48 (0.327)	2.65 (0.430)	1.80 (0.479)	0.70 (0.109)	2.50 (0.351)	1.21 (0.210)	2.12 (0.342)	3.99 (0.512)	40.2 (5.806)	11.4 (1.584)	1.70 (0.224)	2.23 (0.354)	16.3 (2.312)	35.6 (2.952)	65.7 (8.273)	1.09 (0.166)	5.01 (0.665)	22.4 (3.260)
5	DF	10.9 ** (1.303)	16.0 ** (2.305)	5.67 ** (0.618)	5.99 ** (0.638)	12.9 ** (1.315)	14.2 ** (1.708)	12.7 ** (1.222)	22.1 ** (1.813)	249. ** (31.22)	78.1 ** (9.486)	8.06 (0.902)	17.7 ** (2.263)	105. ** (8.886)	204. ** (17.60)	244. * (33.14)	7.53 ** (1.086)	29.6 ** (2.309)	102. ** (13.75)
	HA	5.89 (0.367)	9.24 (0.887)	2.74 (0.226)	1.66 (0.135)	6.02 (0.622)	6.14 (0.544)	4.72 (0.464)	13.3 (1.614)	137. (27.07)	36.6 (4.716)	7.60 (0.567)	5.76 (0.488)	29.3 (3.991)	112. (20.58)	152. (28.15)	3.43 (0.294)	10.9 (0.770)	46.4 (10.56)
Grand Mean	DF	6.04 (1.269)	7.15 (2.235)	3.48 (0.569)	3.16 (0.722)	6.05 (1.745)	6.76 (1.902)	7.27 (1.561)	14.3 (2.361)	121. (32.35)	36.8 (10.54)	4.02 (1.011)	8.13 (2.410)	75.2 * (15.86)	131. (22.74)	151. (28.27)	3.80 (0.949)	17.5 (3.733)	57.6 (15.44)
Grand Mean	HA	3.77 (0.606)	4.69 (1.224)	2.07 (0.187)	1.38 (0.183)	3.70 (0.718)	3.31 (0.804)	3.49 (0.553)	8.46 (1.539)	69.9 (18.91)	16.7 (5.188)	3.27 (1.108)	3.71 (0.620)	29.5 (5.942)	63.5 (15.55)	93.4 (18.34)	2.18 (0.440)	8.05 (1.167)	34.5 (9.149)

Note: Averages with a "*" adjacent to them indicate that the difference between maple and Douglas-fir is significant at the p=.10 level for that nutrient on that site.
Averages with a "**" adjacent to them indicate that the difference between maple and Douglas-fir is significant at the p=.05 level for that nutrient on that site.
Numbers in parentheses are standard errors for the individual plots or for the whole study.

their effect could not be completely eliminated. The presence of rodent tunnels in some samples may account for the low bulk density values encountered (Table 10). For example, bulk density averaged from 0.69 to 0.88 g/cm³ under Douglas-fir and 0.63 to 0.84 g/cm³ under bigleaf maple.

Chemical Properties of A1 Horizons of Mineral Soil

As with the litter and forest floor components, both concentrations and total nutrient weights are important for developing an understanding of the nutrient dynamics of the system, hence both are reported here (Tables 11 and 12). The nutrient weights are calculated as the products of concentrations in the soil and bulk densities.

Nitrogen concentration is significantly greater ($p < 0.1$) under maple at all sites (valid for $p < 0.05$ at four sites), ranging from .14 to .23 % under Douglas-fir and from .21 to 0.28% under maple. On a weight basis, there is more nitrogen in the top ten cm of soil under maple on all sites, though the differences are significant on only three. Weights of N in the top 10 cm of mineral soil ranged from 1140 to 1790 kg/ha on the five Douglas-fir plots and 1560 to 1970 kg/ha on the five maple plots (Table 12).

The concentration of mineralizable nitrogen was greater under maple on all five sites, and on a weight basis it was greater on four of them. Since only one sample per plot was analyzed for mineralizable N (Table 11), it is impossible to

Table 10. Soil C:N ratio, pH, Cation exchange capacity (CEC), base saturation (BS), and bulk density (BD) in top 10 cm of mineral soil.

SITE	PLOT	C:N	pH	CEC	BS	BD
				meq/100	%	g/cc
1	DF	19.5	6.32 **	34.4	75.5 **	0.72 **
		(0.866)	(0.047)	(1.454)	(1.322)	(0.027)
	MA	17.5	6.60	37.6	89.0	0.63
		(0.288)	(0.081)	(1.235)	(2.943)	(0.012)
2	DF	20.2	6.20	34.1	68.0	0.79 **
		(0.629)	(0.040)	(1.075)	(2.738)	(0.014)
	MA	19.5	6.32	38.2	77.5	0.66
		(0.288)	(0.062)	(2.192)	(5.545)	(0.030)
3	DF	19.7		34.6 **	77.5 *	0.69
		(0.478)	not	(0.512)	(5.795)	(0.020)
	MA	21.2	available	41.2	64.5	0.67
		(1.030)		(1.383)	(3.329)	(0.014)
4	DF	20.7 **	5.90	33.8 *	64.0 **	0.75
		(0.478)	(0.040)	(0.699)	(2.857)	(0.010)
	MA	28.5	5.75	39.2	41.0	0.70
		(3.068)	(0.086)	(2.268)	(0.912)	(0.047)
5	DF	19.5 *	6.40 **	39.5	86.0	0.88
		(0.866)	(0.040)	(1.190)	(3.219)	(0.085)
	MA	17.0	6.67	40.3	88.2	0.84
		(0.707)	(0.062)		(3.759)	(0.075)
Grand Mean	DF	19.9	6.21	35.5	72.0	0.77
		(0.242)	(0.110)	(0.998)	(5.534)	(0.032)
Grand Mean	MA	20.7	6.34	35.8	85.6	0.70
		(2.079)	(0.210)	(2.128)	(16.74)	(0.036)

Note: Averages with a "*" adjacent to them indicate that the difference between maple and Douglas-fir is significant at the $p=.10$ level for that nutrient on that site.

Averages with a "**" adjacent to them indicate that the difference between maple and Douglas-fir is significant at the $p=.05$ level for that nutrient on that site.

Numbers in parantheses are standard errors for the individual plot or for the whole study.

Table 11. Concentrations of nutrients in top 10 cm of mineral soil.

SITE	PLOT	C %	TOTAL N %	MIN. N ppm	P ppm	K ppm	Ca ppm	Mg ppm
1	DF	3.08 ** (0.189)	0.15 ** (0.004)	18.9	756. ** (23.66)	628. ** (42.01)	3527 ** (70.71)	814. (53.65)
	MA	4.45 (0.319)	0.25 (0.014)	20.1	1018 (53.40)	1011 (28.31)	4749 (354.5)	887. (19.18)
2	DF	3.93 ** (0.115)	0.19 ** (0.002)	18.7	1000 (10.20)	565. ** (36.02)	3366 ** (144.2)	613. ** (4.819)
	MA	4.56 (0.044)	0.23 (0.002)	24.8	1075 (60.38)	786. (53.21)	4078 (120.5)	835. (20.56)
3	DF	4.26 ** (0.191)	0.21 * (0.011)	22.9	1762 (26.02)	296. * (36.09)	3507 (173.6)	1041 (120.4)
	MA	5.30 (0.214)	0.25 (0.002)	32.5	1706 (51.41)	668. (151.1)	3352 (145.8)	985. (83.91)
4	DF	4.91 ** (0.099)	0.23 ** (0.004)	18.8	1756 (37.32)	522. (46.16)	2930 ** (139.1)	689. (12.96)
	MA	8.23 (1.264)	0.28 (0.015)	53.3	1706 (6.250)	543. (41.14)	2225 (92.42)	433. (15.99)
5	DF	2.89 (0.237)	0.14 ** (0.008)	14.4	1162 ** (23.93)	344. (39.58)	4729 (183.1)	1145 (5.837)
	MA	3.58 (0.339)	0.21 (0.011)	15.7	1312 (16.13)	478. (57.19)	4864 (318.2)	1212 (47.45)
Grand Mean	DF	3.81 (0.373)	0.19 * (0.016)		1287 (203.2)	454. (63.24)	3537 (346.8)	836. (113.8)
Grand Mean	MA	5.22 (0.799)	0.24 (0.011)		1363 (148.2)	695. (95.59)	3894 (455.2)	865. (131.9)

Note: Averages with a "*" adjacent to them indicate that the difference between maple and Douglas-fir is significant at the $p=.10$ level for that nutrient on that site.

Averages with a "**" adjacent to them indicate that the difference between maple and Douglas-fir is significant at the $p=.05$ level for that nutrient on that site.

Numbers in parentheses are standard errors for the individual plots or for the whole study.

Table 12. Weights of nutrients in top 10 cm of mineral soil.

SITE	PLOT	C	TOTAL N	MIN. N	P	K	Ca	Mg
		g/m ²	g/m ²	g/m ²	g/m ²	g/m ²	g/m ²	g/m ²
1	DF	2228. *	114. **	1.380	54.8 *	45.4 **	256.3	59.2
	MA	2814. (60.43)	159. (3.49)	1.327	64.3 (1.167)	63.7 (2.030)	299.5 (9.251)	55.8 (4.601)
2	DF	3100. (55.81)	152. (2.05)	1.421	78.9 (1.570)	44.5 (2.430)	265.5 (8.783)	48.4 *
	MA	3034. (142.07)	156. (7.73)	1.711	71.7 (6.106)	52.5 (5.282)	270.5 (10.73)	55.5 (2.825)
3	DF	2964. **	149. **	1.557	122.8	20.8 *	244.2	72.5
	MA	3597. (60.99)	171. (5.89)	2.308	115.7 (2.360)	45.1 (2.841)	227.7 (11.47)	66.7 (8.179)
4	DF	3722. **	179. (5.20)	1.429	133.0 (3.121)	39.6 (3.968)	222.4 **	52.2 **
	MA	5622. (654.64)	197. (7.59)	3.838	119.4 (8.368)	37.6 (2.113)	155.3 (10.79)	30.4 (2.564)
5	DF	2504. **	128. **	0.907	102.6	29.7	413.9	101.3
	MA	2937. (94.00)	176. (7.92)	1.178	110.4 (9.481)	40.4 (3.095)	403.4 (28.14)	100.9 (9.851)
Grand Mean	DF	2904. (257.69)	144. (11.18)		98.4 (14.28)	34.7 (4.643)	274.8 (36.89)	64.9 (10.40)
Grand Mean	MA	3601. (522.77)	172. (7.36)		96.3 (11.70)	47.7 (4.758)	274.3 (38.91)	61.3 (11.82)

Note: Averages with a "*" adjacent to them indicate that the difference between maple and Douglas-fir is significant at the p=.10 level for that nutrient on that site.

Averages with a "**" adjacent to them indicate that the difference between maple and Douglas-fir is significant at the p=.05 level for that nutrient on that site.

Numbers in parantheses are standard errors for the individual plots or for the whole study.

establish significant differences; however, the consistency of the trend and the large difference at some sites indicates that more intensive sampling of this soil property could result in detection of significant differences.

The strongest differences in cation contents were found for K, which averaged 21 to 45 g/m² under Douglas-fir and 37 to 64 g/m² under maple (Table 12). Concentration of K (Table 11) was significantly greater under maple at the .05 level at two sites and at the .10 level at another. On the basis of total nutrient weight, K was more abundant under maple on four sites, but significantly so on only one at the 0.05 level and one at the .01 level.

There were no consistent trends for Ca or Mg on either a concentration or weight basis. For example, on site #2, Mg was significantly ($p < .10$) greater under maple at 56 g/m² vs. 48 g/m² while on site #4, the comparison was 28 g/m² for maple and 43 g/m² for Douglas-fir and no statistically significant difference at the .1 level. The high variation in most bases and the closeness in values for some of them preclude conclusive comparisons. Values for P also have high variability and no statistically significant differences.

Total carbon concentration, an index of organic matter, was greater under maple on all sites, significantly so ($p < .05$) on four. Douglas-fir plots had 2.9 to 4.9 % C while maple plots had 3.6 to 8.2 % C in the soil. There was

22,200 to 37,200 kg/ha of C in the top 10 cm under Douglas-fir and 28,100 to 56,200 kg/ha under bigleaf, maple and there was more total carbon under maple on four sites (3 for $p < 0.05$; 1 for $p < 0.10$). The C:N ratio was significantly ($p < .05$) greater under maple on site #4, significantly ($p < .10$) greater under Douglas-fir on site #5 and not significantly different between species on the other sites.

Cation exchange capacities (CECs) were slightly greater on the maple plots and base saturation did not differ consistently (Table 10).

DISCUSSION

The data lead us to conclude that bigleaf maple has a dramatic effect on the dynamics of nutrient cycling by circulating more biomass with greater concentrations of some nutrients through the forest-soil system. The total litterfall biomass and nutrient content were generally greater than those found in other studies (Rickard, 1975; Tarrant and Chandler, 1951) for both Douglas-fir and bigleaf maple, probably because of site differences and our method of stratifying litter samples by time period, prior to nutrient analysis.

Not surprisingly, considering the similar results reported for other hardwood/conifer comparisons (Challinor, 1968; MacLean and Wein, 1978; Gessel and Turner, 1974; Tappeiner and Alm, 1975), maple litter is richer in bases, and is decomposed more rapidly, presumably a result of lower lignin content compared to Douglas-fir litter. The extremely slow (>100 years) turnover rates calculated for Al and Fe indicate an accumulation in the forest floor beyond the contribution of litterfall, since the stands in the study were not much older than 50 years.

Large concentrations of both cations are common at the soil surface, especially on soils derived from mafic parent material (Bohn, et al, 1979) and it is likely that the forest floor samples became enriched in these elements

through 1) the mixing activity of rodents, 2) translocation from roots in the soil to roots in the forest floor, or 3) from inclusion of small amounts of mineral soil during sample collection.

Total forest floor biomass weights and nutrient weights and concentrations on our Douglas-fir plots were within the ranges reported by others (Youngberg, 1966; Grier and McColl 1971; Cole et al, 1968). The strong, consistent differences in nutrient content of the litterfall were not found in the forest floor. This may be partly attributable to the high variability which characterized the forest floor weights and nutrient contents; however, site specific factors may also be the cause.

The presence of moss in the forest floor samples on some plots could complicate the nutrient dynamics by retaining nutrients that would otherwise become incorporated into the soil. Some of the variability could be due to differences in the rates of decomposition among sites. On some sites, tree roots were observed in the forest floor layer; they certainly withdraw some nutrients directly from the forest floor. When subjected to the strong leaching action of winter rains, highly mobile elements in the forest floor, like K and Na, might be expected to remain only in small amounts with little difference between forest floor types; the data confirm this.

Even though the mass of forest floor was greater under

maple on some sites and under Douglas-fir on others, the turnover was uniformly more rapid under bigleaf maple. The rapid turnover under maple helps explain the lack of consistent differences in the forest floor. The rapid cycling rates of maple litter could benefit surrounding Douglas-fir trees by making bases more readily available to the tree roots instead of being sequestered in the forest floor.

Even though there were no discernable differences in the forest floor, maple did affect some soil properties in the top 10 cm of soil. Organic matter, N content and CEC were greater under maple, probably because of the heavier input of litter and the more rapid incorporation of residues under this species. It is likely that the presence of more soil organic matter contributes to the trend towards lower bulk density under maple.

The presence of larger quantities of N in the soils under maple was consistent and significant, ranging from 40 to 400 additional kg/ha compared with Douglas-fir and representing an increase of 3 to 38%. Perhaps the roots of bigleaf maple access a larger volume of soil either from a larger area or from deeper soil horizons and the greater N values are a consequence of concentration of litterfall in the smaller zone under the crown. However, if this were the sole mechanism, one might expect larger amounts of other nutrients under the maple as well, and the data do not support this hypothesis. It is likely that the additional and

nutrient rich substrate provided by the organic matter under maple results in larger populations of nitrogen-rich microorganisms occurring there and this might account for at least some of the differential in N levels. Conceivably, there could be more N fixation by free-living and/or symbiotic nitrogen fixers, although we have no evidence to support this.

Although the magnitude of the nitrogen effect varies widely between sites, in no case does it indicate large differences in average annual increment. For example, on the site with 400 additional kg/ha under bigleaf maple, the maple has probably been influencing soil development for at least two 50 year generations of maple; if so, the average annual addition amounts to only 4 kg/ha/yr. This assumes, of course, that none of the added N has been transported away from the site during this period by mechanisms such as Douglas fir roots from the surrounding stand.

One might expect somewhat greater CEC under maple because of more soil organic matter, and the data indicate that maple may have this effect; however, the differences are not very large.

Differences in nutrients in the mineral soil were not unequivocal for K and were not clearly evident for Ca, Mg and P. One possible explanation is maple's capacity to cycle nutrients more rapidly. The rate of uptake by maple roots might be sufficient to offset the additional nutrient

input from the litter. Also, since the maple plots were actually patches within Douglas-fir stands, it is likely that Douglas-fir roots have access to the soil on the maple plots and the surrounding stand of Douglas-fir might act as a reservoir of tissue capable of absorbing any "excess" soil nutrients. Also, since both above- and below-ground woody tissues of maple generally would be expected to have greater concentrations of nutrients than Douglas-fir, there may be more of each element "stored" in the standing maple biomass on each plot. We made no attempts to estimate biomass of trees on our plots and do not have available reliable prediction equations for both species. This hypothesis would require further evaluation.

Another potential explanation for the apparent lack of soil nutrient differences stems from our uncertainty as to the length of the period of influence of maple on the maple plots, since it was impossible to determine true ages for the maple trees. The maples on sites 2 and 4 may be only 50 to 60 years old, starting from seeds or small sprouts at the same time as the origin of the Douglas-fir. Those on the other three sites were clearly derived from large sprout clumps and therefore may be over 200 years old.

Although there were few differences in the content of bases in the soil between Douglas-fir and bigleaf maple, there appeared to be differences in soil N and organic matter content and there were striking differences in the

annual input and cycling of all nutrients. It still seems wise to examine these differences more closely and to fully understand their implications before eliminating this hardwood from commercial Douglas-fir forests.

LITERATURE CITED

- Alban, D.H. 1969. The influence of western hemlock and western redcedar on soil properties. *Soil Sci. Soc. Am. Proc.* 33:453-457.
- Bohn, H. L., B. L. McNeal and G. A. O'Connor. 1979. Aluminum and transition metals. In *Soil Chemistry*. John Wiley & Sons, New York.
- Bray, J. R. and E. Gorham. 1964. Litter production in the forests of the world. p. 101-157. In J. B. Cragg [ed] *Advances in Ecological Research*. Vol. 2. Academic Press, London.
- Bray, R.H., and L.T. Kurtz. 1945. Determination of organic and available forms of phosphorous in soils. *Soil Sci.* 59:39-45.
- Bremner, J. M. 1965. Total nitrogen, Chap. 83 of *Methods of Soil Analysis, Part 2*, (Agron. Monogr. 9), Amer. Soc. Agron., Madison, Wisconsin, pp. 1149-1176.
- Bremner, J. M. and D. R. Keeney. 1966. Determination and isotope-ratio analysis of different forms of nitrogen in soils:3. Exchangeable ammonium, nitrate and nitrite by extraction-distillation methods. *Soil Sci. Soc. Am. Proc.* 30:577-582.
- Challinor, D. 1968. Alteration of surface soil characteristics by four tree species. *Ecology* 49:286-290.
- Cole, D. W., S. P. Gessel, and S. F. Dice. 1968. Distribution and Cycling of nitrogen, phosphorous, potassium, and calcium in a second growth Douglas-fir ecosystem. In *Proceedings of Symposium on Primary Productivity and Mineral Cycling in Natural Ecosystems*. Amer. Asso. Adv. Sci., 13th annual meeting, Dec. 27, 1967. New York. Univ. of Maine Press. p. 193-197.
- Crocker, R. L. 1959. The plant factor in soil formation. *Austr. J. Sci.* 21(6):180-193.
- Doescher, P.S.; Miller, R. F. and A. H. Winward. 1984. Soil chemical patterns under Eastern Oregon plant communities dominated by big sagebrush. *Soil Sci. Soc. Am. J.* 48:659-663.

- Gessel, S. P. and A. N. Balci. 1965. Amount and composition of forest floors under Washington coniferous forests. In C. T. Youngberg [ed] *Forest-soil relationships in North America*. State University Press.
- Gessel, S. P. and J. Turner. 1974. Litter production by red alder in Western Washington. *Forest Science* 20:4.
- Grier, C. C. and J. G. McColl. 1971. Forest floor characteristics within a small plot in Douglas-fir in Western Washington. *Soil Sci. Soc. Am. J.* 35:988-991.
- Hall, J. K. and P. B. Alaback. 1982. Preliminary Checklist of the Vascular Flora of McDonald and Paul Dunn State Forests. Oregon State University, Forest Research Laboratory. Special Publication #3.
- Jackson, M. L. 1958. *Soil Chemical Analysis*. Englewood Cliffs, NJ. Prentice-Hall, pp151-154.
- Jenny, Hans. 1958. Role of the plant factor in pedogenic functions. *Ecol.* 39:5-16.
- Jensen, E. C. and J. N. Long. 1983. Crown structure of a codominant Douglas-fir. *Canadian Journal of Forest Research*, Vol 13 No. 2, pp. 264-269.
- Jones, J. B. Jr. 1977. Elemental analysis of soil extracts and plant tissue ash by plasma emission spectroscopy. *Commun. in Soil Science and Plant Analysis*, 8(4), pp. 349-365.
- Keeney, D. R. and J. M. Bremner. 1966. Comparison and evaluation of laboratory methods of obtaining an index of soil nitrogen availability. *Agron. J.* 58:498-503.
- Knezevich, Clarence A. 1975. *Soil Survey of Benton County Area, Oregon*. U.S. Dept. of Agriculture, Soil Conservation Service, in cooperation with Oregon Agricultural Exper. Station. Oregon State University, Corvallis. 119 p.
- MacLean, D. A. and R. W. Wein. 1978. Litter production and forest floor nutrient dynamics in pine and hardwood stands of New Brunswick, Canada. *Holarctic Ecology* 1:1-15.
- Ovington, J. D. 1956. Studies of the development of woodland conditions under different trees. IV. The ignition loss, water, carbon and nitrogen content of the mineral soil. *J. Ecol.* 44:171-179.

- Peech, M. L., T. Alexander, L. A. Dean, and J. F. Reed. 1947. Methods of soil analysis for fertility investigations. USDA Circ. 757, p.25.
- Peterson, D. L. and G. L. Rolfe. 1982. Precipitation components as nutrient pathways in floodplain and upland forests of central Illinois. *Forest Science* 28:321-332.
- Rickard, W. H. 1975. Litterfall in a Douglas-fir forest near the Trojan Nuclear Power Station, Oregon. *Northwest Science* 49:183-189.
- Schollenberger, C. J., and R. H. Simon. 1945. Determination of exchange capacity and exchangeable bases in soils -- ammonium acetate method. *Soil Sci.* 59:13-24.
- Stone, E. L. 1975. Effects of species on nutrient cycles and soil change. *Phil. Trans. R. Soc. Lond. B.* 271:149-162.
- Tappenier, J. C. and A. A. Alm. 1975. Undergrowth vegetation effects on the nutrient content of litterfall and soils in red pine and birch stands in Northern Minnesota. *Ecology* 56:1193-1200.
- Tarrant, R. F. and R. F. Chandler, Jr. 1951. Observations on litter fall and foliage nutrient content of some Pacific Northwest tree species. *Journal of Forestry* 49:914-915.
- Tarrant, R. F. and R. E. Miller. 1963. Accumulation of organic matter and soil nitrogen beneath a plantation of red alder and Douglas-fir. *Soil Sci. Soc. Am. Proc.* 1963. pp. 231-234.
- Waring, S. A. and J. M. Bremner. 1964. Ammonium production in soil under waterlogged conditions as an index of nitrogen availability. *Nature* 201:950-951.
- Youngberg, C. T. 1966. Forest floors in Douglas-fir forests:I: Dry weight and chemical properties. *Soil Sci. Soc. Am. J.* 30:406-409.
- Zinke, P. J. 1961. The pattern of influence of individual forest trees on soil properties. *Ecology* 43:130-133.
- Zinke, P. J. and R. L. Crocker. 1962. The influence of giant sequoia on soil properties. *Forest Science* 8:2-11.

THE ECOLOGY OF BIGLEAF MAPLE SEEDLING ESTABLISHMENT AND
EARLY GROWTH IN DOUGLAS-FIR FORESTS

by

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ABSTRACT

The establishment phase of bigleaf maple, a ubiquitous, deciduous, hardwood in western Oregon's Douglas-fir forests, was studied in a variety of stands ranging from 1 to 150 years of age to identify the stages in Douglas-fir forest succession where bigleaf maple is most likely to become successfully established from seed. Germination rates of seed protected from rodents averaged from 30 to 40 % in all environments but typically less than 2 % of the unprotected seed germinated, indicating that seed predators play an important role in regulating seedling establishment.

Seedling survival was highly dependent on light, and mortality after one growing season was particularly high in stands with greater than 90 % overstory cover. At least half (63 %) of the first year mortality was due to browsing by burrowing rodents and invertebrates, with dessication as the second greatest cause of mortality during the first year.

On plots that were monitored over two growing seasons, overwinter mortality was the second most frequent classifi-

cation. Seedling survival was not related to soil moisture content or soil moisture tension. The highest survival rates (90 %) were in clearcuts and very open stands and the lowest (0 %) were in dense, young, conifer stands. Maple establishment in clearcuts will likely only be successful if seedlings escape shading by competing shrubs and herbs. Optimum long term survival is most likely in Douglas-fir stands over 40 years of age.

The Ecology of Bigleaf Maple Seedling Establishment
and Early Growth in Douglas-fir Forests

INTRODUCTION

Bigleaf maple (*Acer macrophyllum*) and red alder (*Alnus rubra*) are the two most abundant hardwoods in Douglas-fir forests in western Oregon. Considerable research has been conducted on the ecology and nutrient relations of red alder (for example, Tarrant et al., 1969; Gessel and Turner, 1974), largely because of its importance as a nitrogen fixer. However, bigleaf maple has received comparatively little attention. Although maple does not fix nitrogen, a recent study has shown that maple may enhance soil nitrogen and organic matter by greater annual inputs of litter and turnover rates that are more rapid than those under Douglas-fir (Fried, 1985a).

Although present in the same forests and occurring on both riparian and upland sites, these two hardwoods appear to have markedly different ecological strategies and patterns of establishment. While the light-seeded (1.7 million seeds/kg [Fowells, 1965]) red alder requires bare mineral soil to become established and thrives in fresh clearcuts or other disturbed areas, the heavier seeded (7165 seeds/kg [Olson and Gabriel, 1974]) bigleaf maple's seedlings are usually observed under a forest canopy, rarely found in

clearcuts, and often germinate on thick forest floors. Initially, alder grows very rapidly (up to 2 m per year), quickly overtopping Douglas-fir seedlings, but by age 60, alder stands stagnate and subsequently die and break up as they become overtopped by the surrounding Douglas-fir stand. Bigleaf maple grows more slowly from seed and this deciduous, persistent hardwood occurs in stands of all ages because of stump sprouting and moderate shade tolerance.

Maple sprout clumps, which originate from cut or burned maple trees, rapidly occupy available growing space and with initial growth rates ranging from 1 to 2 meters/year on as many as 50-60 sprouts per stump, easily outpace conifer seedlings in height growth (Roy, 1955). Consequently, forest managers regard bigleaf maple as a serious competitive threat to the slower growing, planted commercial conifer seedlings and often invest heavily in its control.

Knowledge of the initial establishment strategy of bigleaf maple seedlings is needed to understand the process of secondary succession in Douglas-fir forests and, since established maple trees can be killed only with difficulty, the understanding gained in this study could prove invaluable for cost effective control of this competing hardwood species. Such information could also prove useful for devising mixed maple/Douglas-fir management regimes, which may be desirable for achieving goals of soil enhancement and for creation of wildlife browse.

Virtually no attention has been devoted to understanding *Acer macrophyllum*'s early establishment and growth. Thus, forest managers have little information to guide their decisions pertaining to this species. This study contributes to the development of our understanding of this species by identifying the successional stage(s) in which bigleaf maple seeds will germinate and survive and by determining some of the limiting environmental variables which regulate the establishment phase.

The forestry literature contains only two references to bigleaf maple seedlings. An investigation of brush invasion of small openings on the MacDonald Forest determined that bigleaf maple seedlings were significantly more abundant, taller and older in small forest openings than on adjacent sites under a dense forest canopy (Sabhasri and Ferrell, 1960). In an unpublished study of importance values as an indicator of bigleaf maple succession in Washington, Hansen (1984) found an abundance of seedlings and few saplings in the stands that were studied and speculated that bigleaf maple might be an intolerant species requiring canopy openings for successful establishment. He also found that niche partitioning models were not effective in determining successional status and suggested that age structure analysis would prove more useful.

Research conducted on the seedling phase of other species of the genus *Acer* found in the eastern United States,

concentrated on age structure and mortality patterns. For example, striped maple, (*Acer pennsylvanicum*), in Massachusetts exhibited little mortality between ages 2 and 15, after which it was unable to survive in the understory. After 15 years of age, classic J-shaped distributions accurately described stand structure. Unlike the 2 to 15 years olds, first year germinants suffered high mortality (Hibbs, 1979).

Studies of sugar maple (*Acer saccharum*) (Hett and Loucks, 1970; Hett, 1971) revealed that seedling mortality in that species is relatively independent of moderate climatic fluctuations but somewhat influenced by the density of germinating seedlings. Those studies also demonstrated that the classic J-shaped age distributions accurately described the structure of sugar maple stands. These findings appear to have only limited applicability to bigleaf maple because it usually occurs as scattered individuals or groups in conifer stands and comprises less than 20 % of the total basal area.

The principal objective of this study was to test the hypothesis that bigleaf maple seedlings can become established in all stand successional stages. Additional objectives included assessing the effect of stand factors such as overstory age, canopy density, and soil moisture content on maple seed germination, initial seedling survival and causes of mortality, and evaluating the impact of rodents on

seedling densities.

METHODS

Study Sites

The study was conducted principally on the MacDonald and Dunn Forests, College of Forestry, Oregon State University in Benton County, western Oregon (Lat. 44° 40' N., Long. 123° 20'). The sites are in the foothills west of the Willamette Valley, on the eastern fringe of the Coast Range. Annual rainfall averages 130 cm, average annual air temperature is 9 to 12° C and the frost free season is 165 to 200 days (Knezevich 1975). A complete description of the vegetation in this area is given by Hall and Alaback (1982). Elevation of the sites ranges from 175 to 400 m. The soils were derived principally from fractured or weathered basalt, range from 75 to 152 cm in depth and are typical of commercial Douglas-fir/bigleaf maple stands found on the eastern margin of the Coast Range.

Study I: Survival of Natural Seedlings

Two studies were conducted on seedling germination and early survival. In the first, fourteen plots were established to monitor survival on a variety of soil types and in stands with different overstory and understory densities and composition. Equal numbers of plots were installed in stands in each of two broad age classes (40-80 and 80-150 years) in Spring 1983, shortly after emergence of natural

bigleaf maple seedlings. A large 1982 seed crop resulted in many newly germinated bigleaf maple seedlings in a range of environments. Each plot consisted of 30 to 50 seedlings on an area of .04 hectares (ha.) or less, marked with colored stake flags for identification. Seedling mortality was tabulated for two years on each plot along with causes of death.

Study II: Germination and Survival Experiment

In the second study, 12 stands were selected for installation of three germination/survival plots in each to determine the effect of predation on seeds by rodents on seedling abundance and the effect of stand successional stage, age and density on germination and mortality patterns. Each plot consisted of a) an exclosure, 15 cm tall by 75 cm diameter circular cage, (0.2 X 0.2 cm wire mesh), covered on top and set 5 to 10 cm into the ground, designed to prevent predation on seeds prior to emergence, in which 75 maple seeds were planted, and an unprotected row, 3 m long, extending from the exclosure to a wooden stake along which 75 additional seeds were planted at 4 cm intervals.

All seeds were collected in late September, the time of natural seedfall, from 10 randomly selected trees on the MacDonald Forest, and hollow seeds and seeds with externally obvious defects were discarded. Seeds were sown on the day of collection to ensure their viability, since maple seeds

respond poorly to storage (Olson and Gabriel, 1974). Seeds were sown by inserting the de-winged samaras 1 cm into the duff or soil where they overwintered. Seed viability tests, using the tetrazolium method, on a subsample of the seed determined that 60% were sound at the time of planting. A total of 3600 seeds were sown.

Twelve stands were selected to represent a range of successional stages. Exclosures were installed in three old stands (>80 years), three young stands (25-55 years) in which no natural germinants were found, 3 clearcuts and in three stands where germinants had been abundant the previous year (typically 40-80 year old stands and hereafter referred to as stands where maple seedlings were present), to investigate the relationship between stand successional stage and seedling germination and survival. Seedling emergence and mortality were monitored beginning in March 1984 both inside and outside the exclosures, and continuing at two week intervals during the period of emergence until June. Exclosure lids were removed by June after germination had stopped. Germination was estimated by emergence above the forest floor because identifying germinants below the forest floor would have required excessive disturbance. Beginning in June 1984, these plots were monitored every month, the same as the plots in Study I, for survival and causes of mortality.

Measurement of Soil Moisture

Soil water content in the mineral soil was determined gravimetrically at three points (at 1-30 cm, the maximum depth of first year maple seedling root penetration) on each plot in Study I and at one point outside each exclosure in study II during the first year from June to September. Samples (approximately 75-100 g) were sealed in metal containers, weighed, dried at 105 °C for 48 hours, reweighed and then washed through a two mm sieve so that the weight of the rock fraction could be deducted before calculation of percent moisture on a dry weight basis. Three soil samples from each plot in Study I and one from outside each exclosure in study II were analyzed for moisture content at -5 and -15 bars using pressure plate methods (Anonymous, 1982) to develop a water release curve that would allow us to calculate moisture tension values for each summer month on each plot.

Measurement of Canopy Density

Canopy density of all trees was estimated in each stand in Study I by photographing the overstory above each plot with a 35 mm, fisheye lens equipped camera mounted horizontally 1 m above the plot center and analyzing the negative, Kodalith derived slides using a technique described by Chan et al. (1985) that yields estimates of percent sky, the area

not obscured by foliage. Thus percent sky serves as an index of canopy density.

Canopy density was also measured for each exclosure plot in Study II. In all forest stands, canopy photos were taken directly above the exclosures, but in the clearcuts, the camera was placed on and parallel to the ground so that the photos would account for the shading by dense vegetation that occurred in some exclosures in the clearcuts.

Data Analysis

For the plots in the Study I, percent survival (number of live seedlings divided by the number of seedlings initially staked) was calculated for each observation date. For the germination/survival plots, percent germination (maximum number of emerged seedlings divided by 75, the number of seeds sown) was calculated both in and outside the exclosures at each site and percent survival (total number of live seedlings, both in and out of the exclosure, divided by the maximum number of emerged seedlings) was calculated for each plot at each observation date following the conclusion of germination. Soil moisture tension was calculated from soil moisture content using an equation derived separately for each stand from a logistic regression of the three pairs of moisture content values (-5 and -15 bars) for each stand.

The stands in Study I were divided into two stand age

classes: immature (40-80 years) and mature (> 80 years) and t-tests used to test the null hypothesis that there were no significant differences ($p < .05$) in survival after one or two years between stand age classes. Analysis of variance was conducted on the germination/survival plot data to identify significant differences in germination and survival after one year among stand successional stages and exclosure versus open treatments. We used the Tukey test ($p < .05$) to determine significant differences.

The data from all of the plots in each study were combined for a stepwise regression analysis to determine the effect of percent sky, soil moisture and soil moisture tension on first year survival for Study II and on first and second year survival on Study I. We also regressed percent first year survival on a transformation of the percent sky variable for the plots in Study II, which covered a wider range of canopy densities.

RESULTS

Germination

Germination inside the exclosures (Study II) was significantly ($p < .01$) greater than on the adjacent, unprotected rows in every successional stage (Figure 1). Four exclosures had to be excluded from analysis because rodents had burrowed under them and had removed virtually all of the seed. An additional two exclosures in one of the clearcuts were excluded because they had been placed on a steep, south-facing slope with ravelling soil and it appeared that prolonged exposure to direct sunlight, a month of droughty conditions after sowing and ravelling of the soil that had initially covered the seeds accounted for the extremely low germination rates in those exclosures.

Average germination inside the exclosures in which there was no predation ranged from 29% for the clearcuts to 42% in the old stands, whereas germination outside ranged from 0.3% in the old stands to 3.9% in the young stands. Two of the young stands had very low germination rates outside the exclosures, averaging 0.3%, and one fairly open stand with a thick, grassy understory had an average rate of 11%, anomalously high, not only for that successional stage, but for the entire study as well. The maximum germination rate of protected seed for all plots was 51%, somewhat less than the 60% viability rate predicted by the tetrazolium

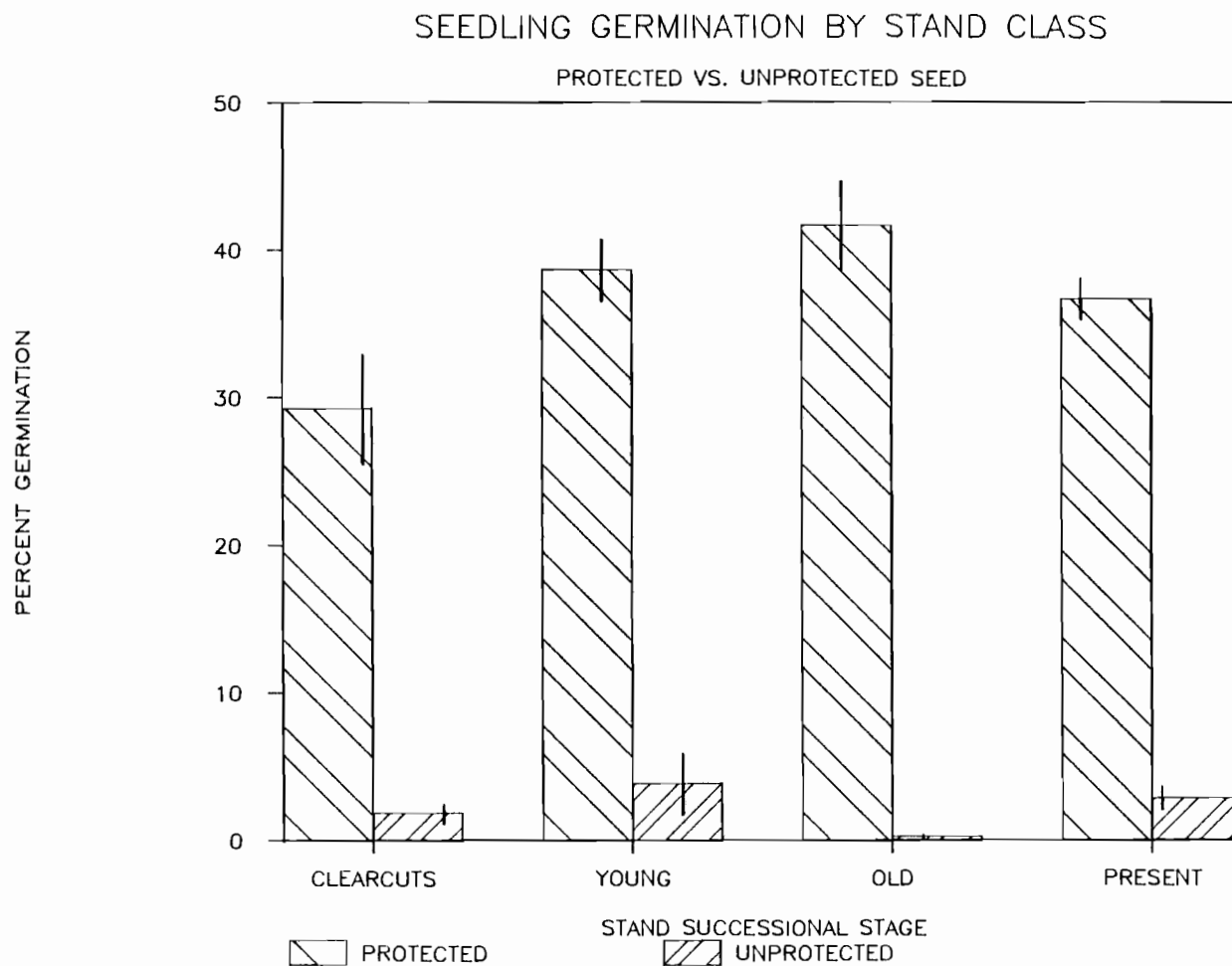


Figure 1. Average maximum germination rates by stand successional stage for protected and unprotected maple seed, with standard error bars.

test, and the maximum germination for unprotected seed was 16%. All seed which was not removed by rodents either germinated the first year or decayed, since there was no germination in the second year in any of the exclosures.

Analysis of variance revealed that average germination was significantly ($p < .05$) greater in the old stands (40%) than in the clearcuts (29%).

Survival and Growth

Average first year survival rates (Study II), measured in early September at the end of the growing season, ranged from 39% in young stands to 85% in clearcuts (Figure 2). Analysis of variance indicated a significant ($p < .05$) difference in survival between clearcuts and young stands; other comparisons of survival by stand type showed no significant differences. Average first year survival for all germination/survival plots was 62% of the seedlings that emerged and ranged from 0% in a dense (8% sky), 25 year old Douglas-fir plantation to 97% in a very open (23% sky), 50 year old mixed Douglas-fir/maple stand.

Most of the mortality (63%) was due to predation, either by rodents which clipped roots underground or, in many cases, even pulled whole seedlings down into rodent burrows, or above ground browsing by slugs (*Ariolimax*) and invertebrates (Figures 3 & 4). Seedlings that vanished without a trace, and were recorded as missing, were presumed

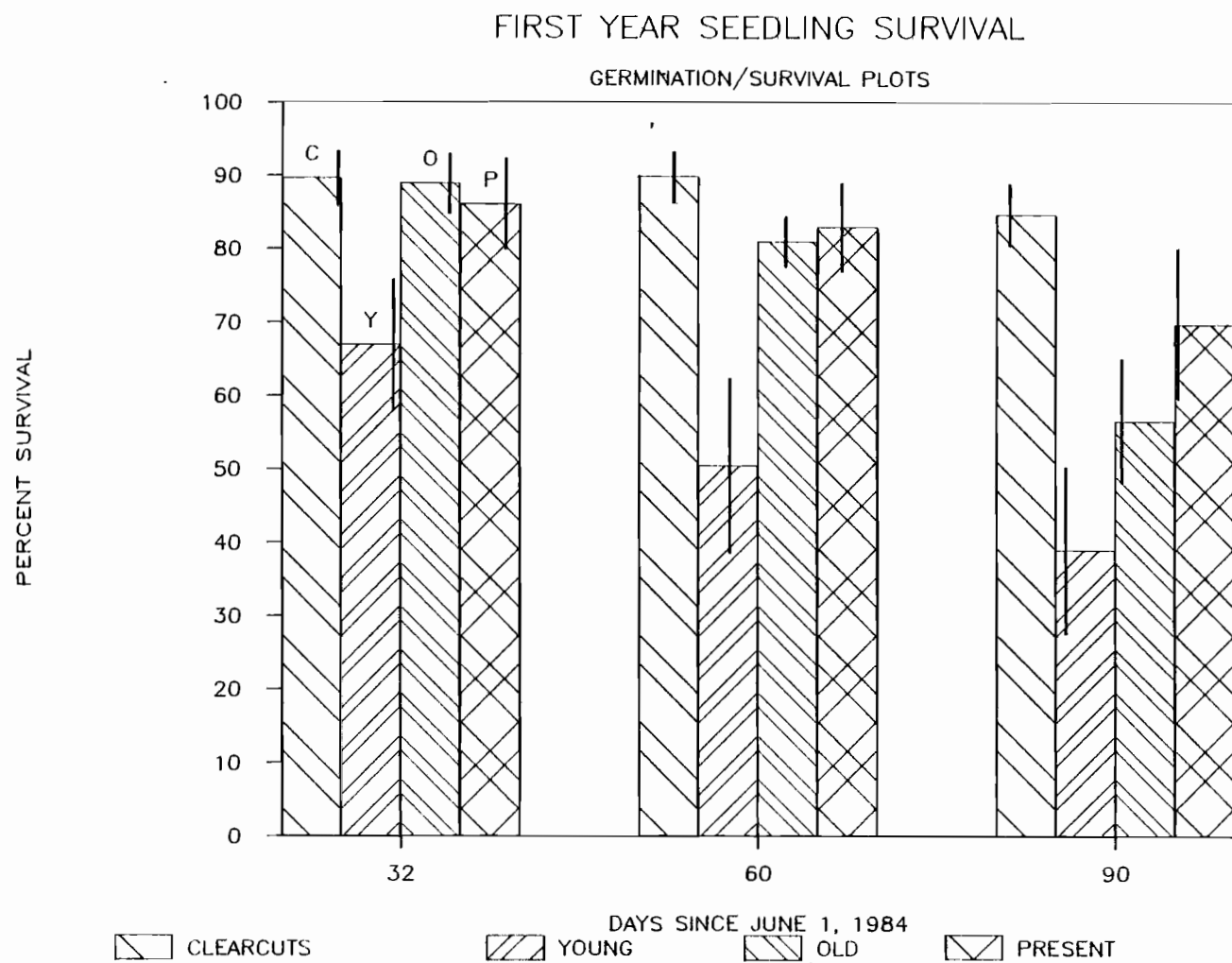
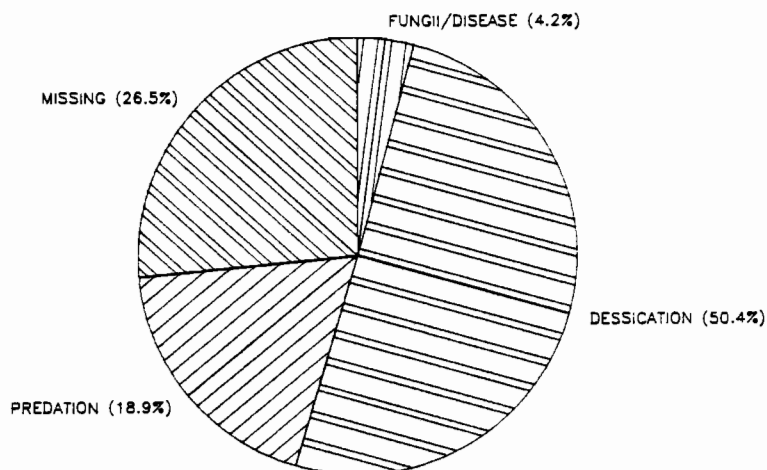
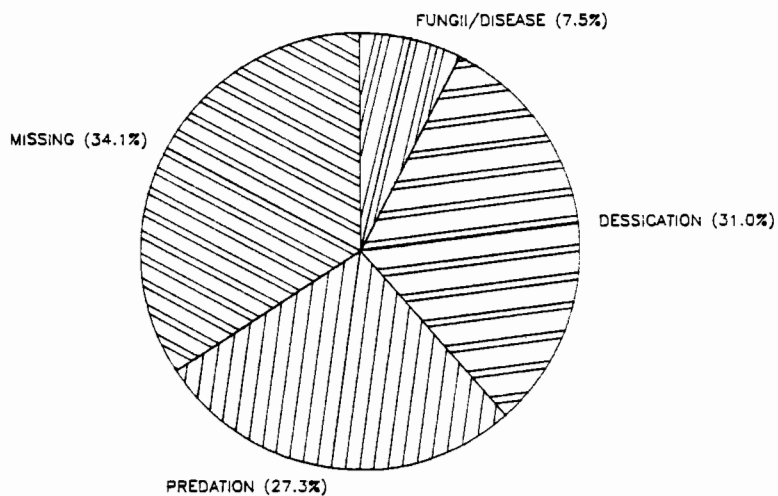


Figure 2. Average survival by stand successional stage on plots in Study II after one growing season, with standard error bars.

CAUSES OF MORTALITY IN STANDS WITH
SEEDLINGS: GERMINATION/SURVIVAL PLOTS



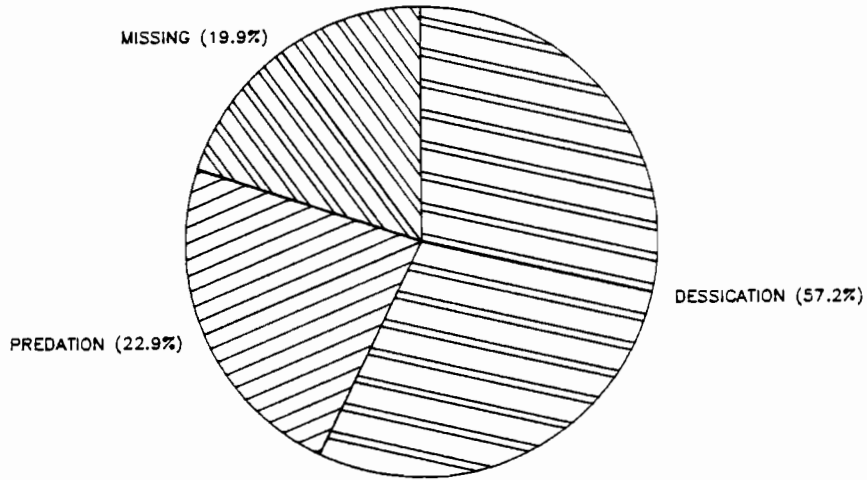
CAUSES OF MORTALITY IN YOUNG
STANDS: GERMINATION/SURVIVAL PLOTS



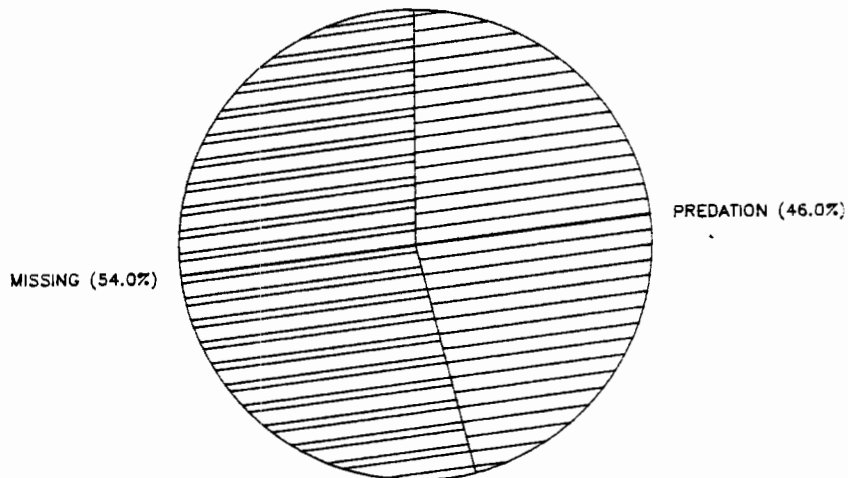
Note: Seedlings recorded as missing were assumed to have been lost to predators.

Figure 3. Causes of death in young stands and stands where seedlings were already present for Study II, expressed as a percentage of total mortality after one growing season.

CAUSES OF MORTALITY IN OLD STANDS
GERMINATION/SURVIVAL PLOTS



CAUSES OF MORTALITY IN CLEARCUTS
GERMINATION/SURVIVAL PLOTS



Note: Seedlings recorded as missing were presumed to have been lost to predators.

Figure 4. Causes of death in old stands and clearcuts for Study II, expressed as a percentage of total mortality after one growing season.

to have been lost to predators. Considerably more seedlings were attacked, but those that lost only leaves and bud tips usually recovered by producing additional leaves from axillary meristems. Thirty-five percent of the mortality appeared to be caused by dessication, and this mode of death occurred principally in old stands (60%) and stands where maple seedlings were already present (51%). No seedlings died of dessication in the exposed clearcuts during the first growing season. The remaining mortality (3%) was due to fungi or disease and this occurred only in young stands and stands with seedlings already present.

First year survival on the plots established in 1983 for Study I was significantly ($p < .01$) greater in the immature (40-80 years) stands (97%) than the mature (>80 years) stands (75%) (Figure 5). Survival in both stand classes was higher than in 1984 and the fact that some of the plots for Study I were not established until June, and thus some early mortality may have been missed, may at least partly account for this difference. Survival after two growing seasons, however, was not significantly different between immature (45%) and mature (36%) stands and ranged from < 2% on a shady plot with a thick, maple litter forest floor and considerable subterranean rodent activity to 90% in a very open stand (Study I stand #8) that had suffered substantial windthrow loss of overstory trees and had been treated with a large, mechanical mower that had removed all understory

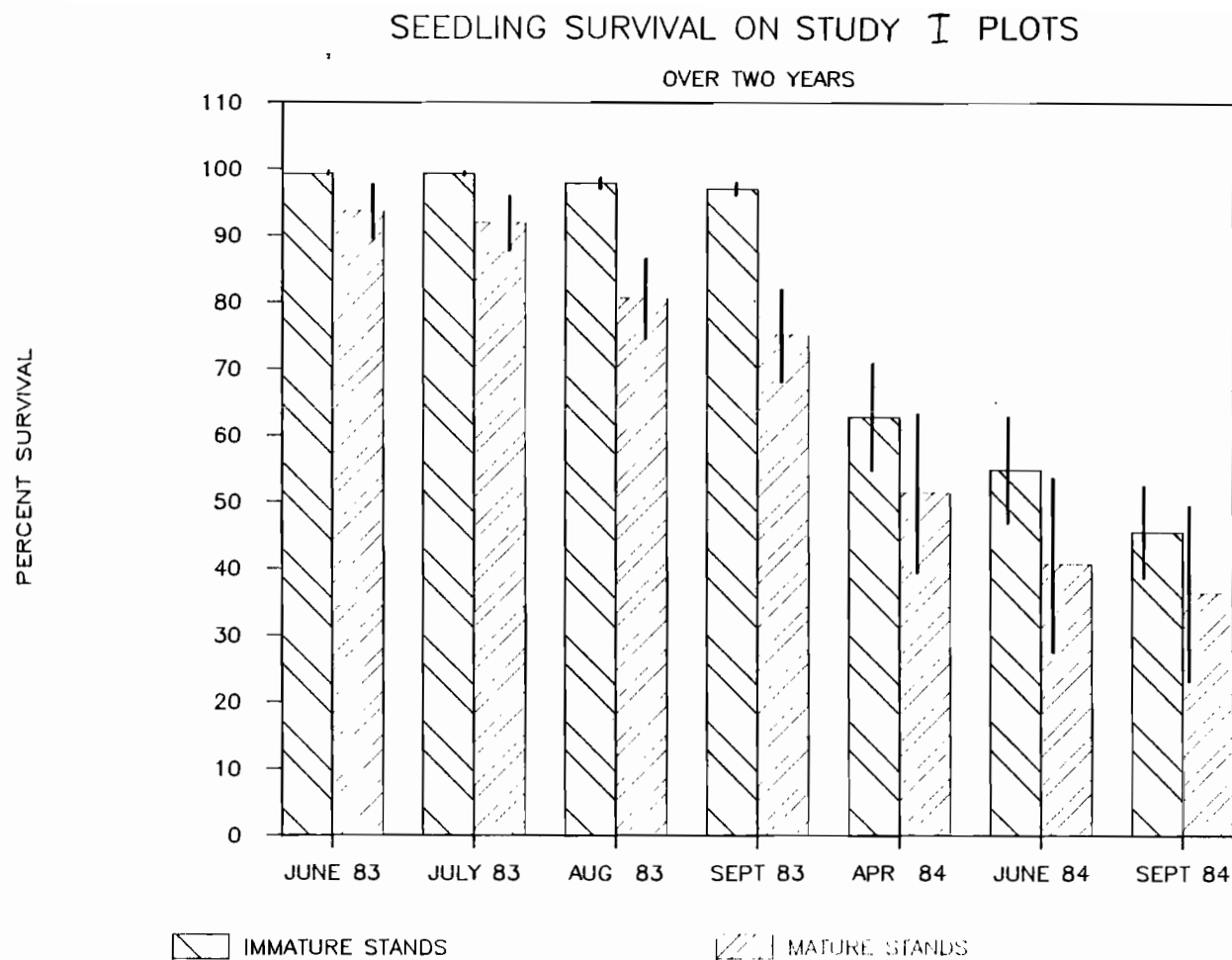
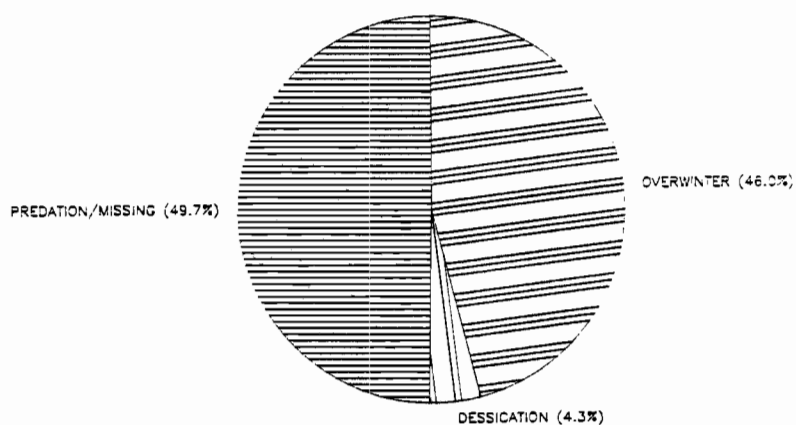


Figure 5. Average survival in immature and mature stands over the course of two growing seasons, with standard error bars.

CAUSES OF MORTALITY IN IMMATURE STANDS



CAUSES OF MORTALITY IN MATURE STANDS

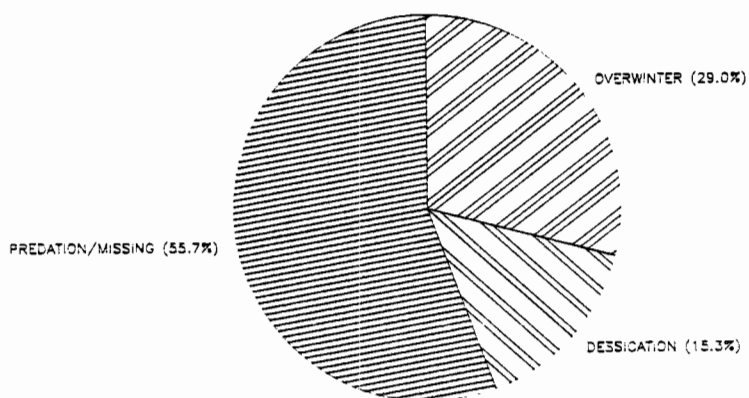


Figure 6. Causes of death on Study I plots, expressed as a percentage of total mortality after two growing seasons.

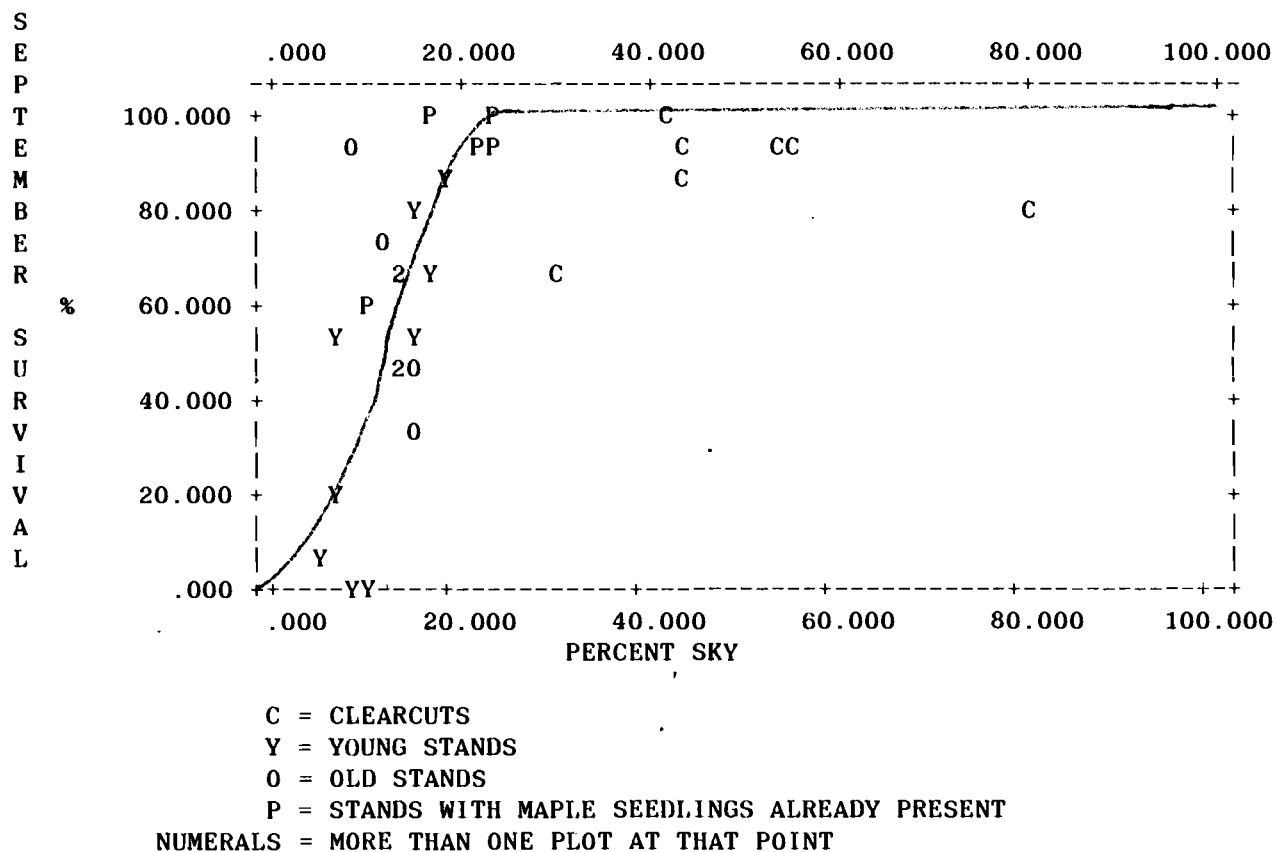
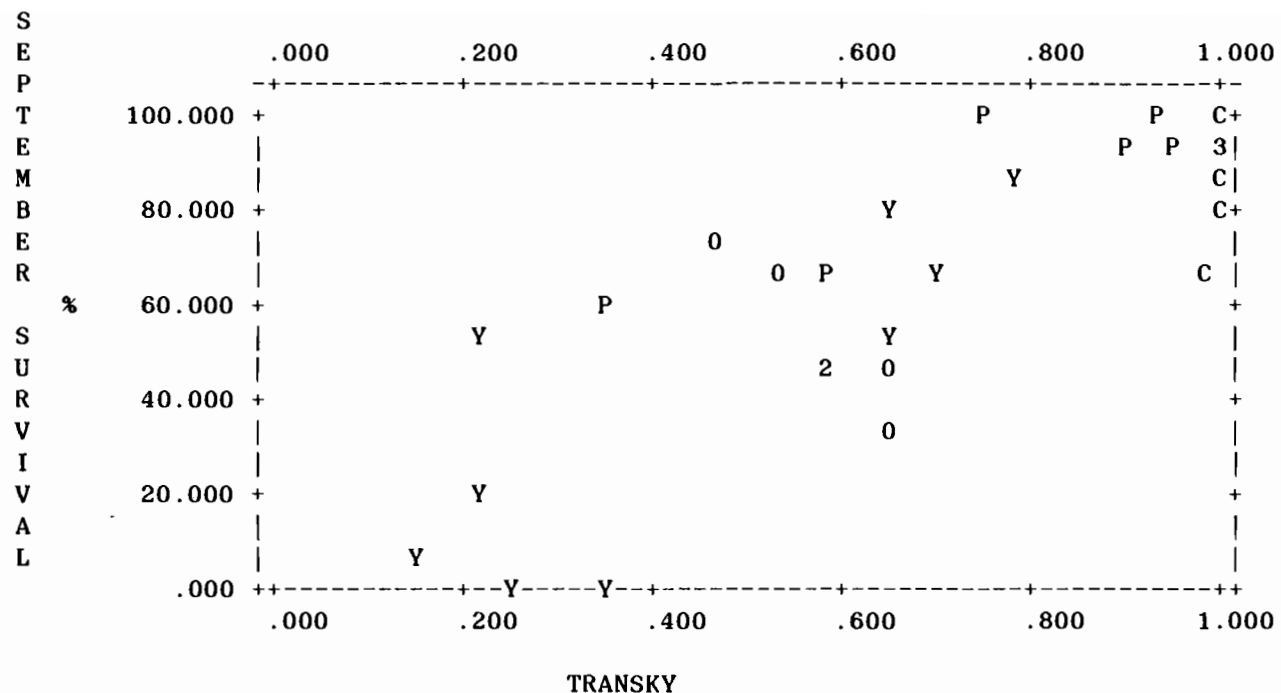


Figure 7. Survival after one growing season on Study II plots plotted against canopy photo determined percent sky.



C = CLEARCUTS
 Y = YOUNG STANDS
 O = OLD STANDS
 P = STANDS WITH MAPLE SEEDLINGS ALREADY PRESENT
 NUMERAL = NUMBER OF DATA POINTS AT ONE LOCATION

Figure 8. Survival after one growing season on germination/survival plots plotted against an inverse exponential transformation of percent sky.

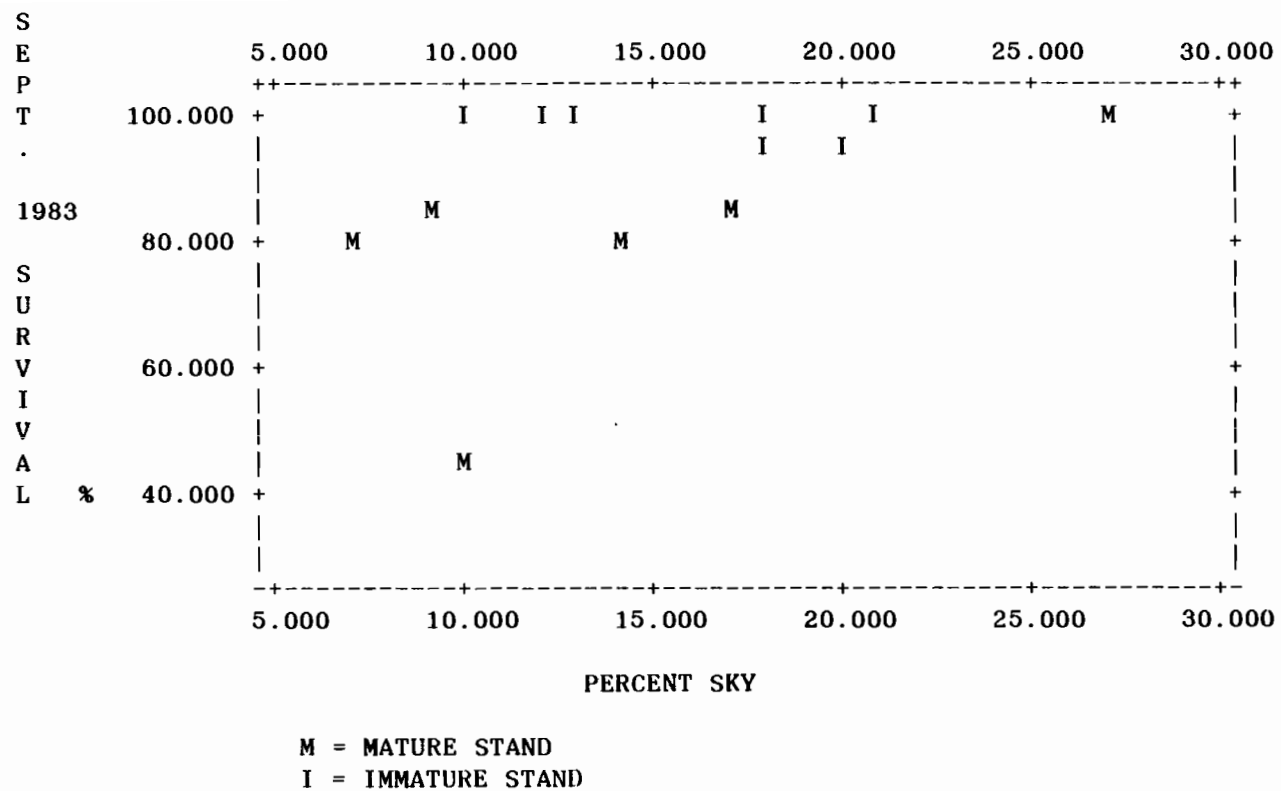
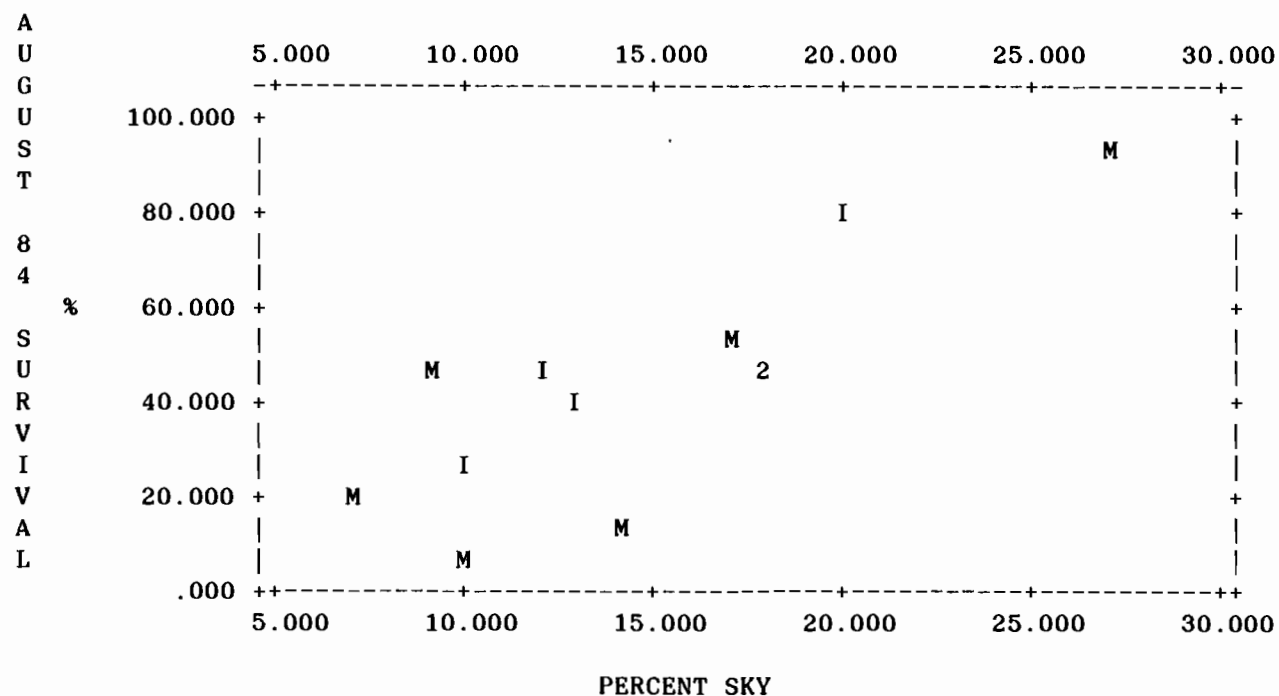


Figure 9. Survival on Study I plots after one growing season plotted against percent sky.



M = MATURE STAND
 I = IMMATURE STAND
 2 = TWO STANDS AT ONE POINT

Figure 10. Survival on Study I plots after two growing seasons plotted against percent sky.

three years earlier. The primary cause of mortality after two growing seasons was predation (53%) followed by overwinter mortality of unknown origin (38%). The remainder (10%) was due to dessication (Figure 6).

Although September 1984 survival on the germination/survival plots was moderately correlated with the percent sky values derived from the canopy photos, a plot of survival against percent sky (Figure 7) shows a relationship that is not strictly linear. A transformation of percent sky, $\text{transky} = 1/(1 + \exp(3 - 24(\% \text{sky}/100)))$, has a relationship to survival in the form of a step function and is linearly related to survival, with an $R^2 = .94$, as $Y = 91.428 X$ ($Y =$ September 1984 survival; $X = \text{transky}$) (Figure 8), and the regression is significant ($p < .01$). The transformation assumes an inflection point at 12.5% sky, an indication that there may be a threshold above which most maple seedlings will survive and below which most will die.

It is not surprising that there is little evidence of a step function in the survival data from Study I (Figures 9 & 10) since there are few data points from either the low or the high ends of the % sky range, (because clearcuts and young stands were not part of this study) and because of the high survival rates which may be due to tardy plot establishment. Survival relates poorly to % sky after one growing season, but after two growing seasons, a reasonably linear relationship emerges as $Y = 2.898 X$, ($Y =$ September

1984 survival; $X = \%sky$), which is significant ($p < .01$) and has an $R^2 = .90$. This model was forced through the origin because, if a constant is included, its estimated value is not significantly different from 0, and because we anticipated 0% survival at 0 % sky. One might expect a somewhat poorer relationship on Study I plots because the canopy photos, taken at only one point on a large plot (up to .04 ha.), may not accurately reflect the availability of light on the entire plot whereas the photos for the germination/survival study were taken directly over the exclosures and should accurately represent the radiation environment of those seedlings. Because of stand heterogeneity, percent sky often varied greatly within a stand, sometimes by as much as 50% of the value, between two exclosures spaced a few meters apart.

Neither soil moisture content nor calculated soil moisture tension were correlated with survival on the germination/survival plots and, in a stepwise regression, neither contributed any additional predictive power to the model based solely on the inverse exponential transformation of % sky. Soil moisture measured at the beginning of September varied among stand successional classes with old stands having significantly ($p < .05$) greater average moisture content (29.6%) than stands where maple seedlings were already present (21.2%) (Figure 11). Computed moisture tension values also varied significantly among stands with signifi-

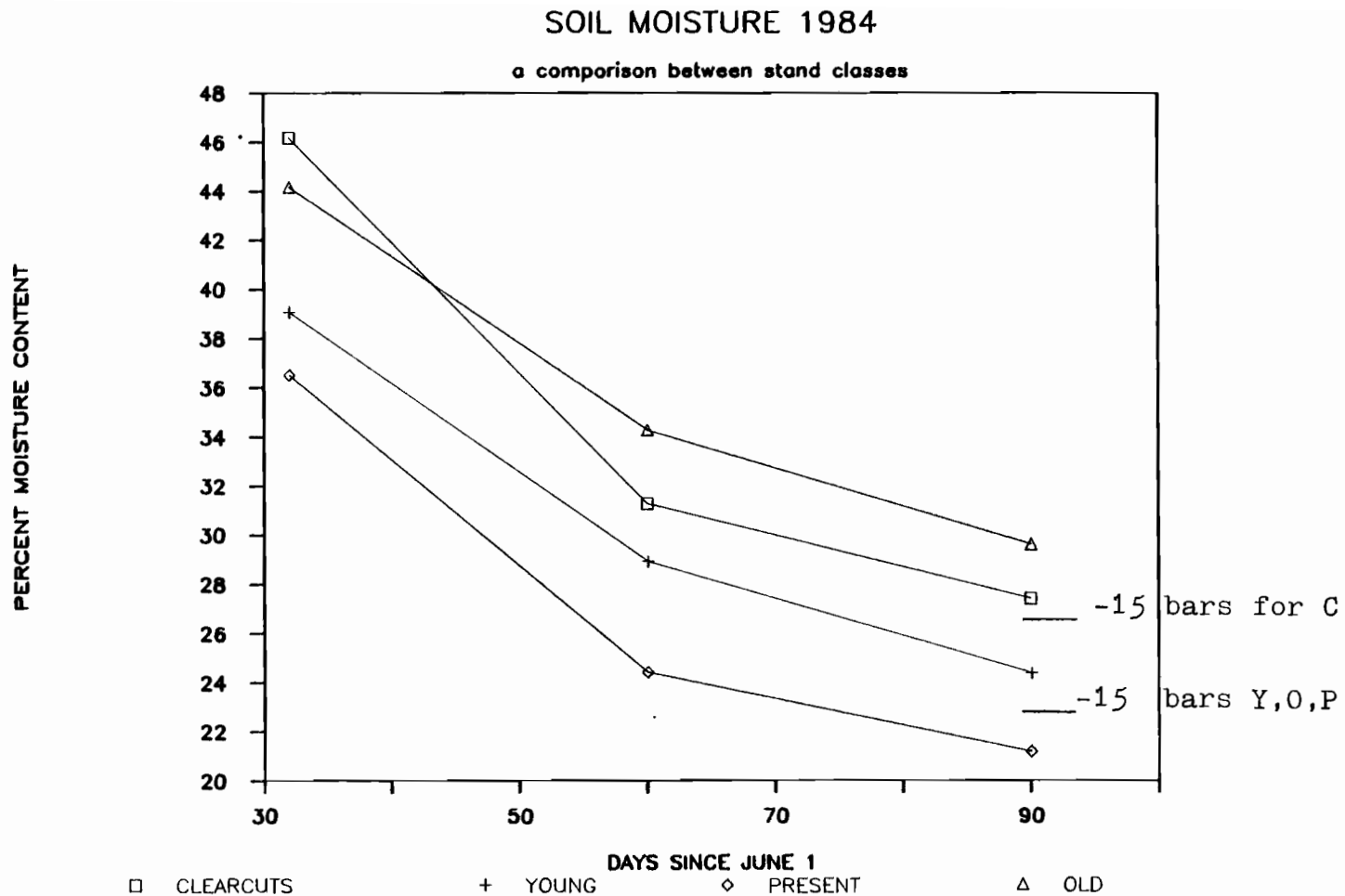


Figure 11. Average soil moisture content on the plots in Study II, by stand class.

cantly lower ($p < .05$) moisture tension in old stands (-3.2 bars) than stands with maple seedlings already present (-11.5 bars). Average moisture content at the permanent wilting point (-15 bars) was 27.2% in the clearcuts and 23.8% in the other stands. End of first growing season moisture content in Study I (Figure 12) was significantly ($p < .01$) greater in the mature stands (30.8%) than the immature stands (23.2%) and, while second year survival was weakly negatively correlated ($R^2 = .40$) with soil moisture content at the end of the first growing season, this variable added no predictive power to the model based on percent sky alone.

Soil moisture regimes for the two growing seasons covered by this study were strikingly different (Figure 13). Rain fell intermittently during the summer of 1983 until mid-July and was followed by a dry spell that, except for three days of rain in late August, remained unbroken until early October. In 1984 there was no rainfall from late May until mid-September.

In both Study I and Study II, survival didn't appear to be related to either overstory basal area or stand age (Figures 14 & 15).

Average seedling height after one year of growth ranged from 6.0 cm in clearcuts to 7.7 cm in old stands and differences between stand classes were not significant. Seedling height growth on the plots in Study I during the second

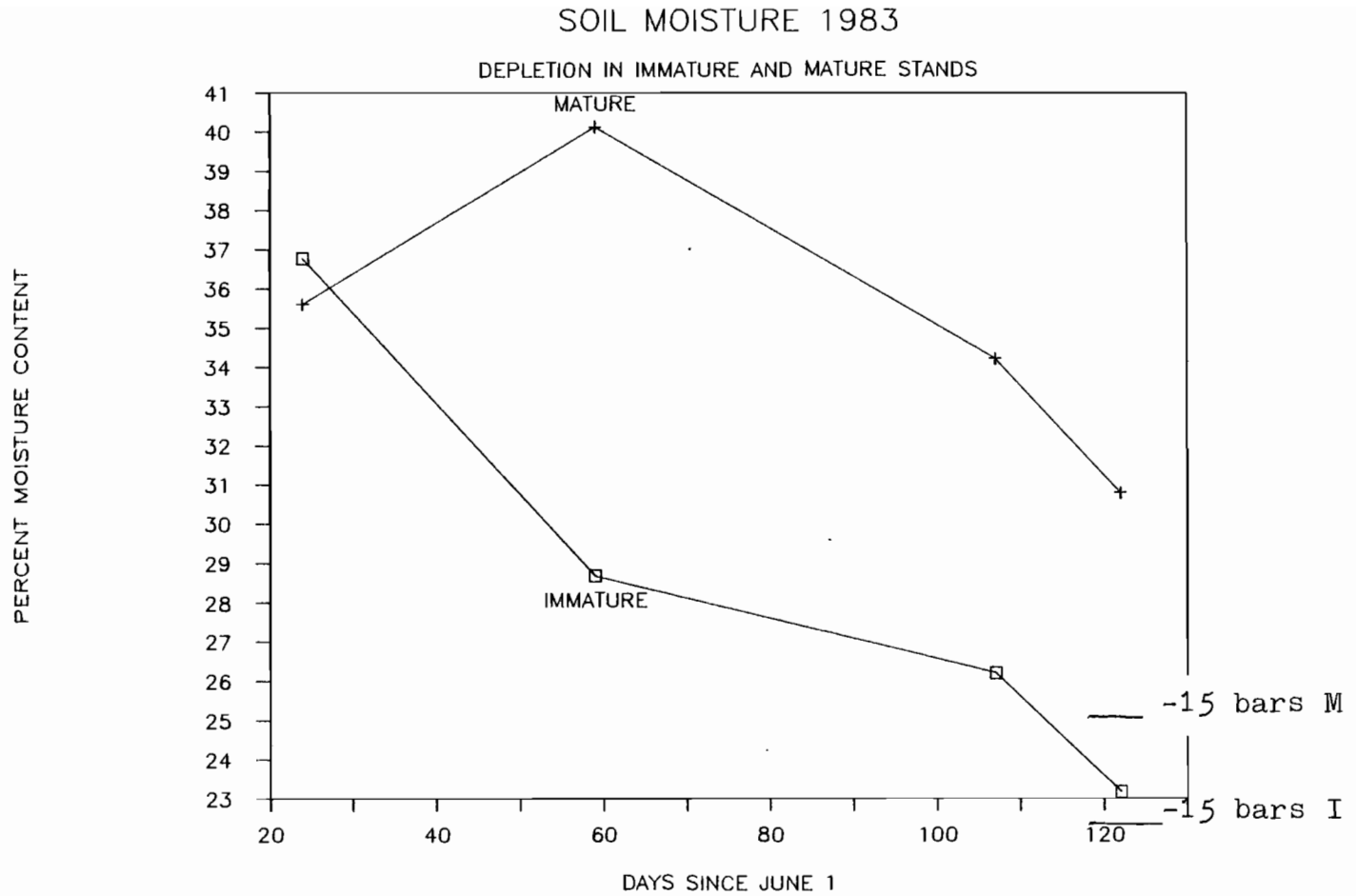


Figure 12. Average soil moisture content on the plots in Study I, by stand class.

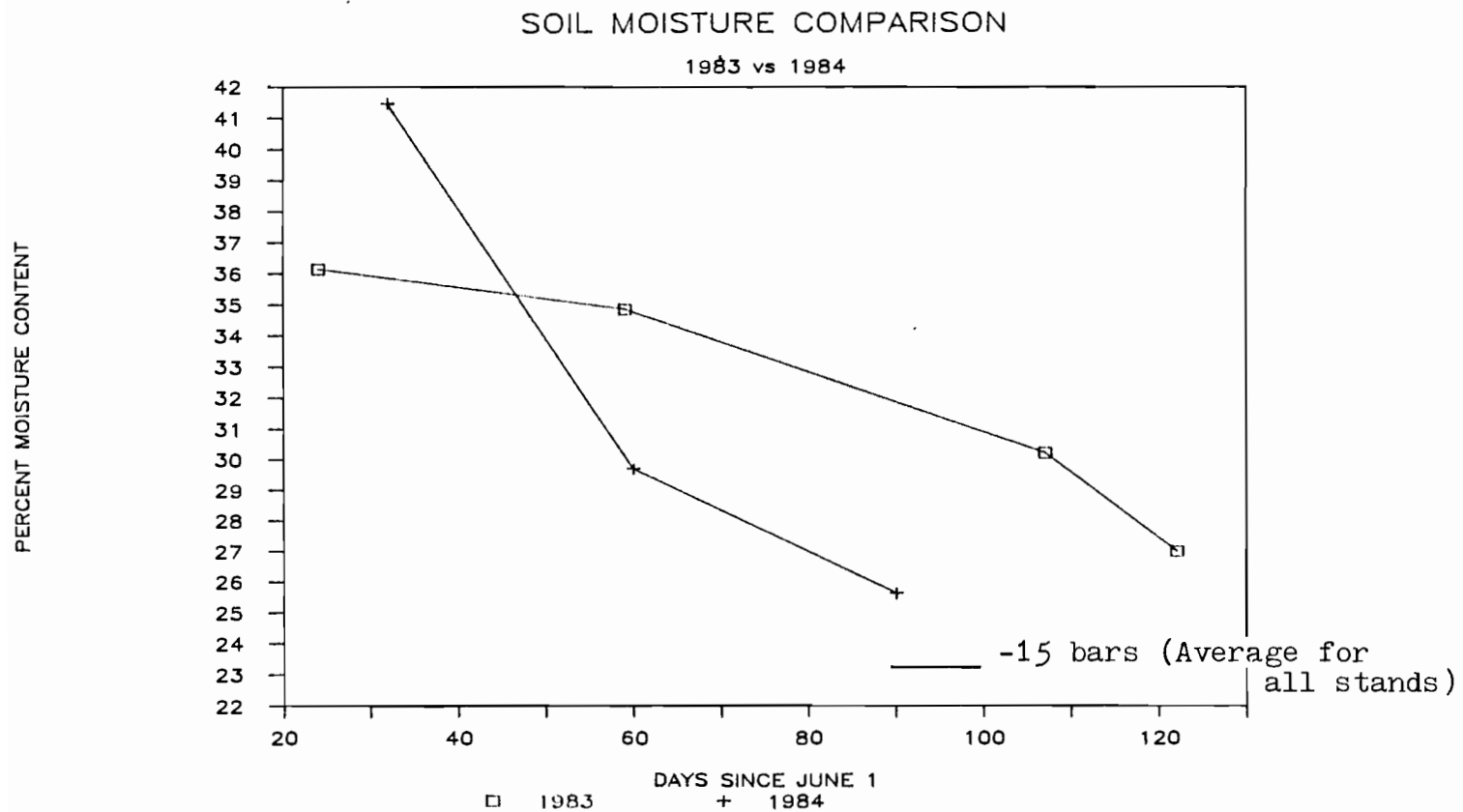
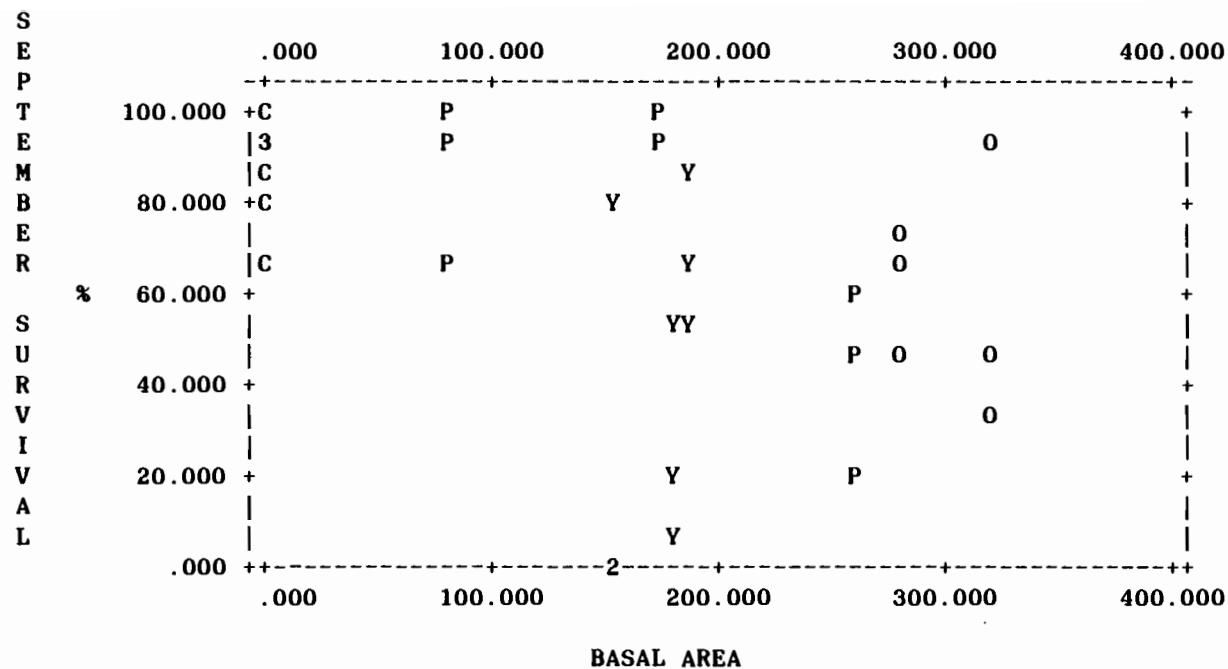
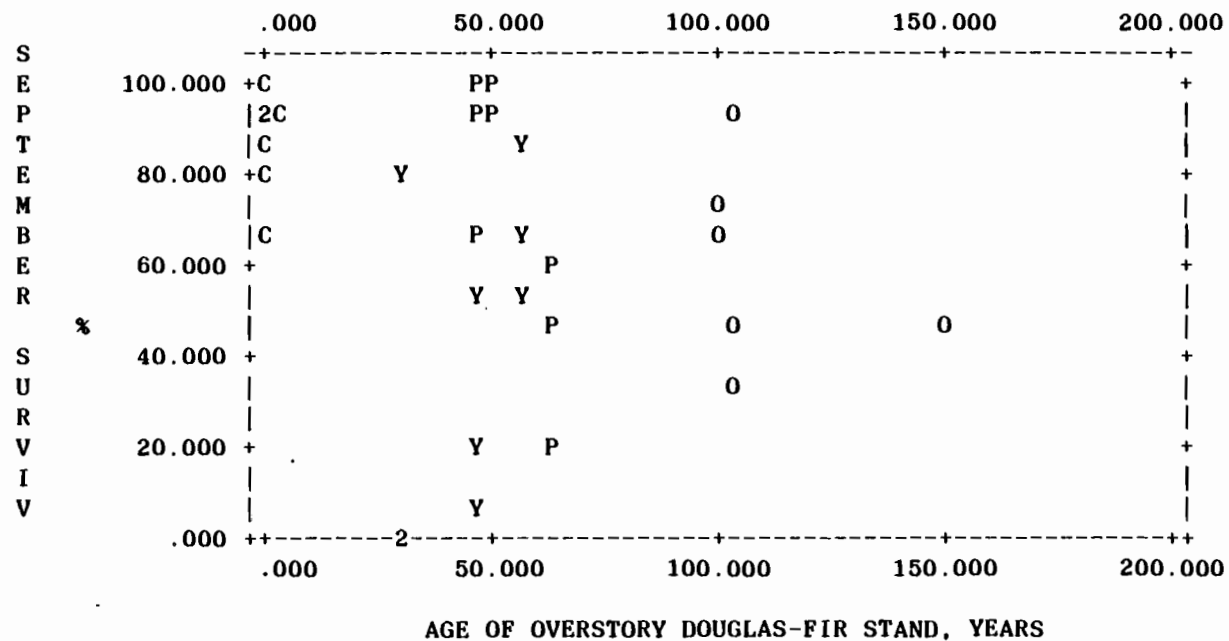


Figure 13. Comparison of soil moisture regimes on the MacDonald Forest between 1983 and 1984; data from all stands.



C = CLEARCUTS
 Y = YOUNG STANDS
 O = OLD STANDS
 P = STANDS WITH MAPLE SEEDLINGS ALREADY PRESENT
 NUMERALS = MORE THAN ONE STAND AT THAT POINT

Figure 14. Survival on the germination/survival plots at the end of one growing season plotted against stand basal area



C = CLEARCUTS
 Y = YOUNG STANDS
 O = OLD STANDS
 P = STANDS WITH MAPLE SEEDLINGS ALREADY PRESENT
 NUMERALS = MORE THAN ONE STAND AT THAT POINT

Figure 15. Survival on the germination/survival plots at the end of one growing season plotted against stand age.

growing season was very slow and average total seedling height and standard errors were only 6.8 (+/- .5) cm in immature stands and 6.1 (+/- .7) cm in mature stands. The tallest seedlings 12.6 (+/- 1.2) cm were found on Study I plot #8, the plot with the highest survival after two years. Average taproot length after 2 years was 19.8 cm and the range was 11 to 39 cm.

DISCUSSION

The impact of predation on seeds by rodents on bigleaf maple establishment appears to be substantial. Coupled with the seedling mortality due to browsing by rodents and invertebrates, predators exert a profound influence on the distribution and abundance of maple seedlings in the early establishment phase. Considering the dramatic suppression of height growth on much older, taller seedlings by browsing ungulates (Fried, 1985b), it appears that the ecology of this species is closely tied to populations of various animals. For example, the high rates of seed predation in the old stands may be related to the higher degree of complexity in those ecosystems and their ability to support larger or more diverse populations of small mammals.

Germination rates were not significantly different among the forested stands and the somewhat lower rate on clearcuts could be due to a combination of the droughty month following sowing, the southern exposure of the plots, frost heaving in winter and the high solar radiation load and soil temperatures in the spring. Thus, we can infer that our inability to find natural seedlings in clearcuts or young stands in 1983 stems from a lack of maple seed source in those successional stages. Between one third and one half of the viable (as tested in Fall 1983) seeds failed to germinate, even in the exclosures, presumably because over-

winter predation by small insects, rot or defects in the seed coat that led to dessication impaired their viability.

Although stand age was not a good predictor of survival, stand successional stage was, probably because stands were selected for the old and young categories based on characteristics like degree of crown closure, stem spacing and tree size rather than chronological age alone.

Despite the more prolonged period of high moisture stress in the 1984 growing season, the proportion of mortality attributable to dessication was equal (35%) in 1983 and 1984, although average dessication rates for the two years were 7 and 14% respectively.

Apparently, light is the most limiting environmental variable in the closed canopy forests that we studied. While seedlings in the open clearcuts had small, tough, reddish, almost sclerophyllic leaves, those under all but the closed canopy stands had broad, deep green, thin leaves, a contrast similar to sun versus shade leaves. In the closed canopy stands, seedlings usually appeared weak and spindly and the leaves were often riddled with holes from invertebrate browsing. Since none of the mortality was positively identified as being directly caused by too little light, it seems that low light levels must trigger other mechanisms that ultimately lead to seedling death. Perhaps seedlings surviving tenuously in dark conditions because of limited photosynthate have little or no energy available to

expend on the production of protective chemicals, and as a result, they are more palatable to predators. Maybe seedlings growing in low light are unable to generate primary or secondary leaves if their cotyledons are eaten by predators soon after emergence whereas seedlings receiving more sunlight build sufficient starch reserves to regenerate new leaves after predation occurs. Seedlings under low light may lack the vigor to develop taproots sufficiently deep to gain access to limited soil moisture as the growing season progresses and consequently die of dessication. These are but a few possibilities and many other explanations could be postulated.

Light seems to play an important role in the growth and development of another species of maple. Wilson and Fischer (1977) found that solar radiation regulated primordia development in striped maple seedlings and saplings. Light intensities of 6% of solar radiation in the open induced formation of bud scales while an intensity of 18% promoted development of additional leaves, and maximum height growth and leaf pair formation occurred at 30-60% solar radiation. Perhaps bigleaf maple is less shade tolerant of full shade than previously supposed, at least in the establishment phase. This contrasts strikingly with highly tolerant sugar maple seedlings, whose survival is relatively independent of overstory conditions.

The autecology of bigleaf maple differs from that of

sugar maple in many other ways too. While intraspecific competition strongly affects seedling mortality in sugar maple, bigleaf maple seedlings seldom occur in densities high enough to generate such mortality. Also, while sugar maple recruitment is fairly uniform over time, pilot studies (Fried, 1985b) on bigleaf maple have demonstrated that extreme year-to-year variability typifies their seedling age structure, thereby forcing substantial departures from J-shaped form. Though year-to-year variability of sugar maple seed production is high (Bjorkbom, 1979), the higher mortality rates for years of high input result in an essentially constant net recruitment rate for this species. In any case, unmanaged sugar maple stands contain all age classes from recent germinants to mature trees, a phenomenon never observed with bigleaf maple, despite the reported annual production of large seed crops (Olson and Gabriel, 1974). Actually, the maple seed crop on the MacDonald Forest in 1984 was much smaller than 1983; in fact, it was so small that we were unable to replicate the germination/survival study for a second year because of a dearth of maple seed.

Conclusions

It appears that bigleaf maple germinates in a wide variety of environments but that early survival of bigleaf maple seedlings depends on a minimum threshold of light. Establishment in dense Douglas-fir stands where canopy cover

is greater than 90 % will probably be unsuccessful. In clearcuts and 40-80 year old Douglas-fir stands, environments where light is sufficient, survival is limited by browsing. We don't yet know whether the seedlings in clearcuts will succeed over the long term as competing vegetation invades and dominates these disturbed sites. We expect that thinning Douglas-fir stands would favor bigleaf maple seedling establishment by reducing canopy density and increasing the light reaching the forest floor.

LITERATURE CITED

- Anonymous. 1982. Annual Book of American Society for Testing of Materials Standards, pt. 19 Soil and Rock; Building Stones. D2325 and D3152.
- Bjorkbom, J. C. 1979. Seed production and advanced regeneration in Allegheny hardwood forests. Forest Service Research Paper (435), NE Forest Experiment Station, Broomhall, PA.
- Chan, S. S., R. W. McCreight and J. D. Walstad. 1985. Evaluating forest vegetative cover with computerized fisheye photographic analysis. Submitted to Forest Science, March 1985.
- Fowells, H. A. (ed.) 1965. Silvics of forest trees in the United States. Forest Service Handbook, Washington, p.51
- Fried, Jeremy S. 1985a. The effects of bigleaf maple on soils in Douglas-fir forests. Manuscript being reviewed for eventual submission to Forest Science.
- Fried, Jeremy S. 1985b. An analysis of age structure of bigleaf maple seedlings in western Oregon. Manuscript in preparation for eventual submission to Canadian J. of For. Res.
- Hall, J. K. and P. B. Alaback. 1982. Preliminary Checklist of the Vascular Flora of McDonald and Paul Dunn State Forests. Oregon State University, Forest Research Laboratory. Special Publication #3.
- Hansen, David. 1984. Age structure and importance values as indicators of comparative successional status of red alder (*Alnus rubra*) and bigleaf maple (*Acer macrophyllum*). Unpublished manuscript by David Hansen, Dept. of Biology, Pacific Lutheran University, Tacoma, WA, 98447.
- Hett, Joan M. and Orle Loucks. 1970. Sugar maple seedling mortality. J. Ecology 59:507-520.
- Hett, Joan M. 1971. A dynamic analysis of age in sugar maple seedlings. Ecology 52:6:1071-1074.
- Knezevich, Clarence A. 1975. Soil Survey of Benton County Area, Oregon. U.S. Dept. of Agriculture, Soil Conservation Service, in cooperation with Oregon Agricultural Exper. Station. Oregon State University, Corvallis. 119 p.

- Minore, Don. 1984. Silvical characteristics of bigleaf maple, preliminary draft intended for eventual inclusion in the updated version of USDA Silvical Series 13. Pacific Northwest Forest and Range Experiment Station, Portland, OR.
- Olson, David F. Jr. and W. J. Gabriel. 1974. *Acer L. Maple*. In *Seeds of woody plants in the United States*. C. S. Schopmeyer, tech. coord. U.S. Dept. of Agric., Agricultural Handbook 450. Washington, D.C. p. 187-194.
- Roy, D. F. 1955. Hardwood sprout measurements in northwestern California. PSW For. and Range Exper. Sta. Forest Res. Note 95. Berkeley, CA. 6 p.
- Ruth, Robert H. and Gerhard F. Muerle. 1958. Silvical characteristics of bigleaf maple. USDA Forest Service silvical series 13. PNW Forest and Range Exper. Sta., Portland, OR. 10 pp.
- Sabhasri, Sangs and William K. Ferrell. 1960. Invasion of brush species into small stand openings in the Douglas-fir forsts of the Willamette Foothills. *Forest Science* 34:3:77-88.
- Wilson, B. F. and B. C. Fischer. 1977. Striped maple: shoot growth and bud formation related to light intensity. *Canadian Journal of Forest Research* 7:1:1-7.

OVERALL CONCLUSIONS

If bigleaf maple is eliminated from commercial conifer forests, the most likely effects on nutrient cycling would be an increase in the amount of nutrients bound in the forest floor, and a decrease in mineral soil nitrogen and organic matter in the patches where Douglas-fir replaces bigleaf maple. The time in which these changes would become evident is unclear. Additional research is needed to determine whether the conifers surrounding or planted in eliminated patches of bigleaf maple benefit from the soil amendment by faster growth, and if so, how much the increased growth offsets the loss of potential conifer growing sites because of occupancy by bigleaf maple. In forests managed for multiple uses, a net loss of conifer growth could be at least partially offset by the possible wildlife and commercial value of maple.

This research sheds light on the seedling establishment "strategy" of bigleaf maple. This knowledge can be used to develop silvicultural techniques that prevent maple seedling establishment, thereby reducing the need for costly control of maple trees. Maintaining a closed canopy by planting conifers at close spacing and limiting thinning operations to minimize the amount of light reaching the forest floor would extend the period in which maple seedlings are excluded. These benefits, of course, would have to be weighed

against possible timber value losses due to dense stand characteristics and/or deferred commercial thinnings. Caution should be exercised in killing or felling mature maple trees in a stand because, if maple seedlings are already established underneath them, they will probably be released and thrive.

BIBLIOGRAPHY

- Alban, D.H. 1969. The influence of western hemlock and western redcedar on soil properties. Soil Sci. Soc. Am. Proc. 33:453-457.
- Anonymous. 1982. Annual Book of American Society for Testing of Materials Standards, pt. 19 Soil and Rock; Building Stones. D2325 and D3152.
- Bjorkbom, J. C. 1979. Seed production and advanced regeneration in Allegheny hardwood forests. Forest Service Research Paper (435), NE Forest Experiment Station, Broomhall, PA.
- Bohn, H. L., B. L. McNeal and G. A. O'Connor. 1979. Aluminum and transition metals. In Soil Chemistry. John Wiley & Sons, New York.
- Bray, J. R. and E. Gorham. 1964. Litter production in the forests of the world. p. 101-157. In J. B. Cragg [ed] Advances in Ecological Research. Vol. 2. Academic Press, London.
- Bray, R.H., and L.T. Kurtz. 1945. Determination of organic and available forms of phosphorous in soils. Soil Sci. 59:39-45.
- Bremner, J. M. 1965. Total nitrogen, Chap. 83 of Methods of Soil Analysis, Part 2, (Agron. Monogr. 9), Amer. Soc. Agron., Madison, Wisconsin, pp. 1149-1176.
- Bremner, J. M. and D. R. Keeney. 1966. Determination and isotope-ratio analysis of different forms of nitrogen in soils:3. Exchangeable ammonium, nitrate and nitrite by extraction-distillation methods. Soil Sci. Soc. Amer. Proc. 30:577-582.
- Challinor, D. 1968. Alteration of surface soil characteristics by four tree species. Ecology 49:286-290.
- Chan, S. S., R. W. McCreight and J. D. Walstad. 1985. Evaluating forest vegetative cover with computerized fisheye photographic analysis. Submitted to Forest Science, March 1985.

- Cole, D. W., S. P. Gessel, and S. F. Dice. 1968. Distribution and Cycling of nitrogen, phosphorous, potassium, and calcium in a second growth Douglas-fir ecosystem. In Proceedings of Symposium on Primary Productivity and Mineral Cycling in Natural Ecosystems. Amer. Asso. Adv. Sci., 13th annual meeting, Dec. 27, 1967. New York. Univ. of Maine Press. p. 193-197.
- Crocker, R. L. 1959. The plant factor in soil formation. Austr. J. Sci. 21(6):180-193.
- Doescher, P.S.; Miller, R. F. and A. H. Winward. 1984. Soil chemical patterns under Eastern Oregon plant communities dominated by big sagebrush. Soil Sci. Soc. Am. J., 48:659-663.
- Fowells, H. A. [ed.] 1965. Silvics of forest trees in the United States. Forest Service Handbook, Wahington, p.51
- Fried, Jeremy S. 1985a. The effects of bigleaf maple on soils in Douglas-fir forests. Manuscript being reviewed for eventual submission to Forest Science.
- Fried, Jeremy S. 1985b. An analysis of age structure of bigleaf maple seedlings in western Oregon. Manuscript in preparation for eventual submission to Canadian J. of For. Res.
- Gessel, S. P. and A. N. Balci. 1965. Amount and composition of forest floors under Washington coniferous forests. In C. T. Youngberg [ed] Forest-soil relationships in North America. State University Press.
- Gessel, S. P. and J. Turner. 1974. Litter production by red alder in Western Washington. Forest Science 20:4.
- Grier, C. C. and J. G. McColl. 1971. Forest floor characteristics within a small plot in Douglas-fir in Western Washington. Soil Sci. Soc. Am. J. 35:988-991.
- Hall, J. K. and P. B. Alaback. 1982. Preliminary Checklist of the Vascular Flora of McDonald and Paul Dunn State Forests. Oregon State University, Forest Research Laboratory. Special Publication #3.
- Hansen, David. 1984. Age structure and importance values as indicators of comparative successional status of red alder (Alnus rubra) and bigleaf maple (Acer macrophyllum). Unpublished manuscript by David Hansen, Dept. of Biology, Pacific Lutheran University, Tacoma, WA, 98447.

- Hett, Joan M. and Orle Loucks. 1970. Sugar maple seedling mortality. *J. Ecology* 59:507-520.
- Hett, Joan M. 1971. A dynamic analysis of age in sugar maple seedlings. *Ecology* 52:6:1071-1074.
- Jackson, M. L. 1958. Soil Chemical Analysis. Englewood Cliffs, NJ. Prentice-Hall, pp151-154.
- Jenny, Hans. 1958. Role of the plant factor in pedogenic functions. *Ecol.* 39:5-16.
- Jensen, E. C. and J. N. Long. 1983. Crown structure of a codominant Douglas-fir. *Canadian Journal of Forest Research*, Vol 13 No. 2, pp264-269.
- Jones, J. B. Jr. 1977. Elemental analysis of soil extracts and plant tissue ash by plasma emission spectroscopy. Comun. in Soil Science and Plant Analysis, 8(4), pp. 349-365.
- Keeney, D. R. and J. M. Bremner. 1966. Comparison and evaluation of laboratory methods of obtaining an index of soil nitrogen availability. *Agron. J.* 58:498-503.
- Knezevich, Clarence A. 1975. Soil Survey of Benton County Area, Oregon. U.S. Dept. of Agriculture, Soil Conservation Service, in cooperation with Oregon Agricultural Exper. Station. Oregon State University, Corvallis. 119 p.
- MacLean, D. A. and R. W. Wein. 1978. Litter production and forest floor nutrient dynamics in pine and hardwood stands of New Brunswick, Canada. *Holarctic Ecology* 1:1-15.
- Minore, Don. 1984. Silvical characteristics of bigleaf maple, preliminary draft intended for eventual inclusion in the updated version of USDA Silvical Series 13. Pacific Northwest Forest and Range Experiment Station, Portland, OR.
- Olson, David F. Jr. and W. J. Gabriel. 1974. Acer Maple. In Seeds of woody plants in the United States. C. S. Schopmeyer, tech. coord. U.S. Dept. of Agric., Agricultural Handbook 450. Washington, D.C. p. 187-194.

- Ovington, J. D. 1956. Studies of the development of woodland conditions under different trees. IV. The ignition loss, water, carbon and nitrogen content of the mineral soil. *J. Ecol.* 44:171-179.
- Peech, M. L., T. Alexander, L. A. Dean, and J. F. Reed. 1947. Methods of soil analysis for fertility investigations. USDA Circ. 757, p.25.
- Peterson, D. L. and G. L. Rolfe. 1982. Precipitation components as nutrient pathways in floodplain and upland forests of central Illinois. *Forest Science* 28:321-332.
- Rickard, W. H. 1975. Litterfall in a Douglas-fir forest near the Trojan Nuclear Power Station, Oregon. *Northwest Science* 49:183-189.
- Roy, D. F. 1955. Hardwood sprout measurements in northwestern California. PSW For. and Range Exper. Sta. Forest Res. Note 95. Berkeley, CA. 6 p.
- Ruth, Robert H. and Gerhard F. Muerle. 1958. Silvical characteristics of bigleaf maple. USDA Forest Service silvical series 13. PNW Forest and Range Exper. Sta., Portland, OR. 10 pp.
- Sabhasri, Sangs and William K. Ferrell. 1960. Invasion of brush species into small stand openings in the Douglas-fir forests of the Willamette Foothills. *Forest Science* 34:3:77-88.
- Schollenberger, C. J., and R. H. Simon. 1945. Determination of exchange capacity and exchangeable bases in soils -- ammonium acetate method. *Soil Sci.* 59:13-24.
- Stone, E. L. 1975. Effects of species on nutrient cycles and soil change. *Phil. Trans. R. Soc. Lond. B.* 271:149-162.
- Tappeiner, J. C. and A. A. Alm. 1975. Undergrowth vegetation effects on the nutrient content of litterfall and soils in red pine and birch stands in Northern Minnesota. *Ecology* 56:1193-1200.
- Tarrant, R. F. and R. F. Chandler, Jr. 1951. Observations on litter fall and foliage nutrient content of some Pacific Northwest tree species. *Journal of Forestry* 49:914-915.

- Tarrant, R. F. and R. E. Miller. 1963. Accumulation of organic matter and soil nitrogen beneath a plantation of red alder and Douglas-fir. Soil Sci. Soc. Am. Proc. 1963. pp. 231-234.
- Waring, S. A. and J. M. Bremner. 1964. Ammonium production in soil under waterlogged conditions as an index of nitrogen availability. Nature 201:950-951.
- Wilson, B. F. and B. C. Fischer. 1977. Striped maple: shoot growth and bud formation related to light intensity.
- Youngberg, C. T. 1966. Forest floors in Douglas-fir forests:I: Dry weight and chemical properties. Soil Sci. Soc. Am. J. 30:406-409.
- Zinke, P. J. 1961. The pattern of influence of individual forest trees on soil properties. Ecology 43:130-133.
- Zinke, P. J. and R. L. Crocker. 1962. The influence of giant sequoia on soil properties. Forest Science 8:2-11.