GROWTH AND NUTRIENT RELATIONS IN BLACK COTTONWOOD IN SOUTH-COASTAL BRITISH COLUMBIA

by

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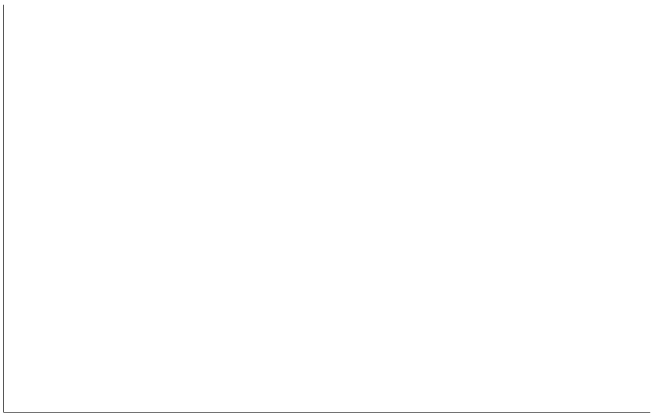

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Abstract

Initially, the study examined within and among site temporal and spatial variation of foliar nutrients, and spatial variation of soil nutrients to assess the sampling methods employed, and to provide background for the interpretation of nutrient-site index interactions. The study then examined relationships between the growth of black cottonwood, expressed as site index, and site units, understory vegetation, soil nutrient contents, and foliar nutrient concentrations in 29 black cottonwood stands in south-coastal British Columbia. The final phase of the study was a fertilizer trial in three juvenile black cottonwood stands, with treatments based on used DRIS diagnosis of limiting nutrients.

Significant levels of variability in foliar nutrient concentrations were identified within tree canopies, and from tree-to-tree within stands. A protocol was suggested to standardize sampling procedures to reduce spatial variability. Sample size requirements for different levels of accuracy and precision were presented. Important variation in foliar nutrient concentrations was also recorded seasonally, and from year to year, in foliage samples collected according to the same protocol. It was shown that the temporal variability was sufficient to alter the interpretation of foliar nutrient concentrations for the stands.

Spatial variation in soil nutrient concentrations was high and was attributed to order-of-magnitude concentration differences between soil strata in each pedon. Spatial variation of soil nutrient contents (expressed in kg/ha over a 1 m sampling depth) was generally higher than soil nutrient concentrations, because of factors such as bulk density and percent coarse fragments that were used to calculate soil contents, and that are themselves subject to variation. It was shown that the compositing procedure used to reduce costs approximately doubled the variability seen in the intensively sampled sites, and alterations to the compositing procedure were

suggested. It was also argued that sampling over a depth of 1 m, and not over the main rooting depth, provided the most biologically meaningful estimates of soil nutrients available to black cottonwood.

The ANOVA comparing black cottonwood growth within site units was highly significant ($p < .001$), and explained 87% of the variance in site index within the 29 study sites. This general result suggests that, relative to the ecological requirements of black cottonwood, the site classification provided an ecologically-meaningful differentiation of the edatopic gradients sampled. For operational purposes, this result predicts that black cottonwood site index can be estimated with considerable accuracy by identifying the site unit on which a stand is located. Growth was best on the high bench of alluvial floodplains (Ss-Salmonberry site association), and on moist upland sites with seepage (Cw-Foamflower site association). Growth was poorest on the low bench of alluvial floodplains (Ac-Willow site association), and on gleyed, marine site units (Cw-Salmonberry and Cw-Black twinberry site associations). About 50% of the variation in site index could be accounted for using understory vegetation from within the stands as predictors. This relatively low explanatory power was attributed to the fact that black cottonwood site index changed significantly across the indicative range of many of the understory plants.

All methods of analysis revealed consistent relationships between measures of site nutrient status and site index. Sample stands with high pH, high levels of exchangeable Ca and Mg, and low levels of soil N, P, and K, had foliar concentrations of N, P, and K diagnosed as limiting to black cottonwood growth, and had the lowest site index. High site index was recorded in stands with more or less opposite soil and foliar properties. Site index was seen to decrease in site units with increasing flooding frequency and duration on alluvial floodplains. The decrease was attributed to the negative impact of flooding on the rate of organic matter mineralization, on nutrient uptake, and on the negative effect of high levels of soil Ca and high soil pH on the availability of soil P. On upland sites, soil gleying and prolonged rooting zone

flooding during the growing season was correlated with low site index. Using DRIS analysis based on foliar norms from the 25 fastest-growing, fertilized trees at the Squamish 23 site, it was concluded that black cottonwood stands in the high site index class were limited by K, and then P.

In three juvenile black cottonwood stands, the application of fertilizer based on diagnosis of foliar nutrient concentration using DRIS norms had the following 3 year responses - basal area increment increased by 65%, and height growth increment by 15% at the Squamish 23 site; basal area increment increased by 65% and height growth increment increased by 30% at the Strawberry site; and basal area increment increased by 27% without a significant height growth response at the Soowahlie site. At the Squamish 23 and Soowahlie trials, response was attributed to fertilization with K and P, as suggested from the foliar nutrient diagnosis of the fast-growing group. Given that relatively low dosages (ca. 100 kg/ha) of P were required to achieve a significant growth response, and acknowledging that, in many forest fertilization programs response to P fertilization occurs for a considerable period of time, the results suggest that the fertilization of fast-growing, juvenile black cottonwood stands in coastal British Columbia may be economically justified. Significant correlations between measures of foliar response and wood production were not seen in the study, and this finding limits the usefulness of the graphical procedure for interpretation of the experimental results. Foliar concentrations from the 25 fastest-growing black cottonwoods at the Squamish 23 site are presented as DRIS standards that will be useful in the diagnosis of the nutrient status of black cottonwood stands in coastal British Columbia.

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Acknowledgements

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CHAPTER 1

INTRODUCTION

1.1 STUDY RATIONALE

Black cottonwood [*Populus trichocarpa* L. ssp. *trichocarpa* (Torrey and Gray) Brayshaw] is the largest, and most rapidly-growing broadleaf tree in western North America (Roe, 1958; DeBell, 1990). Given the availability of soil moisture and abundant soil nutrients, the species is capable of very rapid height growth (Smith, 1980) and biomass accumulation (Heilman et al., 1972; Heilman and Peabody, 1981; Heilman and Stettler, 1983, 1985b). Although many studies have been carried out that examine ecological aspects of the growth of coniferous species in western North America (Carter and Klinka, 1990; Eis, 1962; Kabzems and Klinka, 1987a; Green *et al.*, 1989; Kayahara, 1991; Klinka *et al.*, 1989; Monserud, 1984; Wang, 1992), there have been fewer studies on broad-leaved species such as red alder (Harrington, 1986; Courtin, 1992), and none on black cottonwood, except for a brief overview by Smith (1957). There have also been a number of evaluations of soil and foliar nutrient status and diagnosis of conifers (Ballard and Carter, 1986; Courtin *et al.*, 1988; Kabzems and Klinka, 1987b; Klinka *et al.*, 1984, 1990a), but none have been conducted in broad-leaved ecosystems, with predominantly Mull humus forms and rich soils. Many of the studies cited have shown that site index of the species studied is well correlated with soil moisture, soil nutrient, and regional climatic classes of the biogeoclimatic classification, but this work has not been done for black cottonwood.

Within the biogeoclimatic classification, the ecological site quality of a forest site can be summarized by determining its subzone, soil moisture regime, and soil nutrient regime, to account for the climatic, soil moisture, and soil nutrient factors affecting site productivity (Pojar *et al.*, 1987). In this study the availability of soil nutrients is assessed both qualitatively, as soil nutrient regime, and quantitatively, through the measurement of soil nutrient contents (kg/ha), and of concentrations of foliar nutrients. The rationale for employing only qualitative measures

of soil moisture and climate is that meaningful quantitative measures of these factors are difficult to acquire. A model of growing season soil water deficit using an energy-driven model with climatic normals and soil physical parameters (Spittlehouse and Black, 1981) has been used successfully by other workers (Carter and Klinka, 1990; Giles *et al.*, 1985; Wang, 1992), but is less useful in a study such as this where almost all sites receive additional, and relatively unpredictable inputs of soil moisture from flooding and seepage. The site units identified in Banner *et al.* (1990) develop special-case classes to account for variation in flooding, and thus, given the limited range of soil nutrient regimes sampled, site unit served as a measure of soil moisture regime in the present study. The acquisition of meaningful climatic data that would differentiate among the sites sampled would require on-site instrumentation and measurement over a much longer time period that this study. Compared to climate and soil moisture, it is relatively easier to acquire estimates of the absolute amounts of soil nutrients, using methods that have been correlated with productivity of trees on a given site (Curran, 1984; Klinka *et al.*, 1980; Powers, 1980).

A precise measure of the plant nutrients available in the soil at a given time is very difficult to assess directly. A major problem in attempting to measure the availability of soil nutrients for a forest stand is the large spatial variability that exists within the soil, and hence the large sampling effort required to acquire accurate estimates of the properties measured (Ball and Williams, 1968; Carter and Lowe, 1986; Courtin *et al.*, 1983; Mader, 1963; McFee and Stone, 1965; Quesnel and Lavkulich, 1980; Troedesson and Tamm, 1969). An important finding from this research is the lack of any consistent pattern in the variability of the nutrients measured. As a result, previous studies are difficult to extrapolate, unless they have been carried out on soils and stands very similar to the ones being studied (Blyth and MacLeod, 1978; Carter and Lowe, 1986; Courtin *et al.*, 1983). For this reason, the nature of spatial variability of soil nutrient contents in black cottonwood ecosystems is investigated in this study.

Evaluations of foliar nutrient concentrations bypass some of the problems associated with soil nutrient evaluations by providing direct measures of nutrients that have actually been

taken up by the tree (Ballard and Carter, 1986; Leaf, 1973; van den Driessche, 1974; Weetman and Wells, 1990). A variety of methods have been developed to use foliar nutrient concentrations for stand nutrient diagnosis including critical levels (Ballard and Carter, 1986; Everard, 1973; Leyton, 1958; Richards and Bevege, 1972), Diagnosis and Recommendation Integrated System (DRIS) ratios (Beaufils, 1973; Leech and Kim, 1979a, 1981; Schutz and de Villiers, 1986), nutrient ratios (Ballard and Carter, 1986; Ingestad, 1962), and graphical interpretations (Heinsdorf, 1968; Timmer, 1985; Timmer and Stone, 1978; Timmer and Morrow, 1984). Although some foliar nutrient diagnoses and interpretations have been carried out on other *Populus* species and on hybrid poplars (Bonner and Broadfoot, 1967; Leech and Kim, 1981; White and Carter, 1970), there is a very limited amount of information for black cottonwood (Heilman, 1985). Evaluation of foliar nutrient status was one of the major tools used to interpret relationships between black cottonwood growth and soil nutrient status in this study.

As for evaluations of soil nutrients, obtaining accurate estimates of foliar nutrient concentrations for a forest stand is also complicated by spatial variability, both within and among trees, and from stand to stand (Ellis, 1975; Guha and Mitchell, 1965 a,b; Lea *et al.,* 1979 a,b; Mitchell and Chandler, 1939; Verry and Timmons, 1976). In addition to spatial variation, seasonal, and year to year variation has also been documented (Day and Monk, 1977; Hoyle, 1965; Lea *et al.*, 1979 a,b; Verry and Timmons, 1976; White, 1954), and this component of variability has special importance for foliar sampling in broad-leaved species, because samples must be acquired during the growing season. For this reason the temporal and spatial variability of black cottonwood foliar nutrients was also investigated in this study.

The study examined relationships between ecological site quality of black cottonwood stands, and the growth of the species along a productivity gradient that included an almost four-fold increase in site index. The approach taken in the study was to use both qualitative and quantitative assessments of ecosystem nutrient status to ascertain relationships between these factors and the growth of black cottonwood. A major objective of this study was to better

understand the factors responsible for its observed range of productivity by establishing quantified relationships between site index and measurements of soil nutrient contents and foliar concentrations. A second major objective was to correlate observations of site index and site nutrient status with site units so that the information could have operational application. Quantitative relationships between measurements of soil and foliar nutrients and site units will also help provide a better understanding of the productivity of black cottonwood within the site units sampled.

A major focus of these analyses is the identification and diagnosis of nutrient limitation in black cottonwood stands. If it is concluded that a certain nutrient or combination of nutrients were limiting growth in a particular stand, then the validity of the diagnosis can be tested by applying the nutrients thought to be limiting, and then measuring the response of fertilized trees. Fertilization of fast-growing black cottonwood stands will also provide information on the potential for increasing growth in stands that are already growing rapidly.

1.2 STUDY OBJECTIVES

The rationale for conducting the research, and the general objectives have been discussed above. The specific objectives for each component of the study are listed in the chapters that follow. The overall objectives of the study were:

1) to examine spatial and temporal aspects of the variability of foliar nutrients in juvenile black cottonwood stands;

2) to examine spatial aspects of the variability of soil nutrients;

3) to develop relationships among site index, foliar and soil nutrients, understory vegetation, and site units, and to develop diagnoses of nutrient limitations; and,

4) to test diagnoses of nutrient limitation through fertilization of three black cottonwood stands.

1.3 ORGANIZATION OF THE THESIS

The thesis was written so that each chapter is as independent as possible from other chapters, and so that each represents a distinct component of research. Where methodologies overlap they were not repeated and reference is made to where they first appear in the thesis. Chapter 2 provides an overview and ecological description of the 29 black cottonwood ecosystems sampled in the study. Chapter 3 uses foliar data from intensive sampling in a subset of study sites to examine spatial and temporal variability of foliar nutrients in black cottonwood trees. The presentation and analysis of spatial variation in the chapter has been published previously (McLennan, 1990). Chapter 4 also utilizes intensive sampling in a subset of study sites to examine and evaluate soil nutrient variability. Chapter 5 uses a variety of quantitative and qualitative ecological variables to assess factors that determine the range of black cottonwood site index in the 29 sites sampled. Chapter 6 is a fertilization study carried out in 3 of the study sites, and examines the response of test trees to the application of fertilizers based on diagnosis of foliar nutrients. The last chapter briefly discusses some of the more general results, and summarizes the major findings of the study.

CHAPTER 2

DESCRIPTION AND CLASSIFICATION OF STUDY SITES

2.1 STAND SELECTION

Twenty nine stands were selected to represent the range of sites on which black cottonwood commonly grows in south coastal British Columbia (Tables 2.1, 2.2, and 2.3). The majority of sites were situated on alluvial floodplains, although upland landforms such as glaciomarine, glaciofluvial, and loess over till landforms were also sampled (Table 2.2). Alluvial floodplain sites were dominated by different Subgroups of Regosol soils, while soils on upland landforms were Gleyed, Sombric, or Orthic Humo-ferric Podzols and Orthic Humic Gleysols. Soils were mostly coarse fragment free, although a few sites had a significant amount of coarse fragments (Table 2.3). Soil textures ranged from clay to sand, but generally soils had predominantly loamy (silt loam to sandy loam) soil textures. Most sites had Mull humus forms although some Moder humus forms were described.

Most of the sites selected for sampling supported well-stocked (500-900 stems/ha) deciduous stands dominated by black cottonwood (Table 2.1). However, to sample across the edatopic range of sites on which black cottonwood occurs, it was necessary to include a number of stands where black cottonwood was not the dominant species. At several sites, black cottonwoods sampled were scattered among well-stocked plantations of *Populus 'robusta'* (Table 2.1), and these were considered to be ecologically very similar to pure black cottonwood stands. On upland sites, natural stands of black cottonwood do not occur, and black cottonwood is common as scattered individuals in a mixture of other deciduous and coniferous species. Stands of this nature were also sampled.

Table 2.1: Site index, site index class, stand age, and relative coverage of trees in the upper canopy at 29 black cottonwood study sites. Sites are listed in order of increasing black cottonwood site index and are divided into low (L=8.0-14.9 m/15 years), medium (M=15.0-21.9 m/15 years), and high (H=22.0-30.8 m/15 years) black cottonwood site index classes.

Site	Site Index (m/15 yrs)	Site Index Class	Stand Age (years)[1]	Relative % Tree Cover in Main Canopy[2]
1 Herrling	8.5	L	18	Ac (100)
2. Polygon 19	10.3	L	22	Ac (100)
3. Murphy 2	11.5	L	27	Ac (72) / Dr (28)
4. Straw 1	11.8	L	23	Ac (100)
5. Oyster	12.2	L	49	Dr (60) / Ac (30) / At (10)
6. Polygon 20	13.0	L	43	Ac (87) / Dr (13)
7. Chilliwack	13.6	L	47	Fd (53)-/ Dr (27) / Ac (20)
8. Murphy1	13.9	L	19	Ac (85) / Dr (15)
9. Elk 3	14.5	L	49	Ac (75) / Dr (25)
10. Elk 1	15.0	M	49	Dr (82) / Ac (9) / Mb (9)
11. Chipmunk	16.3	M	44	Fd (50) / Mb (25) / Ac (13) / Bg (12)
12. Elk 2	17.2	M	49	Dr (62) / Ac (38)
13. Straw 2	18.5	M	25	Ac (83) / Dr (17)
14. Pierce	20.4	M	46	Ac (40) / Dr (25) / Cw (20 / Hw (15)
15. Island 12	20.9	M	31	Ac (62) / A rob (30) / Dr (8)
16. Squam 38	21.1	M	22	Arob (69) / Ac (31)
17. Mercer	21.2	M	38	Arob (65)/ Ac (25) / Dr (5) / Mb (5)
18. Carey	21.9	M	25	Arob(80) / Ac (18) / Dr (2)
19. Salmon	23.0	H	27	Ac (85) / Dr (15)
20. Soowahlie	23.0	H	12	Ac (90) / Mb (8) / Dr (2)
21. Squam 23	24.4	H	14	Ac (85) / Dr (10) / Mb (5)
22. Borden	24.6	H	25	Ac (37) / Dr (60) / Cw (3)
23. Tamihi Fan	25.2	H	18	Ac (100)
24. Chester	25.7	H	28	Arob (80) / Ac (15) / Dr (3) / Mb (2)
25. Tamihi Cr.	26.2	H	15	Ac (83) / Mb (12) / Dr (5)
26. Sumas	27.1	H	30	Arob (75) / Ac (15) / (Dr (10) / Mb (5) / Cw (5)
27. Squam 29	28.1	H	19	Ac (53) / Dr (35) / Arob (6) / Cw (6)
28. Ashlu	28.4	H	21	Ac (60) / Dr (40)
29. Ryder	30.8	H	25	Arob (75) / Ac (15) / Ep (8) / Dr (2)

[1] refers to total age of the stand in 1989 based on the mean age of site index trees

[2] codes for species are; Ac = black cottonwood; Arob = 'Robusta' hybrid; Dr = red alder; Mb = bigleaf maple; Ep = paper birch; At = trembling aspen; Fd = Douglas-fir; Bg = grand fir; Cw = western redcedar; Hw = western hemlock

Table 2.2: Location, landform, soil, and ecological classification of 29 black cottonwood study sites.

Site	Location	Elevation (masl)	Landform	Soil Subgroup[1]	Humus Form[2]	Subzone/ Variant[3]	Site Association[4]
1 Herrling	Lower Fraser R.	30	floodplain/lb	CU.R	t.D	dm	Ac-Willow
2. Polygon 19	Lower Fraser R.	30	floodplain/lb	CU.R	t.D	dm	Ac-Willow
3. Murphy 2	Lower Fraser R.	30	floodplain/mb	O.HR	J.VL	dm	Ac-Red osier dogwood
4. Straw 1	Lower Fraser R.	20	floodplain/lb	CU.R	O.ZL	dm	Ac-Willow
5. Oyster	Oyster R.	200	glaciomarine	GL.HFP	J.VL	xm1	Cw-Salmonberry
6. Polygon 20	Lower Fraser R.	30	floodplain/mb	CU.R	t.D	dm	Ac-Red osier dogwood
7. Chilliwack	Chilliwack R.	250	glaciofluvial	GL.HFP	J.VL	dm	Cw-Foamflower
8. Murphy1	Lower Fraser R.	30	floodplain/lb	O.R	O.ZL	dm	Ac-Willow
9. Elk 3	Elk R.	200	glaciomarine	O.HG	t.D	xm1	Cw-Black twinberry
10. Elk 1	Elk R.	200	glaciomarine	GL.HFP	K.VL	xm1	Cw-Salmonberry
11. Chipmunk	Chilliwack R.	250	glaciofluvial	O.HFP	O.TD	dm	Cw-Swordfern
12. Elk 2	Elk R.	200	glaciomarine	O.HG	K.VL	xm1	Cw-Black twinberry
13. Straw 2	Lower Fraser R.	25	floodplain/mb	O.R	O.VL	dm	Ac-Red osier dogwood
14. Pierce	Chilliwack R.	250	glaciofluvial	GL.HFP	O.TD	dm	Cw-Foamflower
15. Island 12	Lower Fraser R.	30	floodplain/mb	O.R	O.VL	dm	Ac-Red osier dogwood
16. Squam 38	Squamish R.	150	alluvial fan	O.R	t.D	ds1	Cw-Foamflower
17. Mercer	Lower Fraser R.	30	floodplain/mb	O.HR	O.VL	dm	Ac-Red osier dogwood
18. Carey	Lower Fraser R.	25	floodplain/mb	O.HR	K.VL	dm	Ac-Red osier dogwood
19. Salmon	Salmon R.	50	floodplain/hb	O.HR	O.VL	xm1	Ss-Salmonberry
20. Soowahlie	Chilliwack R.	90	floodplain/hb	O.HR	K.VL	dm	Ss-Salmonberry
21. Squam 23	Squamish R.	75	floodplain/hb	O.HR	K.VL	ds1	Ss-Salmonberry
22. Borden	Chilliwack R.	100	floodplain/hb	O.R	tu.L	dm	Ss-Salmonberry
23. Tamihi Fan	Chilliwack R.	100	alluvial fan	O.R	t.D	dm	Cw-Foamflower
24. Chester	Lower Fraser R.	15	floodplain/mb	O.HR	K.VL	dm	Ac-Red osier dogwood
25. Tamihi Cr.	Chilliwack R.	100	floodplain/mb	O.HR	K.VL	xm1	Ss-Salmonberry
26. Sumas	Lower Fraser R.	150	loess/till	SM.HFP	K.VL	dm	Cw-Foamflower
27. Squam29	Squamish R.	45	floodplain/hb	CU.HR	tu.L	ds1	Ss-Salmonberry
28. Ashlu	Squamish R.	30	floodplain/hb	CU.HR	tu.L	dm	Ss-Salmonberry
29. Ryder	Lower Fraser R.	150	loess/till	SM.HFP	K.VL	dm	Cw-Foamflower

[1] Soil subgroups are identified using Agriculture Canada Committee on Soil Survey (1987); O.R=Orthic Regosol; O.HR=Orthic Humic Regosol; CU.R=Cumulic Regosol; CU.HR=Cumulic Humic Regosol; O.HFP=Orthic Humo-Ferric podzol; SM.HFP=Sombric Humo-Ferric Podzol; O.HG=Orthic Humic-Gleysol.

[2] Humus forms are identified using Klinka *et al.* (1981) with abbreviations from Luttmerding et al. (1990); t.D=tenuic Moder; O.VL=Orthivermimull; K.VL=Macrovermimull; J.VL=Microvermimull; tu.L=turbic Mull; O.ZL=Orthirhizomull

[3] CWH subzones and variants identified from Nuszdorfer *et al.* (1985)

[4] Site associations were determined from Banner *et al.* (1990)

Table 2.3: Actual soil moisture regime (aSMR), soil nutrient regime (SNR) and selected soil physical properties of 29 black cottonwood study sites.

Site	aSMR[1]	SNR[2]	Ah Depth (cm)	MRD (m)[3]	ARD (m)[4]	Soil Volume Index[5]	Soil Texture Class[6]	Coarse Fragment (%)	Depth to Gleying or Water Table[7] (m)
1. Herrling	lbF	M	0	0.48	0.67	0.67	LS	0	na
2. Polygon 19	lbSD	M	0	0.22	0.51	0.51	S	0	na
3. Murphy 2	mbM	R	7	0.60	0.79	0.79	SiL	0	na
4. Straw 1	lbM	R	3	0.55	> 1.5	1.00	SL	0	na
5. Oyster	fM	R	7	0.45	0.57	0.43	SL	25	0.42g
6. Polygon 20	mbM	R	0	1.30	> 1.3	1.00	LS	0	na
7. Chilliwack	M	R	7	0.36	0.80	0.78	C	2	0.35g
8. Murphy1	lb/VM	R	3	0.46	1.75	1.00	SL	0	na
9. Elk 3	fVM	R	1	0.34	0.42	0.42	SiL	0	0.28g
10. Elk 1	fM	VR	13	0.40	0.51	0.51	SiL	0	0.40g
11. Chipmunk	SD	M	0	0.26	1.03	0.45	S	45	na
12. Elk 2	fVM	VR	12	0.27	0.35	0.35	SiL	0	0.10g
13. Straw 2	mbM	R	8	0.63	> 2.2	1.00	SiL	0	na
14. Pierce	M	R	0	0.71	> 1.5	1.00	SL	0	1.00w
15. Island 12	mbF	R	6	0.59	> 1.5	1.00	LS	0	na
16. Squam 38	M	R	0	0.49	0.93	0.88	LS	5	na
17. Mercer	mbM	R	9	1.03	1.00	1.00	SL	0	na
18. Carey	mbM	VR	12	0.65	> 1.7	1.00	LS	0	na
19. Salmon	hbM	VR	10	0.83	> 1.5	1.00	L	0	na
20. Soowahlie	hbF	VR	12	0.68	> 2.0	1.00	SL	0	na
21. Squam 23	hbM	VR	11	0.61	> 2.0	1.00	SL	0	na
22. Borden	hbF	R	0	0.68	> 1.0	0.40	LS	60	na
23. Tamihi Fan	M	VR	2	0.66	> 1.5	0.35	LS	65	na
24. Chester	mbM	VR	17	0.58	> 1.7	1.00	SiL	0	na
25. Tamihi Ck.	hbM	VR	9	0.65	> 1.5	1.00	SCL	0	na
26. Sumas	M	VR	14	0.65	0.91	0.91	Si	0	0.85s
27. Squam 29	hbM	R	7	0.77	1.13	1.00	LS	0	na
28. Ashlu	hbM	R	1	0.7	> 2.0	1.00	SL	0	na
29. Ryder	M	VR	10	0.55	1.10	1.00	SiL	0	0.95s

[1] Actual soil moisture regime (aSMR) classes are; SD=slightly dry; F=fresh; M=moist, and; VM=very moist and were identified using Banner *et al.* (1990) and Green *et al.* (1984). For alluvial sites SMRs refer to the moisture conditions when the site is not flooded, and hb, mb, and lb denote flooding regimes for the high, middle, and low bench sites respectively. Sites with poorly-drained, fine textured soils in depressions with winter-summer fluctuating water tables are denoted with an 'f,' and the SMR noted is that during the growing season.

2 Soil nutrient regime (SNR) classes are M=nutrient medium; R=nutrient rich, and; VR=nutrient very rich, and were determined from field observations using Banner *et al.*,(1990) and Green *et al.* (1984)

[3] Main rooting depth (MRD) is defined as that depth of soil more or less completely occupied by roots.

[4] Absolute rooting depth (ARD) is defined as that depth of soil beyond which no roots are found.

[5] Soil Volume Index is a relative estimate of the soil volume available for rooting, and is based on soil rooting depth, and coarse fragment content. A value of 1 represents an area of 1 ha with unrestricted rooting and no coarse fragments to 1 m, i.e., 10,000 m3. Root restricting layers within a depth of 1 m, and coarse fragments reduce the soil volume index relative to this case.

[6] Soil texture classes are based on laboratory analysis of samples collected over the upper 1 m of soil (or to restricting layer) and have been identified using Agriculture Canada Committee on Soil Survey (1987); S=sand; LS=loamy sand; SL=sandy loam; L=loam; SiL=silty loam; Si=silt; SCL=sandy clay loam; and, C=clay.

[7] w=water table; g=gleyed soil; and, s=seepage water.

2.2 BLACK COTTONWOOD SITE INDEX AND STEM ANALYSIS

Black cottonwoods selected for stem analysis were canopy dominants or codominants, without physical damage or evidence of disease or suppression. Stem analysis trees were felled at 0.30 m, after which total height of the tree was measured. Based on the difference between total height and breast height (1.3 m), disks were removed at breast height and at 10 equal length segments to the top of the tree. Height of the section above the ground surface was noted for all disks removed. Stumps were cut off flush with the ground to get an estimate of total age. This involves some error on alluvial sites because trees may be buried by sedimentation, so that the germination point can occur somewhere below ground level. Given the rapid juvenile growth of black cottonwood, this error was considered to be small.

All disks were taken from the field for counting of the annual rings because of the difficulty in obtaining reliable age estimates from the diffuse porous wood of black cottonwood. All disks were dried in a lumber kiln, sanded with a belt sander, and moistened before counting under a 10x power binocular stereoscope. All disks were counted until the same age was arrived at on two separate counts, by two different observers.

Height at an index age of 15 years (breast height age) was estimated by first correcting estimated heights to true heights (Carmean, 1972; Dyer and Bailey, 1987), and then using an interpolation program to calculate total height by 1 year increments. Except for the Strawberry 1, Elk 1, Soowahlie, and Squamish 23, all curves were based on the means of three site trees. At Elk 1, only 2 trees were sampled, and at Strawberry 1, Squamish 23, and Squamish 23, means were based on the control trees (15 at Strawberry 1 and Squamish 23, and 10 at Soowahlie) used in fertilizer experiments conducted at those sites.

Since a sample size of 15 trees was used at Strawberry 1 and Squamish 23, they can be used to estimate the accuracy and precision of black cottonwood site index estimates where only

three trees were collected. The mean CV for Strawberry 1 and Squamish 23 was 8.3%. Using an alpha of 0.90, site index means at the sample sites with 3 trees per plot (assuming that the variances did not differ significantly among sites) were estimated at +/- 15% error.

Breast height ages of the stands were distributed fairly evenly between 12 and 49 years (Table 2.1). Site index of black cottonwood showed an almost four-fold increase from 8.5 to 30.8 m in 15 years. Estimates of site index for the two stands younger than the index age (Soowahlie and Squamish 23) were based on extrapolation of the distinctly linear height-age curves that characterizes juvenile height growth of black cottonwood. By dividing the population of study sites approximately by 3, study sites were assigned to low, medium, and high site index classes. These groups are used in Chapter 5 to analyze relationships between black cottonwood site index and ecological variables.

2.3 ECOLOGICAL DESCRIPTION AND CLASSIFICATION

Within black cottonwood stands, plots were located by excavating exploratory soil pits to ensure sample plots were uniform in general soil properties such as landform, soil subgroup, and humus form. Plots were also determined to be uniform in the composition and structure of tree and understory vegetation. Such an area delineates a forest ecosystem (Pojar *et al.*, 1987) and served as the basic sampling unit for the study. At each sample location a 0.04 ha plot that typified vegetation, site and soil conditions within the area was used for sampling ecosystem properties as outlined in Luttmerding *et al.* (1990). This involved descriptions of site properties (slope, aspect, elevation, landform, mesoslope position, and microtopography), soil properties (soil depth, texture, structure, horizonation, and colour, coarse fragment content, rooting depth, mottling and gleying, and humus form characteristics), and vegetation (percent coverage of all species by strata, except epiphytic and epilithic vegetation). Using these observations of site,

soil and vegetation properties, the soil moisture regime (SMR) and soil nutrient regime (SNR) were determined for the plots (Table 2.2) using keys provided in Banner *et al.*, (1990). Estimates of relative soil moisture regime were converted to absolute soil moisture regime following Banner *et al.* (1990), after which site associations were assigned to each plot (Table 2.2).

2.3.1 Climate

All sample sites were located below 250 masl, and across a relatively limited range of the climatic gradient in coastal British Columbia (Table 2.2). The majority of sites were located in the CWHdm subzone, with relatively fewer sites in the CWHxm and ds subzones. Also, sample sites in the CWHds and xm subzones were close to the boundary with the CWHdm subzone. Thus, sample sites were all located in cool mesothermal climates with mild, humid winters, and cool, relatively dry summers. In most sample locations sites were level or gently sloping and few alterations in regional climate due to slope or aspect were anticipated.

2.3.2 Soil Nutrient Regime

Medium sites were distinguished from rich and very rich sites by humus forms that were either poorly-developed (poor structure) and less than 1 cm in depth (classified as Tenuic Moders), or well-developed Moders with distinct ecto-organic horizons. Soil colour in nutrient medium soils was generally light and soil texture coarse. Sample sites assigned to rich and very rich soil nutrient regimes (SNRs) featured Mull humus forms with different levels of Ah horizon development, and dark, fine-textured soils. Rich sites were distinguished from very rich sites mostly by having Ah horizons less than 10 cm in depth, or where Ah horizons had been buried by sedimentation. Sites judged to be nutrient very rich featured Ah horizons deeper than 10 cm and often had an Ah_2 horizon below the Ah_1 horizon, where soils were darkly stained by organic matter, but where the characteristic crumbly structure was not present. Soil textures in nutrient very rich sites were always loam or finer, at least at the surface. Except for the three nutrient

medium sites, study locations were divided relatively equally between nutrient rich and very rich SNRs (Table 2.3). No sites with poor or very poor SNRs supporting suitable black cottonwood stands were found for sampling. Thus, although sites compared in this study represent only half of the complete spectrum of SNRs in south coastal British Columbia, the sample represents the range of SNRs on which black cottonwood commonly occurs.

2.3.3 Soil Moisture Regime

As for SNR, black cottonwood occurs on only a restricted portion of the soil moisture gradient in coastal British Columbia (Table 2.3). Based on qualitative field evaluations of soil physical properties (Banner *et al.*, 1990; Green *et al.*, 1984; Luttmerding *et al.*, 1990), the SMR for most sites studied were either fresh or moist (Pojar *et al.*, 1987). Only the Chipmunk site had a SMR that was estimated to include a period of soil drought. Most soils sampled also receive flooding or laterally-moving, sub-surface seepage water that provides additional inputs of soil moisture. The site classification of Banner *et al.* (1990) provides special-case classification units to identify sites that receive additional moisture inputs that complicate an evaluation of soil moisture regime based solely on soil physical properties. Sites located on alluvial floodplains (Ac-Willow, Ac-Red-osier dogwood, and Ss-Salmonberry site associations) were inundated either annually, or much more infrequently, depending on their elevation relative to the flooding characteristics of the river on which they are located. Study sites identified as Cw-Salmonberry or Cw-Black twinberry site associations were situated in low-relief, poorly drained upland landscapes that were subjected to an annually-fluctuating water table. Winter SMRs in these site associations were very moist and wet, and summer SMRs are fresh and moist, respectively.

To provide information on the differences in flooding characteristics on different benches within alluvial landforms, on several occasions, water levels were surveyed relative to a bench mark established within study sites on the Fraser River (Carey 1 and 2, Strawberry 1 and

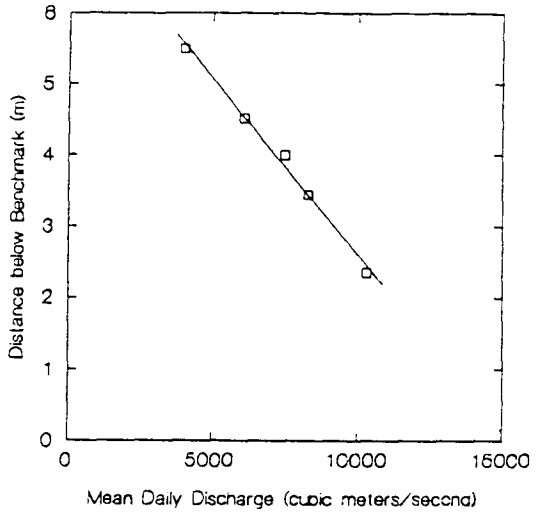
2), and at Squamish 23 on the Squamish River. These observations were then regressed against historical discharge records from Water Survey of Canada gauging stations (Figure 2.1) near the study sites. Because the number of observations was low, the regressions should be considered as preliminary. However, the very strong linear relationships (R^2s > 0.97) suggested that this method provided valid information on flooding parameters within the sites studied. A further validation of the analysis was provided by reference to Hicken and Sichingabula (1988), who estimated that bankful discharge in the Squamish River occurred at approximately 1,200 m^3/sec, and this corresponded almost exactly with overbank flows at the Squamish 23 site, as calculated from the regression shown in Figure 2.1.

Using the regression models shown in Figure 2.1, the discharges that corresponded to flooding at the soil surface, and at a depth of 60 cm in the soil, were calculated. Soil water at 60 cm was considered as an index, above which prolonged flooding may be biologically significant in reducing the amount of rooting volume for black cottonwood. For the period of the growing season (April 15 to September 30) all discharges in excess of these amounts were tabulated, and flooding parameters were summarized for the period of record (Table 2.4).

Although the flooding duration at the soil surface for low and middle bench sites was similar, flooding frequency was much higher in the low bench sites. On average, the 2 low bench sites have been flooded above the surface at least once every two years, whereas the middle bench sites have been flooded above the surface only once every 4 to 6 years. The duration of soil flooding above 60 cm soil depth has been much higher at the low bench sites, with durations up to a month, on average over the last 24 years. The high bench site sampled (Squamish 23) has had a similar flooding frequency as middle bench sites, but the flooding duration has been much shorter. The high bench site has been flooded above the surface for an average of only 1.3 days during the growing season, compared to 17 days for middle bench sites.

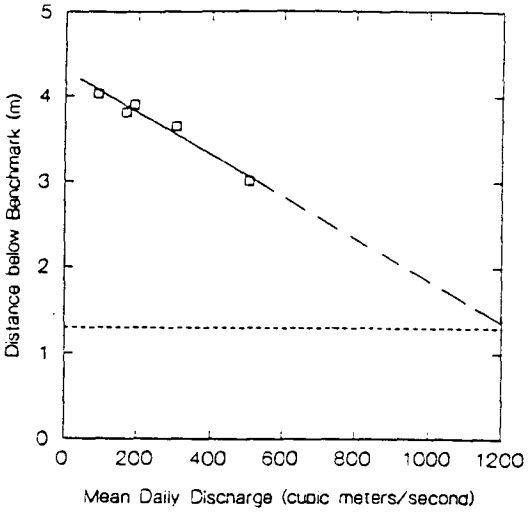
Strawberry 1

(r^2 = .998)



Squamish 23

(r^2 = .969)



Carey 1

(r^2 = .995)

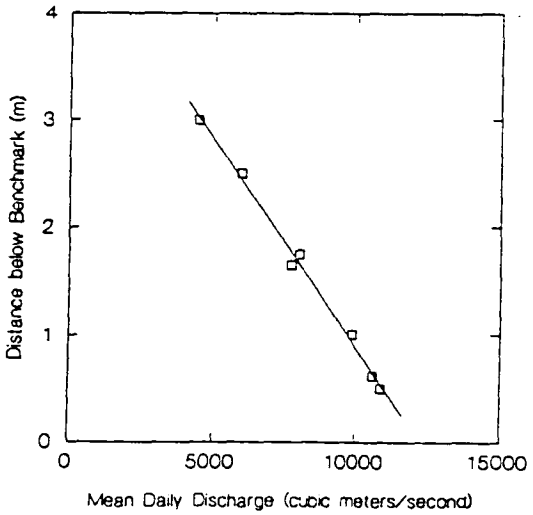


Figure 2.1: Regressions of the distance of the soil surface below the benchmark on mean daily discharge at three alluvial sites. The horizontal line at the Squamish 23 site shows the soil surface, and indicates the discharge correlated with a bank full situation.

Table 2.4: Frequency and duration of flooding during the growing season (April 15 to September 30) at selected low bench (Ac-Willow), middle bench (Ac-Red-osier dogwood), and high bench (Ss-Salmonberry). Flooding data have been calculated for a soil depth of 60 cm and for flooding at the soil surface. Statistics are based on regressions (Figure 2.2) of historical discharge data for the Fraser River at Mission, and the Squamish River at Power House gauging stations (Water Survey Of Canada).

Low Bench (Ac-Willow sa.)	Straw berry 1		Carey 2	
	soil surface	60 cm.	soil surface	60 cm.
Years of record	24	24	24	24
Years flooded	13	20	9	12
Frequency (flood/ x yrs)	1.2	1.85	1.4	2
Mean Duration (days)	17	27	17	30

Middle Bench (Ac-Red osier dogwood sa.)	Straw berry 2		Carey 1	
	soil surface	60 cm.	soil surface	60 cm.
Years of record	24	24	24	24
Years flooded	6	13	4	9
Frequency (flood/ x yrs)	1.85	4	2.6	6
Mean Duration (days)	17	17	17	19

High Bench (Ss-Salmonberry sa.)	Squamish 23	
	soil surface	60 cm.
Years of record	39	39
Years flooded	6	16
Frequency (flood/ x yrs)	2.4	6.5
Mean Duration (days)	1.3	2.1

2.3.4 Vegetation

The black cottonwood communities sampled in this study represented primary, as well as post-logging secondary successional stages on mostly fresh and moist, nutrient rich to very rich sites. The plant species that occurred with black cottonwood reflected this range of site quality - most had nutrient rich to very rich indicator values, and fresh to moist, or wetter, soil moisture

regime indicator values (Klinka *et al.*, 1989b). *Alnus rubra*, *Cornus sericea*, *Lonicera involucrata*, and *Symphoricarpos albus* occurred with black cottonwood on almost all study sites (Table 2.5). Table 2.5 shows the species that can be used to differentiate the sites, given the hierarchical structure of the site associations into upland and floodplain groups. The differential species listed in Table 2.5 had presence class values of III or greater, and were at least 2 classes greater than that of the group to which they were compared (Mueller-Dombois and Ellenberg, 1974). Given the small number of sample plots for each unit, no attempt has been made to develop a formal diagnostic table for the vegetation data.

Floodplain site associations were distinguished from upland site associations by a group of species indicating nutrient medium (*Mahonia nervosa*, *Rosa gymnocarpa*, *Rubus ursinus*) and rich (*Achlys triphylla* group) SNRs, and a range (moderately dry to very moist-wet) of SMR indicator status. The floodplain group at this hierarchical level was weakly represented by 3 species typical of middle and low bench site associations. For the two upland site associations an *Acer circinatum* group, almost all of which had fresh to very moist soil moisture indicator status, differentiated the Cw-Foamflower site association from the 'Gleyed' site association, that are differentiated by species that have very moist to wet (*Spiraea douglasii*, *Viola glabella*, *Maianthemum dilatatum*), and wet to very wet (*Malus fusca*, *Angelica genuflexa*, *Carex obnupta*) soil moisture indicator status, and reflect the winter flooding that characterizes these site units. The Ss-Salmonberry s.a. is differentiated from the other floodplain site associations by a list of species indicative of nutrient rich SNR status, and primarily fresh to very moist, or very moist to wet, soil moisture status. The Ac-Red osier dogwood s.a. was poorly-differentiated by semi-agricultural species such as *Rubus discolor*, *Rubus laciniatus*, and *Populus robusta*, which suggest a history of agricultural land use on Fraser River, middle bench sites. Species that differentiated the Ac-Willow s.a. were weedy, annual herbs that occupy exposed mineral surfaces created by frequent flooding and sedimentation in low bench sites.

Table 2.5: Presence class[1]/mean percent cover of common and differentiating species for 5 site associations sampled in the study, using upland and floodplain site groups as a primary hierarchical level. The Cw-Swordfern site has been excluded from the analysis because of only one site (Chipmunk) in the unit.

		Site Association	A.1	A.2	B.1	B.2	B.3
		Number of Plots	n=6	n=4	n=7	n=5	n=6
ALL STANDS		**Common Species**					
	Trees	*Alnus rubra*	V/10	5/38	V/17	4/3	IV/8
		Populus trichocarpa	V/30	5/13	V/37	5/26	V/40
	Shrubs	*Cornus sericea*	III/1	4/13	III/5	4/10	V/3
		Lonicera involucrata	IV/5	4/11	IV/3	4/10	V/3
		Symphoricarpos albus	V/7	4/10	IV/5	5/17	V/5
A. UPLAND SITES		**Differential Species**					
	Shrubs	*Rosa gymnocarpa*	II/t	3/6			
	Herbs	*Galium triflorum*	IV/t	4/t	III/t	1/T	I/t
		Mycelis muralis	IV/t	5/t	III/t	1/t	I/t
		Polystichum munitum	V/5	5/11	V/4	2/1	
		Pteridium aquilinum	III/t	5/3			
		Stachys cooleyae	II/t	3/3	III/t		
	Mosses	*Plagiominum insigne*	III/1	4/1	IV/1	2/1	
A.1 Cw-Foamflower		**Differential Species**					
	Trees	*Acer circinatum*	V/9		III/2	1/1	
		Acer macrophyllum	5/2	2/1	V/6	2/1	II/t
		Thuja plicata	IV/6		V/6		I/t
		Tsuga heterophylla	III/3		III/2		
	Shrubs	*Sambucus racemosa*	V/7		V/6	1/2	1/t
		Corylus cornuta	III/t		1/t	3/5	II/2
	Herbs	*Athyrium filix-femina*	V/2	3/t	V/4	4/t	
		Carex deweyana	V/2	3/t	V/1	3/4	II/t
		Dryopteris expansa	III/t		II/t		
		Geranium robertianum	III/4		III/1		
		Geum macrophyllum	III/t		IV/t		
		Tellima grandiflora	III/2		III/t	1/t	
		Tolmiea menziesii	V/5		II/1	1/3	
		Urtica dioica	III/1		II/t	1/1	
A.2 Fluctuating Water Table ('Gleyed') Sites		**Differential Species**					
	Trees	*Malus fusca*		4/3			
	Shrubs	*Holodiscus discolor*	I/t	3/1			
		Mahonia nervosa	I/1	4/2	I/t		
		Rubus ursinus		5/21	II/2		
		Spiraea douglasii		3/7		1/1	
	Herbs	*Achlys triphylla*	I/t	5/4	1/t		
		Angelica genuflexa		3/4			
		Carex obnupta		4/13			
		Maianthemum dilatatum	II/t	4/t	III/1	1/t	
		Pteridium aquilinum	III/t	5/3			
		Viola glabella		4/t			
	Mosses	*Isothecium stoloniferum*	I/t	4/t	IV/1	4/t	II/4

Table 2.5 (continued):Presence class[1]/mean percent cover of differentiating species for 5 site associations sampled in the study, using upland and floodplain sites as a primary hierarchical level. The Cw-Swordfern site has been excluded from the analysis because of only one site (Chipmunk) in the unit.

		Site Association Number of Plots	A.1 n=6	A.2 n=4	B.1 n=7	B.2 n=5	B.3 n=6
B. FLOODPLAIN SITES		**Differential Species**					
	Shrubs	*Rubus discolor*		2/7	1/t	5/13	III/1
	Herbs	*Equisetum arvense*		2/t	III/t	4/t	IV/2
	Mosses	*Isothecium stoloniferum*	1/t	4/t	IV/1	4.t	II/4
B.1 Ss-Salmonberry (High Bench)		**Differential Species**					
	Trees	*Acer circinatum*	V/9		III/2	1/1	
		Acer macrophyllum	V/1	2/1	IV/6	2/1	II/t
		Thuja plicata	IV/6		V/6		1/t
		Tsuga heterophylla	III/3		III/t		1/t
	Shrubs	*Oplopanax horridus*	II/3		III/3		
		Ribes bracteosum	I/t		III/2		
		Rubus parviflorus	IV/9	4/10	V/6	2/2	II/3
		Sambucus racemosa	V/5		V/6	1/2	1/t
	Herbs	*Carex deweyana*	V/2	3/t	V/1	3/4	II/t
		Disporum hookeri	III/t	2/t	III/t		
		Elymus glaucus	II/1	2/t	III/t	1/t	I/t
		Galium triflorum	IV/t	4/t	III/t	1/t	1/t
		Geranium robertianum	III/4		III/1		
		Geum macrophyllum	III/t		IV/t		
		Maianthemum dilatatum	II/t	4/t	III/1	1/t	
		Mycelis muralis	IV/t	5/t	III/t	1/t	I/t
		Polystichum munitum	V/5	5/11	V/4	2/1	
		Smilacina stellata	II/t		III/t		
		Stachys cooleyae	II/t	3/3	III/t		
		Tellima grandiflora	III/t		III/t	1/t	
	Mosses	*Plagiomnium insigne*	III/1	4/1	IV/1	2/1	
B.2 Ac-Red osier dogwood (Middle Bench)		**Differential Species**					
	Trees	*Populus robusta*	II/13		II/1	4/30	
	Shrubs	*Rosa nutkana*		2/1		3/2	1/t
		Rubus discolor		2/7	I/t	5/13	III/1
		Rubus laciniatus	II/t			3/t	
B.3 Ac-Willow (Low Bench)		**Differential Species**					
	Herbs	*Agrimonia striata*				1/t	IV/2
		Agrostis stolonifera		2/t	I/t		IV/2
		Aster hesperius					III/t
		Dactylis glomerata					III/t
		Hypericum perforatum			I/t		IV/t
		Melilotus alba					III/t
		Plantago lanceolata					III/t

[1] Presence class codes: I = 0-20%; II = 21-40%; III = 41-60%; IV = 61-80%; V = 81-100%. Roman numerals are used only when the number of plots for the group is > 5. Mean percent cover < 1 denoted by t ("trace")

CHAPTER 3

SPATIAL AND TEMPORAL VARIABILITY OF BLACK COTTONWOOD FOLIAR NUTRIENT CONCENTRATIONS

3.1 INTRODUCTION

The use of foliar nutrient analysis for the determination of forest stand nutrient status is complicated by spatial variability in foliar nutrient concentrations both between trees in the stand and within the canopy of individual trees. Although spatial variability of many hardwood species has been investigated by a number of workers in North America (Baker and Russell, 1975; Blackmon and White, 1972; Ellis, 1975; Guha and Mitchell, 1965a,b; Hoyle, 1965; Lea *et al.*, 1979a,b; Mitchell, 1936; Mitchell and Chandler, 1939; Morrison, 1972, 1974, 1985; Tamm, 1951; Wallihan, 1944; Woodwell, 1974) there is little information on black cottonwood. Compared to samples from the lower canopies, Heilman (1985) found significantly higher concentrations of foliar N in the upper canopies of 6 year-old black cottonwood trees. Blackmon and White (1972) showed similar differences between foliage from the upper and lower crowns for foliar N in *Populus deltoides*, although foliar P values did not vary appreciably. Guha and Mitchell (1965a) found lower concentrations of Co, N, Fe, V, Ti, Cr, Pb, and Al in upper canopy foliage of *Acer pseudoplatanus*, *Aesculus hippocastanum*, and *Fagus sylvaticum*, but for Mo, Zn, Ca, Mn, B, Si, Cu, Sr, Ba, Mg, and P intra-canopy differences were insignificant and rarely exceeded 20-30%. In *Betula alleghaniensis* only Ca was significantly higher in the upper canopy foliage, while in *Acer saccharum* Ca, K, Mg, Fe, Zn, and Na were significantly higher in the lower canopy (Morrison 1985). Similar within-canopy variation trends in independent studies of *Acer saccharum* (Ellis 1975; Morrison 1985) show that variation may show some consistent trends within the same species on different sites but more comparative studies are needed to confirm this. As a result of within-canopy variation in foliar nutrient concentrations, most workers standardize their sampling methodologies so that foliage samples are collected from the same canopy position and the same types of leaves.

A second component of spatial variability important for standardizing foliage sampling procedures is the determination of the number of samples required to obtain estimates of population parameters that meet desired accuracy and precision criteria. Coefficients of variation for the different foliar nutrients have been published for a number of hardwood species (Ellis, 1975; Guha and Mitchell, 1965a; Morrison, 1985). Morrison (1985) recommended that 30 *Acer saccharum* trees be sampled for estimates of macronutrient concentrations, and 40-70 trees for micronutrients, at an allowable error of 10% with a 0.95 significance level. A consistent trend in these findings is that foliar nutrient concentrations for macronutrients are considerably less variable than for micronutrients, but that, even in the least variable nutrients, a major sampling effort is required to attain high levels of statistical accuracy and precision.

Foliage nutrient concentrations of both coniferous and hardwood trees have been reported to fluctuate over the growing season as a result of dilution effects as leaves enlarge, internal translocation of mobile nutrient elements, leaching of foliage nutrients, and environmental factors (Day and Monk, 1977; Guha and Mitchell, 1965a,b; Knight, 1978; Lea *et al* 1979a,b; McHargue and Roy, 1933; Mitchell, 1936; Sampson and Samish, 1935; Tamm, 1951; Wells and Metz, 1963; White, 1954; Woodwell, 1974). In conifers, growing season fluctuations in foliar nutrient concentrations have led most researchers to restrict foliar sampling to the fall or winter months (Ballard and Carter, 1986; Leaf, 1973; Lavender, 1970; van den Driessche 1974), although the diagnostic precision of foliar data collected outside of the growing season has been questioned (van den Driessche, 1974).

In hardwoods, foliage collection must occur during the growing season and this has led to a number of investigations that attempt to document seasonal changes and use them to determine the best time for sampling (Lea *et. al*, 1979a,b; Guha and Mitchell, 1965a,b; Leaf, 1973; Leyton, 1948; Mitchell, 1936; Tamm, 1951). A similar pattern in many of these studies is for N, P, and Mg concentrations to decrease in the early part of the growing season as leaves enlarge, remain fairly stable over the growing season, and then decline sharply at the end of the growing season as mobile macronutrients are translocated out of foliage before abscission (Day

and Monk, 1977; Lea *et al.* 1979 a,b, 1974; White, 1954). Considerable fluctuations in K have been reported during all periods of the growing season (Tamm, 1951; Day and Monk, 1977). Non-mobile nutrients such as Ca and many micronutrients, gradually increase in concentration and show a rise in concentration towards the end of the season as mobile nutrients are removed (Lea *et al.* 1979b; Tamm, 1951). Heilman (1985) documented a significant decrease in foliar N concentrations in *Populus trichocarpa* after the middle of August. Based on these trends most researchers have recommended sampling hardwood foliage during the latter period of the growing season but before yellowing begins (Lea *et al.* 1979a,b; Leyton, 1948; Mitchell, 1936; Tamm, 1951), as this is the period of highest stability for most of the important macronutrients.

A related aspect of temporal variability in hardwood foliage concentrations is the amount of variation that can be expected from one year to the next in foliage samples collected in the same manner, from the same trees, and during the same seasonal period (Atterson, 1965 to 1970, reported in van den Driessche, 1974; Bickelhaupt *et al,* 1979; Hoyle, 1965; Leaf *et al,* 1970; Verry and Timmons, 1976). Significant year to year changes in foliar N concentrations have been reported in the first six years of a black cottonwood plantation by Heilmann (1985) but it is not clear how this applies to older trees. Variation from year to year in foliage concentrations have been attributed to internal reactions to external factors. For example, Miller (1966) correlated a number of climatic variables with foliage nutrient concentrations and found that average mean and maximum daily temperatures in the period preceding sampling were consistently correlated with fluctuations in foliage nutrient concentrations. Soil conditions have also been implicated as a factor influencing foliage nutrient concentrations (Hoyle, 1965; Pharis and Kramer, 1964; Walker, 1962). Compared to well-watered clones, Broadfoot and Farmer (1969) documented significantly higher N and slightly higher P foliage concentrations for young *Populus deltoides* grown under conditions of moisture stress. Based on a review of the literature, van den Driessche (1974) concluded that the reports of significant year to year fluctuations in foliar nutrient concentrations were to be expected since the factors which determine these variables also fluctuate from year to year.

Clearly, knowledge of spatial variability of the different foliar nutrients within the population being studied is a prerequisite for drawing reliable conclusions from foliar nutrient data (Morrison 1985; Woodwell 1974). Also, since sampling of black cottonwood foliage must be carried out during the growing season when considerable temporal variation in foliar concentrations may occur, seasonal and year to year fluctuations in foliar nutrient concentrations should also be studied (Tamm, 1951; van den Driessche, 1974). The specific objectives of this study were;

1) to evaluate the magnitude and nature of within tree, among tree, and among site variation in foliar nutrients of black cottonwood, in stands of various ages and from a range of locations;

2) to evaluate the magnitude and nature of seasonal and year to year temporal variation at some of the study sites to test the assumption of relative stability of foliar nutrient concentrations in the latter half of August, and;

3) to utilize these observations to recommend the most efficient sampling strategies for evaluating the nutrient status of black cottonwood stands using foliar nutrient sampling.

3.2 METHODS

3.2.1 Site Selection and Description

Sites were selected to represent a range of different-aged black cottonwood stands on alluvial sites in several locations in coastal British Columbia. Stands ranged in age from 2 to 43 and represented both naturally-regenerated stands and plantations. Black cottonwood stands from a wide geographic range encompass considerable genetic variation and Heilman (1985) has shown how clone effects can influence concentrations of foliar nutrients. By including genetic and age variation in the sample design, estimates of foliar variability from this study can be used to estimate sample size requirements for a wide range of black cottonwood stands in coastal

British Columbia. All sites sampled had fresh to moist soil moisture regimes (Pojar *et al.* 1987) with variations in the frequency and duration of flooding, medium to rich soil nutrient regimes (Pojar *et al.* 1987), and were located within a cool, mesothermal climate (see Tables 2.1 - 2.3).

3.2.2. Foliar Sampling

At each of the seven locations the stand was divided into 15 (13 at the Carey II site) approximately even-area plots and a random process was used to select a sampling point within each; the closest healthy, dominant or codominant black cottonwood was selected for foliar sampling. Foliage samples were collected between August 23 and 27, 1985 by a variety of methods (clipping with a pole pruner, tree felling, and shooting) depending on stand height and canopy characteristics, and followed recommendations of Mitchell (1936). Black cottonwood is characterized by heterophyllous foliage so that two types of leaves, preformed, early leaves and late leaves, are found within the same branch. Critchfield (1960) has shown that the preformed leaves are formed in the bud in the previous year and expand rapidly with spring growth initiation. The first late leaves develop from arrested primordia in the bud, while those formed later in the growing season are initiated from the apical meristem as internodes elongate. Late leaves continue to develop as long as growing conditions remain favorable Critchfield (1960). In this study, black cottonwood late leaves were easily distinguishable from early leaves by their larger size and darker green colour. For comparisons among the seven sites only the most recently matured late leaves were sampled and this meant avoiding both the early leaves and the newly-formed, apical late leaves. Using these sample selection criteria, 30 g fresh weight foliage samples were collected from lateral branches within the upper one third of the canopy at all locations. To compare variation within individual trees, samples of recently matured, late leaves were also collected from the middle one third and the lower one third of the canopy at the Soowahlie site, and from the lower one third of the canopy at the Carey II site. At Carey II, foliage samples were also collected from newly formed, apical late leaves for comparison with recently matured, late leaves.

Samples for the within-year analysis were collected in 1985 from 15 sample trees at the Soowahlie site on June 4, July 5, August 1, August 25, September 28, and October 15. These samples were collected from the upper canopy using the protocol described above. All samples except the August 25 sample were composited into one sample for analysis, and thus an estimate of sample variability is only possible for the August sample. Samples for the year to year comparisons were based on foliar analyses of control trees at the three sites (Strawberry 1, Squamish 23, Soowahlie) used for the fertilizer experiments (Chapter 6). All 1985, 1986, and 1988 concentrations are means of 15 (Strawberry 1 and Squamish 23) or 10 (Soowahlie) individual samples. In 1987 a composited sample was collected, so no estimates of variability are available for the 1987 samples.

All foliage samples were placed in paper bags and air-dried briefly until they could be oven-dried at 70°C for 24 hours, and then ground to pass a 20-mesh screen.

3.2.3 Laboratory Analysis

Foliar concentrations of N, P, K, S, SO_4-S, Ca, Mg, Cu, Zn, Fe, active-Fe, Mn, and B were determined using the following procedures. One-gram samples were wet ashed following Parkinson and Allen (1975), followed by colorimetric analysis for N (phenol-hypochlorite method) and P (unreduced vanadomolybdate complex), and atomic absorption spectrophotometry for K, Ca, Fe, Mg, Mn, Zn and Al. Copper was determined by digestion in nitric acid and hydrogen peroxide followed by atomic absorption spectrophotometry. Boron was determined by dry ashing followed by colorimetric analysis by the azomethine H method (Gaines and Mitchell, 1979). Active-Fe was extracted by a modification of the method of Oserkowsky (1933) using 1 *M* HCl and analyzed using atomic absorption spectrophotometry. Sulphur was analyzed using a Fisher Sulphur Analyzer, as described by Guthrie and Lowe (1984). The method of Johnson and Nishita (1952) was used to assess concentrations of SO_4-S. Macronutrients were expressed as percentage concentration and micronutrients as parts per million (ppm) of oven-dry mass.

3.2.4 Statistical Analysis

Principal component analysis was used as an exploratory technique to reveal variance trends in within-canopy foliage concentrations and to reduce the overall complexity in the variables measured so that predominant patterns and potential variable groupings could be identified (Gauch 1984; Pielou, 1975). For within-canopy foliage samples 95% confidence ellipses (Jolicoeur and Mosimann, 1960) around centroids of group PCA scores were constructed to evaluate relationships among the different canopy locations.

At both the Carey II and Soowahlie sites the single-factor, one-way ANOVA model was used to test the hypothesis of no significant difference among canopy strata for each of the 13 nutrients. The foliar nutrient concentration data met the criteria of being normally-distributed variables from a random sample and, in most cases, homogeneity of variance was achieved through logarithmic transformations of those samples that did not satisfy the Bartlett test. Since the treatment effect was random and quantitative, and the objective was to compare concentrations of individual nutrients among canopy strata, Duncan's multiple range test was used to compare means (Mize and Schultz, 1985).

The SASCAL program (Marshall 1987) was used to compute the numbers of samples required at several levels of accuracy and precision. Required sample sizes were calculated using both alpha (a) and gamma (g) levels of significance since workers may want to use this information to decide on the numbers of samples to composite for desired levels of precision (Ballard, 1985; Marshall and Jahraus, 1987; Marshall *et al.*, 1992). Gamma significance levels determine the probability that the confidence limit of the sample taken does not exceed the percentage error term used to determine the number of required samples. When g levels are not specified, a value of 0.50 is assumed and this may be an undesirably high probability for composited samples. When a levels alone were considered (g = 0.50) the following formula from Freese (1962) was used to calculate required sample sizes;

[1] $$N_1 = \frac{t^{2}_{(1-a/2,n_{1-1})} \times CV^2}{PE^2}$$

where, N_1 = predicted sample size, t = t statistic for desired *a* and sample n, CV = coefficient of variation, n_1 = size of pilot sample 1, and PE = percentage error. Where both *a* and *g* were considered in the determination of sample size, the following equation (Harris *et al.* 1948) was used;

[2] $$N_2 = \frac{CV^2 \times F_{(1-a)(1,n-1)} \times F_{(1-g)(n-1,Q)}}{PE^2}$$

where N_2 = the predicted sample size adjusted by g, CV and PE are the same as above, F = the value of the F statistic for desired levels of *a* and *g*, and Q = the appropriate degrees of freedom associated with the estimate of the CV. Both equations used assumed that the population of potential foliar samples in the stand was sufficiently large so that finite population corrections were not necessary.

3.3 RESULTS

3.3.1 Within-tree Spatial Variation

Principal components analysis (PCA) using concentrations of 13 foliar nutrients from different locations within the canopies of black cottonwood stands at the Carey II and Soowahlie sites showed similar trends (Tables 3.1 and 3.2, Figure 3.1). The first two principal components accounted for 66% of the variation in the data set at the Carey II site (Table 3.1) and 63% at Soowahlie (Table 3.2). At both locations the first principal component revealed a contrast between foliar nutrients with high positive (N, S, P, Cu, K, SO_4-S) and those with high negative (Mn, Ca, Zn) loadings. Magnesium and B, although positive at both sites, were much lower at Soowahlie than at Carey II. The similar relationships of nutrients along the first PCA axis at both sites demonstrates a consistent gradient from leaves relatively high in N, S, P, Cu, K, and SO_4-S, and low in Mn, Ca, and Zn, to foliage where the relative levels of these two nutrient groups are reversed. At both sites Fe and active-Fe had the highest values on the second PCA axis, suggesting that variation in the concentrations of these nutrients are controlled by different processes than those that determine foliar concentrations of the other nutrients.

The positions of foliage samples with respect to the first and second axes of the PCAs of samples from different locations within the canopies at the Soowahlie (45 samples) and Carey II (39 samples) sites is shown using 95% confidence ellipses in Figures 3.2. At the Soowahlie site (Figure 3.2) ellipses from the upper and lower canopies had very little overlap while the ellipse for the middle canopy samples overlapped both. This pattern shows the distinctness of foliar nutrient concentrations in the upper and lower canopy at this site. The overlapping of middle canopy foliar samples with both upper and lower canopy samples suggests a gradient of changing foliar nutrient concentrations within the canopies of the black cottonwood trees studied. A similar but more pronounced separation of data swarms occurred at the Carey II site (Figure 3.2) where 95% confidence ellipses for the three groups of samples (upper canopy, lower canopy, apical foliage from the upper canopy) did not overlap.

Table 3.1: Component loadings, eigenvalues, and % variance explained for PCA axes 1 and 2 for 13 foliar nutrients at the Carey II site.

Nutrient	PCA 1	PCA 2
N	0.940	0.022
P	0.901	0.000
K	0.735	0.194
Ca	-0.522	0.470
Mg	0.690	0.314
S	0.913	0.159
SO_4-S	0.691	0.064
Cu	0.800	0.142
Zn	-0.676	0.280
Mn	-0.786	0.312
B	0.544	0.373
active-Fe	-0.196	0.874
Fe	-0.031	0.886
Eigenvalues	6.242	2.271
% Variance	48.01	17.47

Table 3.2: Component loadings, eigenvalues, and % variance explained for PCA axes 1 and 2 for 13 foliar nutrients at the Soowahlie site.

Nutrient	PCA 1	PCA 2
N	0.718	0.202
P	0.946	0.088
K	0.829	0.064
Ca	-0.827	-0.008
Mg	0.123	-0.267
S	0.949	0.072
SO_4-S	0.901	-0.053
Cu	0.870	0.020
Zn	-0.448	0.455
Mn	-0.765	0.118
B	0.316	-0.240
active-Fe	-0.014	-0.894
Fe	-0.118	-0.903
Eigenvalues	6.141	2.020
% Variance	47.24	15.54

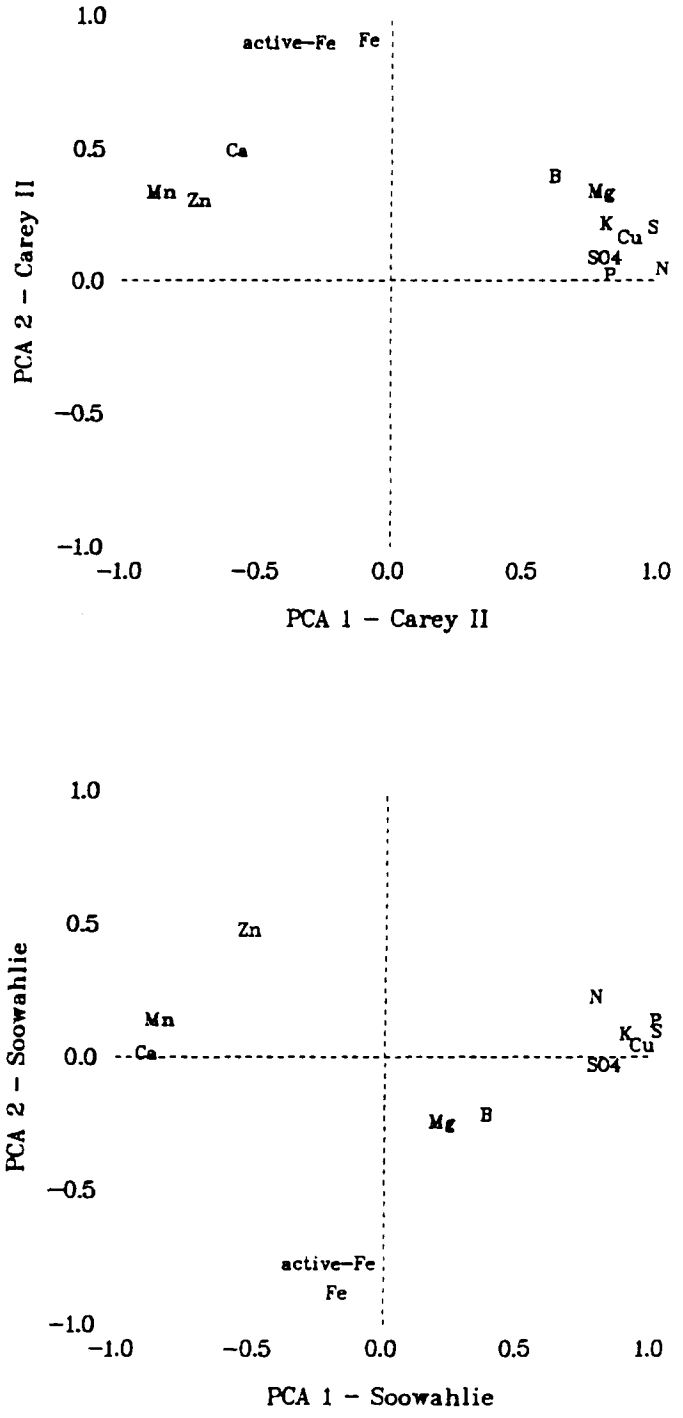


Figure 3.1: Ordinations of within canopy variation of 13 foliar nutrients on the first and second principal component axes at the Carey II (top) and Soowahlie (bottom) sites.

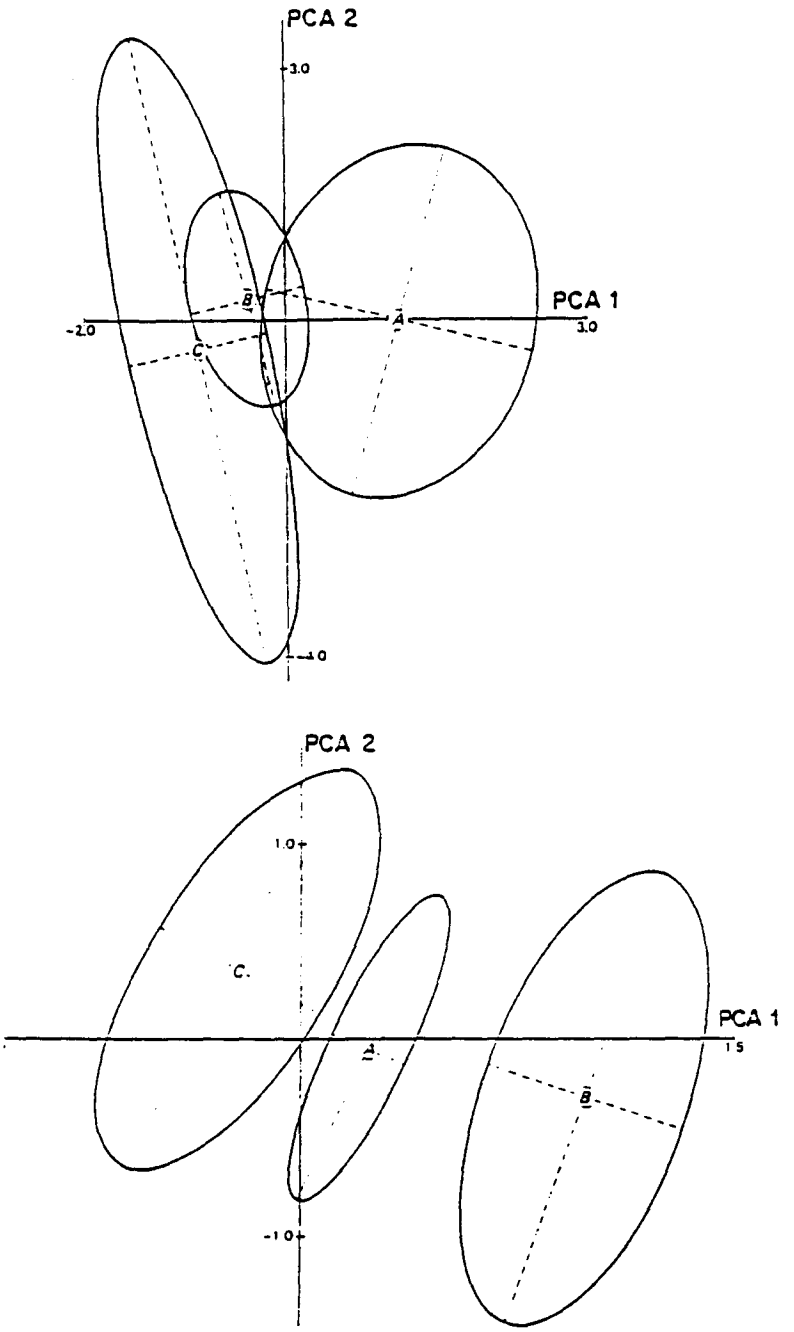


Figure 3.2: (top) Ordination of 45 foliar nutrient samples and 95% confidence ellipses for recently matured late leaves at upper (A), middle (B) and lower (C) canopy positions on the first and second PCA axes at the Soowahlie site.
(bottom) Ordination of 39 foliar nutrient samples + 95% confidence ellipses for recently matured, upper canopy leaves (A), newly-formed, apical upper canopy late leaves (B), and lower canopy late leaves (C) on the first and second PCA axes at the Carey II site.

ANOVA on non-transformed and log-transformed data, and Duncan's multiple range test for 13 nutrients at different positions within black cottonwood canopies at the Carey II and Soowahlie sites, showed that there were significant ($p < 0.05$) differences in concentrations of all nutrients except for Fe at Carey II and Fe, active-Fe, and Mg at Soowahlie (Tables 3.3 and 3.4). A similar trend was observed at both sites in that N, P, K, S, SO_4-S, Mg, and Cu were significantly higher in the upper canopy foliage and Ca, Fe, active-Fe, Mn, and Zn were significantly higher in foliage collected from the lower canopy. Boron concentrations followed a different pattern with highest concentrations in upper canopy foliage at the Carey II site and in the middle canopy samples at Soowahlie. At the Soowahlie site middle canopy foliar nutrient concentrations were intermediate between the upper and lower canopy extremes for all elements except Fe and B. The pattern showed increasing concentrations of N, P, S, SO_4-S, Mg and Cu and decreasing concentrations of Ca, Fe, active-Fe, Mn, and Zn with increasing height in the canopies of black cottonwood trees at the two sites. At Carey II apical foliage contained significantly higher concentrations of N, P, S, and Cu and significantly lower concentrations of Zn and Mn compared to mature late leaves on the same branch in the upper canopy.

3.3.2 Within-site and Among-site Spatial Variation

Mean coefficients of variation (CVs) for 13 elements in black cottonwood foliage at seven sites were lowest for N, P, K, S, Mg, and Ca (12-17%), intermediate for active-Fe (22%), and highest for SO_4-S, Cu, Zn, Mn, B, and Fe (26-37%) (Table 3.5). In general, macronutrient concentrations were characterized by relatively low levels of variation, and variation of foliar micronutrients was generally considerably higher. Foliar SO_4-S was the outstanding exception with a mean CV of 37.4%, the highest of all nutrients studied.

F ratios shown in Table 3.5 compare among-site to within-site variance for the seven sample sites and all were highly significant ($p < .001$). These comparisons suggest that, even though there is considerable variation of foliar nutrient concentrations within sites, variation among sites is significantly and consistently higher.

Table 3.3: Mean foliar nutrient concentrations (n=13) for apical, upper canopy,, and lower canopy foliage, and ANOVA, at the Carey II site. For a given nutrient, figures followed by the same letter are not significantly (p=0.05) different.

Position	N[2] (%)	P (%)	K (%)	Ca (%)	Mg (%)	S (%)	SO_4-S (ppm)	Cu[2] (ppm)	Zn[2] (ppm)	Mn (ppm)	B (ppm)	Active Fe (ppm)	Fe (ppm)
Apical leader	2.47a	0.330a	1.88a	1.15a	0.219a	0.305a	1162a	13.0a	97.7a	64.5a	33.6a	91.0a	156a
Upper canopy	1.79b	0.218b	1.89a	1.22a	0.215a	0.279b	1406b	9.39b	122.7b	84.4b	34.3a	89.3a	168a
Lower canopy	1.33c	0.165c	1.54b	1.46b	0.182b	0.211c	660c	6.85c	170.8c	105.8c	26.8b	106.0b	185a
Significance[1]	***	***	***	***	*	***	*	***	***	***	*	*	NS

[1] significance of the ANOVA at p = .05 (*), p = .01 (**), and p = .001 (***)

[2] variables for which ANOVA was carried out on log-transformed data to statisfy requirements for homogeneity of variance or normality

Table 3.4: Mean foliar nutrient concentrations (n=15) for upper, middle and lower canopy foliage, and ANOVA, at the Soowahlie site. For a given nutrient, figures followed by the same letter are not significantly (p=0.05) different.

Position	N (%)	P[2] (%)	K (%)	Ca (%)	Mg (%)	S[2] (%)	SO_4-S (ppm)	Cu[2] (ppm)	Zn[2] (ppm)	Mn[2] (ppm)	B (ppm)	Active Fe[2] (ppm)	Fe[2] (ppm)
Upper canopy	2.42a	0.239a	2.04a	0.881a	0.227a	0.335a	1648a	14.4a	102a	27.5a	36.7a	88.4a	124a
Middle canopy	2.01b	0.172b	1.33b	1.45b	0.205a	0.225b	752b	8.13b	130ab	43.7b	26.7b	90.0a	112a
Lower canopy	1.83b	0.142c	1.13b	1.60b	0.219a	0.192c	341c	7.47b	153a	46.3b	35.9a	95.5a	158a
Significance[1]	***	***	***	***	NS	***	***	***	*	***	***	NS	NS

[1] significance of the ANOVA at p = .05 (*), p = .01 (**), and p = .001 (***)

[2] variables for which ANOVA was carried out on log-transformed data to statisfy requirements for homogeneity of variance or normality

Table 3.5: Coefficients of variation (CV), mean CVs, and F ratios comparing among- and within-stand variance for foliar nutrient concentrations (n=13 at Carey II: n=15 at all other sites) in upper canopy foliage of black cottonwood at seven alluvial sites. All F ratios are significant at $p < .001$.

Site	N (%)	P (%)	K (%)	Ca (%)	Mg (%)	S (%)	SO_4-S (ppm)	Cu (ppm)	Zn (ppm)	Mn (ppm)	B (ppm)	Active Fe (ppm)	Fe (ppm)
Soowahlie	13.6	16.3	17.0	21.3	15.4	15.4	38.9	38.2	14.0	18.6	20.4	19.7	66.4
Carey I	15.7	8.3	7.7	9.1	12.8	16.1	31.7	19.5	14.3	19.1	14.0	18.7	18.9
Carey II	12.7	11.5	9.5	14.3	10.2	13.0	24.0	42.5	22.9	17.3	26.7	18.4	28.6
Scott Nursery	15.1	25.0	17.1	15.3	12.4	16.6	51.8	17.5	51.1	43.6	11.0	23.9	27.9
Strawberry I	10.8	9.0	18.7	9.6	7.5	9.3	30.9	13.7	32.4	13.8	32.3	15.1	16.6
Squamish 23	12.4	19.4	16.7	27.9	16.3	12.7	45.5	26.2	24.8	43.8	49.4	16.8	22.8
Homathko	5.8	13.0	11.5	20.1	30.4	10.0	39.1	28.0	49.9	22.0	32.2	43.1	44.7
Mean CV	12.3	14.6	14.0	16.8	15.0	13.3	37.4	26.5	29.9	25.5	26.6	22.2	32.3
SD	3.1	5.6	4.0	6.3	6.9	2.7	8.7	9.9	14.3	11.8	12.1	8.9	16.3
F Ratio	20.3	18.1	25.3	12.1	53.2	29.5	15.5	86.4	17.4	33.8	71.3	22.4	13.2

Since the mean CV for each nutrient was used to calculate generalized sample size requirements (Table 3.6), the wide ranges of CVs shown in Table 3.5 for all nutrients has important implications for composited samples, where the CV cannot be calculated. Composited samples collected from sites where the mean CV is exceeded would not meet the expected levels of precision for the nutrient considered and the size of the sample collected.

Table 3.6: Numbers of black cottonwood foliage samples required at various levels of percent allowable error, and significance for 13 foliar nutrients.

	$1-a = 0.95$ $1-g = 0.50$		$1-a = 0.90$ $1-g = 0.50$		$1-a = 0.95$ $1-g = 0.95$		$1-a = 0.90$ $1-g = 0.80$	
Nutrient	5%	10%	5%	10%	5%	10%	5%	10%
N	26	8	18	6	38	13	23	8
P	35	11	25	7	51	17	31	10
K	33	8	23	7	47	16	29	9
Ca	46	13	32	10	65	21	40	12
Mg	37	11	26	8	53	17	32	10
S	30	9	21	7	43	15	26	9
SO_4-S	217	56	153	40	288	79	178	48
Cu	110	29	78	21	149	43	92	26
Zn	140	37	99	26	187	53	116	32
Mn	102	27	72	19	139	40	86	24
B	111	30	78	20	150	43	93	26
Active-Fe	78	21	55	15	107	32	66	19
Fe	163	43	115	30	217	61	135	37

The numbers of samples required for different levels of accuracy and precision for the 13 nutrient elements analyzed in this study are given in Table 3.6. Patterns in the table are similar to patterns in the coefficients of variation (Table 3.5) from which the sample numbers were calculated. In general, for a given level of accuracy and precision, lower numbers of samples are required for N, P, K, Mg, S, and Ca and higher numbers for the other elements. Sample sizes required for high levels of accuracy and precision are large and would be expensive to

collect and analyze, even for the less variable nutrients. For example, a significance level of 0.95 with an allowable error of 5% would require at least 26 samples for N, the least variable element, and 217 samples for SO_4-S, the most variable element. Sample size requirements for N and SO_4-S increase to 38 and 288 respectively if the *a* and allowable error are kept the same and *g* significance raised from 0.50 to 0.95. Changing the allowable error to 10%, and keeping the *a* significance level at 0.95 (g = 0.50), would mean that the least variable elements (N, P, K, S, Mg, Ca) could be reliably estimated with less than 15 samples (Table 3.6). However, a sample of 15 trees would be well under the sampling requirements of the other elements, which range for 21 for active-Fe to 56 for SO_4-S at this level of accuracy and precision. For composited samples the level of *g* significance should be considered; 20 samples would provide estimates within 10% of the mean with an *a* and *g* significance of 95% for N, P, K, Mg, and S. This may represent a desirable level for operational purposes, where these common nutrients are most often considered and where costs of sampling are important.

3.3.3 Seasonal Variation

The foliar concentrations of the 13 nutrients analyzed showed considerable fluctuations over the 1985 growing season at the Soowahlie site (Figure 3.3). Foliar concentrations of N, P, K, and S exhibited an identical pattern in that concentrations were relatively constant from early June to early August, a major concentration peak occurred on the August 25 sampling date, after which concentrations declined rapidly as leaves aged before abscission. The pattern exhibited by foliar concentrations of Mg, Fe, and Cu was to increase up to August 25, decline until mid-September, and then increase in concentration just prior to abscission. SO_4-S, concentrations peaked during the middle of August, then declined, and finally rose during leaf abcission. Ca concentrations showed little change over the growing season, and an increase just prior to abscission. Zn, active Fe, and Mn had only small variations in foliage concentration over the 1985 growing season.

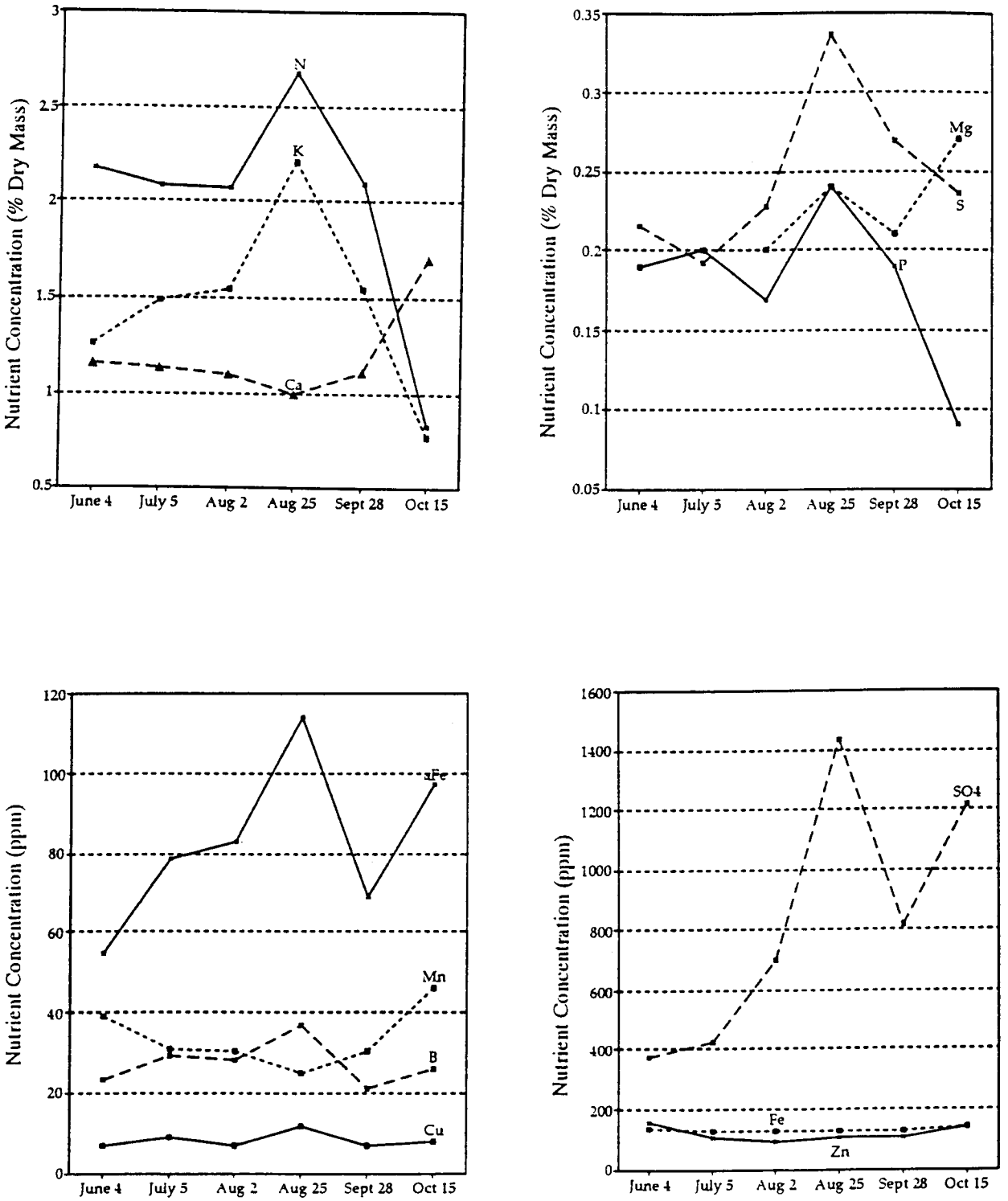


Figure 3.3: Seasonal fluctuations in concentrations of 13 foliar nutrients in the upper canopy of a 10 year old black cottonwood stand (Soowahlie) over the 1985 growing season.

None of the nutrients examined exhibited a pattern of steep concentration decline in the early part of the season (Day and Monk, 1977; Guha and Mitchell, 1965a; Hoyle, 1965, Mitchell, 1936;) and it is assumed that, because leaves emerged on the Soowahlie site in late March, by June 4 there was little dilution effect due to expanding leaf size. The steep concentration decline in N, P, K, and S at the end of the growing season on the October 15 sampling date is well documented for hardwoods (Day and Monk, 1977; Guha and Mitchell, 1965a; Hoyle, 1965; Lea *et al.* 1979 a; Mitchell, 1936) and is interpreted as showing the translocation of important mobile macronutrients out of the foliage for winter storage prior to leaf abscission. Increases in foliar concentrations of Ca, Cu, and Fe are interpreted as a result of the translocation of mobile macronutrients such as N, P, K, and S out of the foliage at that time.

Foliar concentrations of N, P, K, S, Mg, Fe, Cu all demonstrated a pronounced seasonal peak on the August 25 sampling date, and this is almost the same group of nutrients (B and SO_4-S are absent) for which canopy concentrations were significantly higher in the upper canopy foliage at the Soowahlie and Strawberry sites. Given the ability of this group of nutrients to be mobile in the phloem, it appears that their foliar nutrient concentrations may fluctuate in a relatively unpredictable manner over the growing season in black cottonwood stands.

3.3.4 Year to Year Variation

Significant ($p < .05$) fluctuations in the concentrations of P, K, Ca, S, SO_4-S, and Mn occurred at the Soowahlie, Strawberry 1, and Squamish 23 sites from year to year in 1985, 1986, and 1988 in foliar samples collected from the same trees, using the same sampling protocol, with all sampling carried out during the last two weeks of August in each year (Table 3.7). In 1987, samples from the control trees were composited into one sample for analysis and were therefore not used for the ANOVAs shown in Table 3.7. Year to year patterns for all nutrients are shown in Figures 3.4 and 3.5. Significant year to year differences in foliar concentrations of Mg, Cu,

Table 3.7: Mean foliar nutrient concentrations (n=10 at Soowahlie; 15 at Squamish 23 and Strawberry 1) from upper canopy foliage of samples collected in the last 2 weeks of August from the same sample trees in 1985, 1986, and 1988. For a given nutrient, and at the same site, figures followed by the same letter are not significantly (p=0.05) different.

Location	Year	N (%)	P (%)	K (%)	Ca (%)	Mg (%)	S (%)	SO_4-S (ppm)	Cu (ppm)	Zn (ppm)	Mn (ppm)	B (ppm)	Active Fe (ppm)	Fe (ppm)
Soowahlie	1985	2.42a	0.24a	2.04a	0.88a	0.23a	0.34a	1648a	14.4a	102a	27.4a	36.7a	88.4a	124a
	1986	2.47a	0.22a	1.67b	1.13b	0.21a	0.23b	452b	10.0a	107a	30.9a	28.6b	94.5a	128a
	1988	2.41a	0.34b	2.47c	0.69c	0.22a	0.28c	960c	13.3a	95.6a	22.3b	49.5c	84.2a	111a
Significance[1]		NS	***	***	***	NS[2]	***	***	NS[2]	NS[2]	*[2]	**	NS[2]	NS
Squamish 23	1985	2.38a	0.21a	1.76a	0.84a	0.25a	0.31a	994a	15.7a	96.9a	36.8a	17.7a	75.2a	141a
	1986	2.46a	0.19a	1.59b	1.25b	0.22b	0.21b	352b	9.93b	115b	37.4a	15.7a	62.0b	80.5b
	1988	2.39a	0.29b	2.50c	0.51c	0.21b	0.28a	603c	16.7a	87.1a	18.1b	18.9a	61.7b	74.3b
Significance[1]		NS	***	***	***	**	***	***	***	*[2]	***	NS[2]	**	***
Strawberry 1	1985	1.95a	0.18a	1.14a	1.15a	0.33a	0.22a	557a	7.67a	96.3a	66.8a	31.3a	83.2a	148a
	1986	2.09a	0.21b	1.25b	1.07a	0.30a	0.20ab	444ab	7.47a	96.1a	58.9a	26.5a	85.3a	130a
	1988	1.61b	0.19a	1.66c	0.55b	0.24b	0.18b	373b	8.60b	61.7b	15.2b	31.8a	61.6b	73.3b
Significance[1]		***[2]	**	***	***	***	***	*	*[2]	***[2]	***	NS	***	*

[1] significance of the ANOVA at p = .05 (*), p = .01 (**), and p = .001 (***)

[2] variables for which ANOVA was carried out on log-transformed data to satisfy requirements for homogeneity of variance or normality

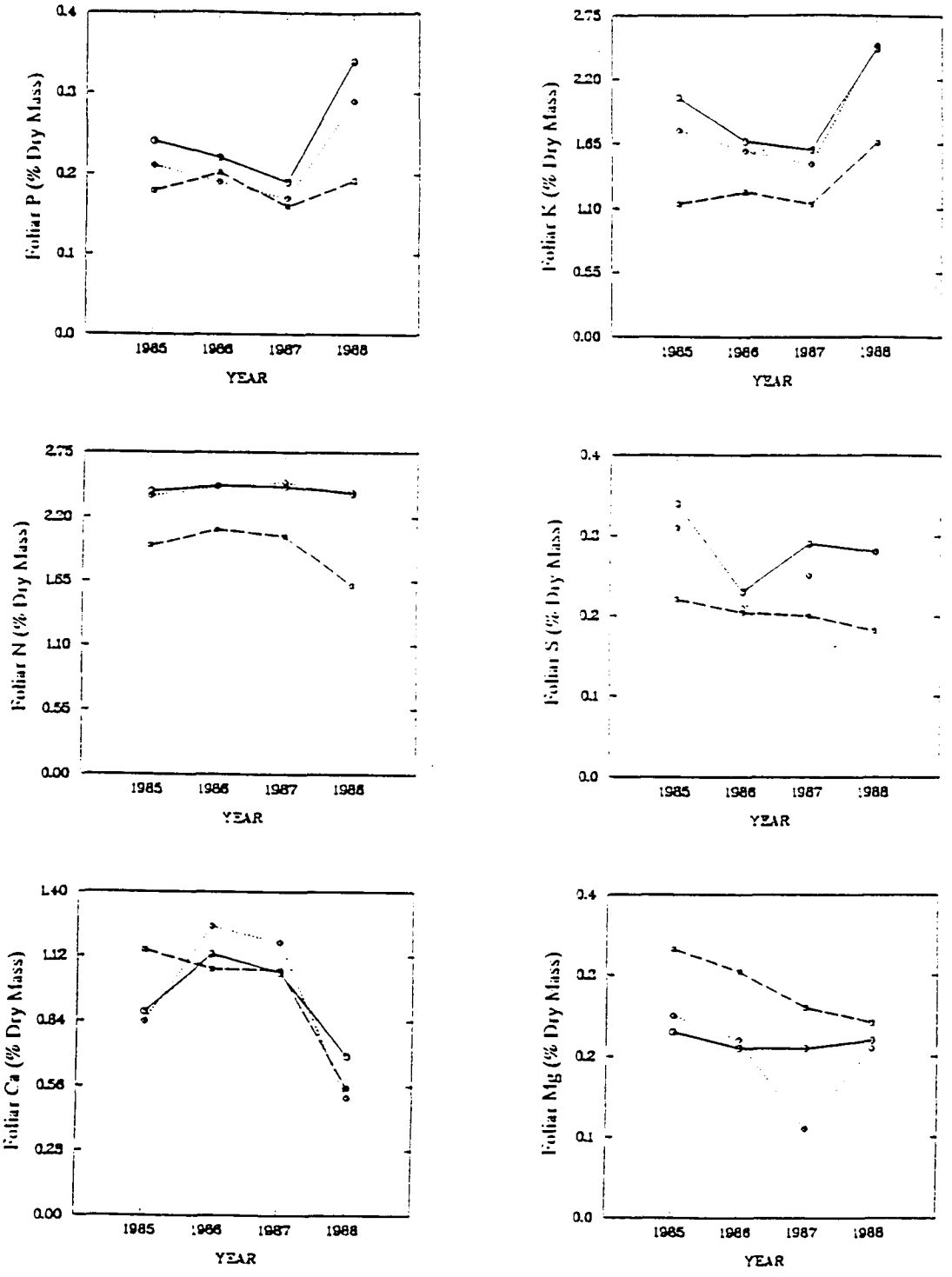


Figure 3.4: Year to year fluctuations in black cottonwood foliar nutrient concentrations of P, K, N, S, Ca and Mg. Data are for samples collected from the upper canopies of the same trees, using the same sampling protocol with all sampling carried out during the last 2 weeks of August.

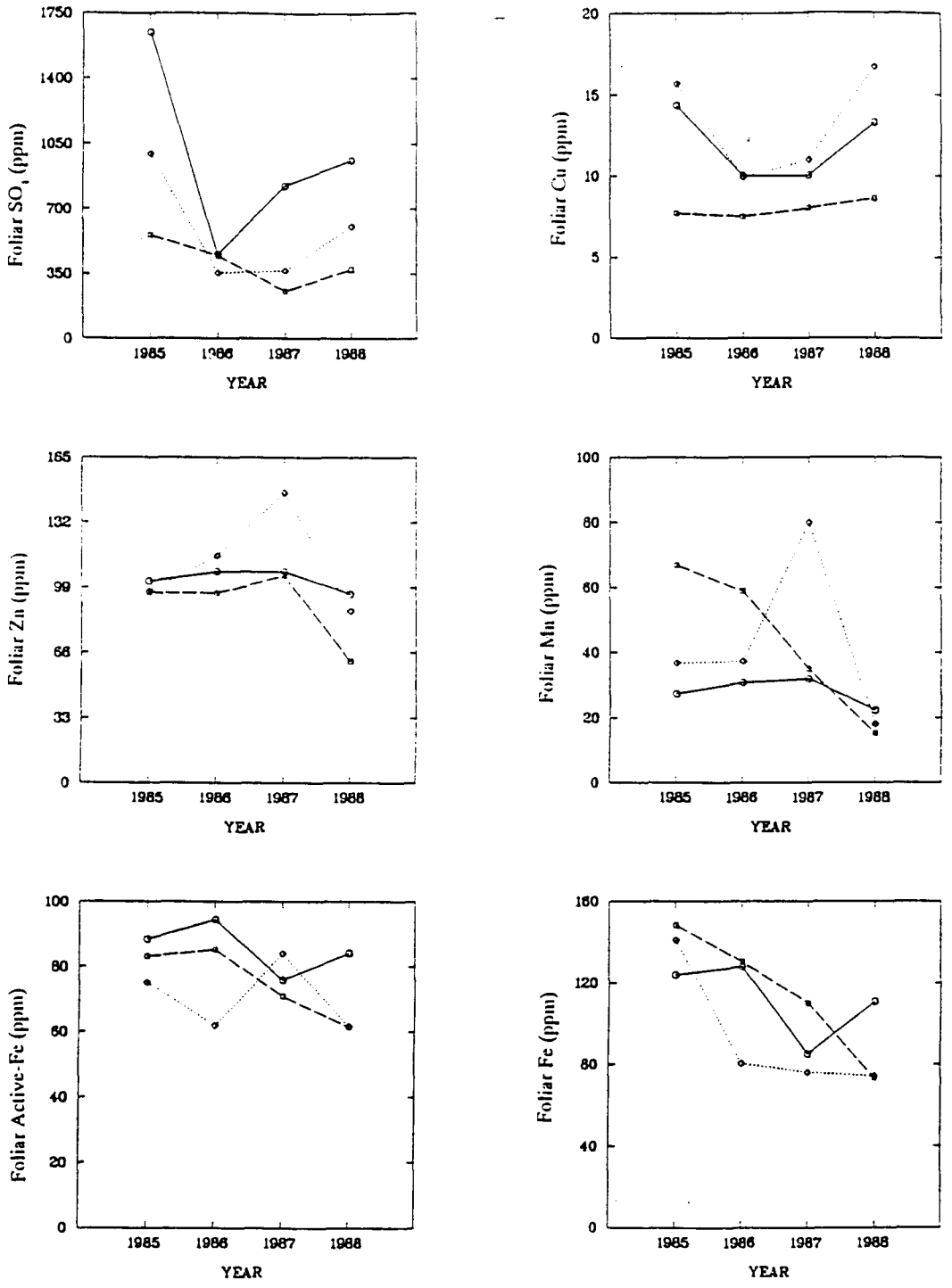


Figure 3.5: Year to year fluctuations in black cottonwood foliar nutrient concentrations of SO_4-S, Cu, Zn, Mn, Active-Fe and Fe. Data are for samples collected from the upper canopies of the same trees, using the same sampling protocol with all sampling carried out during the last 2 weeks of August.

Zn, active-Fe, and Fe were measured at the Squamish 23 and Strawberry 1 sites (Table 3.7). Concentration differences for B were significant only at the Soowahlie site and foliar N concentrations fluctuated significantly only at the Strawberry 1 site. At the Soowahlie and Squamish 23 sites P, K, and Cu demonstrated a similar year to year pattern - their concentrations decreased from 1985 over the 1986-1987 period, and then rose quite sharply in 1988. The trend of Ca was the exact opposite, S fell in 1986 and then rose in 1987 and stayed the same in 1988, and N showed no significant change during the 4 year period at these two sites . Other macro- and micronutrients fluctuated in different ways from year to year.

3.4 DISCUSSION

Principal components analyses of within-canopy variation in foliar nutrient concentrations in two black cottonwood stands revealed two relatively distinct groups of foliar nutrients; the ANOVAs conducted on the same data showed similar trends. On the basis of these observations foliar nutrients in this study are divided into two groups - Group 1 includes N, P, K, S, SO_4-S, Cu, and possibly Mg and B (although the last two are less strongly associated) and had highest concentrations in the upper canopy; Group 2 includes Mn, Zn, and Ca with highest concentrations in foliage of the lower canopy. Due to their distinct patterns in the ordinations at the Carey II and Soowahlie sites, Fe and active-Fe could be considered as a third group with different patterns of variability than all other nutrients studied.

Group 1 nutrients are all highly mobile in the phloem (Devlin, 1966; Fife and Nambiar, 1982; 1984; Ostman and Weaver, 1982; Switzer and Nelson, 1972) and were included in a 'translocated group' by Kumata *et al.* (1988), where, with leaf senescence, translocation of these nutrients from the foliage to the twigs was observed. In this study N, K, P, and S demonstrated a concentration decline at the end of the 1985 growing season and Mg, Fe, Cu, and SO_4-S did not. Concentrations of all Group 1 nutrients (except SO_4-S) showed a pronounced peak on the August 25 sampling data. Group 2 elements are all micronutrients (except Ca) that are relatively immobile in the phloem so that, once metabolized, are not easily transported to other areas

within the canopy (Attiwill, 1986; Kumata *et al.*, 1988). Group 2 nutrients demonstrated much lower levels of seasonal changes, although most showed significant year to year differences.

Differences in element mobility within the phloem has been used to interpret within-canopy variation in other hardwood species, and in conifers (Fife and Nambiar, 1982, 1984; Guha and Mitchell 1965 a,b; Morrison, 1985; Sheriff *et al.*, 1986; Wallihan, 1944). Lack of significant within-canopy variation in macronutrient foliar concentrations, lower coefficients of variation for nutrients in the lower canopy, and ease of sampling, have led some investigators to recommend sampling from the mid-crown of hardwood trees to estimate stand nutrient status (Ellis, 1975; Morrison, 1985). Guha and Mitchell (1965 a,b) stated that canopy sampling location is only important when sampling for immobile micronutrients since they did not observe significant differences in macronutrients within the canopy. None of these studies observed the pattern found for black cottonwood in this study where foliar nutrient concentrations of all macronutrients were higher in the upper canopy, and there is some evidence to suggest that this pattern of within-canopy variation is characteristic of fast-growing *Populus* species. Concentrations and concentration differences in foliar N between the upper and lower crowns of 6-year old black cottonwood trees published by Heilman (1985) are very similar to those revealed in this study. White and Carter (1970), working with *Populus deltoides*, showed a similar pattern for mobile and immobile nutrient groups and recommended sampling both upper and lower crowns for the determination of stand nutrient status of mobile nutrients such as N, P, and K. White and Carter (1970) also recommended that only upper foliage need be sampled for determination of Ca status since the element is highly immobile and thus deficiencies will appear in the youngest foliage.

Higher concentrations of Group 1 nutrients in the upper crown of black cottonwood may be the result of translocation from lower canopy foliage, differential allocation of absorbed nutrients, or both. Whatever the process, variability in foliar nutrient concentrations between the upper and lower crown of black cottonwood trees has important interpretative implications since very different conclusions about stand nutrient status could be drawn from the Carey II and

Soowahlie data, depending on which concentration is considered. For example, Heilman (1985) has suggested that, for black cottonwood, foliar N concentrations below 2.5% indicate a condition of N deficiency (see Table 5.20). Using 2.5% as a critical value, samples collected from the lower canopy at the Carey II and Soowahlie sites would indicate nitrogen deficiency, while upper canopy concentrations are very close to the critical level of 2.5% (Tables 6.4 and 6.5). The significantly lower concentrations of mobile nutrients in foliage of the upper canopy may indicate a condition of nutrient stress in that mobile macronutrients are translocated to more rapidly-growing areas of the tree crown (Devlin 1966; White and Carter, 1970a). However, it is difficult to draw this conclusion from the findings of this study since the 15 black cottonwood trees sampled at the Soowahlie site were growing rapidly and had a mean site index of 23.0 m in 15 years (see Table 2.1). In the absence of more precise information on the diagnostic usefulness of sampling and comparing upper and lower canopy nutrient concentrations, and given the higher costs of foliage sampling and laboratory analysis, it is believed that upper canopy foliage samples from black cottonwood will provide the most useful and economical interpretations of black cottonwood stand nutrient status.

This study revealed significant changes in foliar nutrient concentrations during the growing season at the Soowahlie site, and from year to year at three sites. The most significant aspect of changes in nutrient concentration over the 1985 growing season is the pronounced peak of many Group 1 nutrients (N, P, K, S, Fe, Cu, and to a lesser extent Mg and B) in late August. Foliar concentrations of these nutrients decreased significantly with decreasing canopy position (upper, middle and lower thirds) at the Soowahlie site. A similar gradient of significantly decreasing concentrations of this group of nutrients in apical, upper canopy and lower canopy foliage samples was shown for the Carey II site. Guha and Mitchell (1965b) felt that seasonal variations in foliar concentrations of nutrients appeared to be related to the physiological importance of the nutrients, and that seems to be the case in this study as well. In a review of variability in foliar nutrient concentrations within the crowns of forest trees, van den Driessche (1974) attributed within-canopy variation to auxin-controlled apical dominance, and stated that, in response to competition or environmental stress, it is likely that the apical region of the plant

will maintain a relatively higher foliar nutrient concentration, at the expense of more distal regions. This may be especially true for a highly shade-intolerant species such as black cottonwood, where maintenance of canopy dominance or codominance is a prerequisite for survival.

The relatively high concentrations of the group of mobile nutrients on the August 25 sampling date is contrary to the accepted view that foliar nutrient concentrations in hardwood species remain relatively stable over the latter part of the growing season (Day and Monk, 1977; Lea *et al.* 1979a,b; Mitchell, 1936), and thus is the best period for sampling foliage and applying and interpreting critical foliar standards. The observed year to year changes are to be expected given the significant seasonal fluctuations discussed above and shown in Figures 3.3. Foliar concentrations fluctuated seasonally in response to poorly understood environmental and physiological factors, thus foliar concentrations taken at the same time in different years may show considerable variation.

The year to year fluctuations observed at the three sites become an important aspect of variation in foliar nutrient analysis if they are of sufficient magnitude to alter interpretations based on the data, i.e., if they fluctuate across boundaries of critical limits or alter nutrient ratios significantly. Using the critical levels for P in natural *Populus* stands and plantations (see Table 5.20), the critical value is between 0.17 and 0.24%, which means that, at the Soowahlie site, the foliar analysis interpretations would range from barely sufficient or slightly deficient in 1987, to more than sufficient in 1988. A similar situation arises for K for the same site using the same standards. At the Strawberry 1 site, foliar N concentrations are just above a critical concentration of 2.0 % from 1985 to 1987, and then fall below this critical level in 1988.

A comparison of DRIS indices (Beaufils, 1973; Schutz and de Villiers, 1986) using the 1985 to 1988 foliar concentrations for N, P, K, Mg, and Ca for the Soowahlie site is shown in Table 3.8. Criteria for the DRIS analysis utilized the greenhouse standards of Leech and Kim (1981) given in Table 5.20. Interpreting the indices, in 1985 only P is limiting, in 1986 N, P, and Ca are about equally limiting, 1987 is similar to 1985 in that P is the primary limiting

nutrient, and in 1988 N and P, are interpreted as limiting. In all cases P is seen as a limiting nutrient, but this is mostly because of the high greenhouse standard for the nutrient used in this analysis, so that concentrations never attain the optimal level. Clearly, using a DRIS approach, very different interpretations of black cottonwood nutrient status would be made, depending on the year in which the samples were collected. The observed changes in the DRIS indices (and hence in their interpretation) are a result of relatively independent fluctuations of the different nutrients from year to year, and this altered the nutrient ratios from which the DRIS indices were calculated. These results contradict the assumption that the ratios used to calculate DRIS indices are constant (Leech and Kim, 1979b, 1981; Schutz and de Villiers, 1986; Sumner, 1978, 1979), even though nutrient concentrations may fluctuate.

Table 3.8: Comparisons of DRIS indices at the Soowahlie sites for 1985-1988.

Year	N	P	K	Ca	Mg
1985	8	-112	-3	44	63
1986	-26	-28	47	-28	35
1987	-2	-88	-6	46	50
1988	-14	-78	24	9	60

Using observations of within-year fluctuations in foliar nutrient concentrations in beech, sycamore, and horse chestnut, Guha and Mitchell (1965b) found that there were few elements for which stable periods could be utilized for diagnostic analysis. Based on his review of the foliar analysis literature, van den Driessche (1974) stated that annual variation of foliar concentrations were of sufficient magnitude to contribute substantially to the imprecision of the method. The results of this study support this conclusion for black cottonwood. Accurate interpretations of the nutrient status of black cottonwood using foliar nutrient information must

attempt to account for the fact that significant changes in critical foliar nutrient concentrations may occur seasonally, and from year to year on a given site. Observations of foliage nutrient concentrations over a number of years will be required to accurately evaluate stand nutrient status using foliar nutrient concentration alone. Studies of the physiological ecology of black cottonwood, in conjunction with the monitoring of important environmental factors, are required to attempt to understand, and thus be able to predict, the rapid changes in foliar concentrations within a given tree.

Estimates of the numbers of foliar samples necessary for desired levels of accuracy and precision in this study are comparable to other studies (Ballard, 1985; Ellis, 1975; Guha and Mitchell, 1965a,b; Heilman, 1985; Lavender 1970) for both macronutrients and micronutrients. Estimates of black cottonwood foliar nutrient variability presented in this study are based on samples of most recently matured, late leaves collected from lateral branches within the upper third of the canopies of dominant or codominant trees. Thus the sample size requirements presented here are valid only for samples collected according to this protocol and any deviation from this procedure can be expected to alter sample variability in an unpredictable manner. Samples of 15 trees were used in this study, and the results of within-stand variation show that a sample of this size would estimate the sample mean at an *a* significance level of 0.95, with an allowable error of 10% for the macronutrients N, P, K, Ca, Mg, and S.

Turner *et al.* (1977) have shown the usefulness of SO_4-S in predicting stand response to N fertilization. Foliar SO_4-S concentrations were the most variable (mean CV = 37.4%) of all nutrients studied in this report and this variability should be considered when interpreting foliar SO_4-S data. Both total Fe and active-Fe were measured in this study because of the better ability of active-Fe to diagnose iron deficiencies (Ballard, 1981). In this study active-Fe was shown to be much less variable than Fe so that, at an a significance level of 0.95, with an allowable error of 10%, Fe would require 43 samples and active-Fe only 21.

A sample size of 15 trees has been recommended to estimate macronutrients by several workers (Ballard, 1985; Ellis, 1985; Mitchell, 1936) and the results of this study support this

number as a compromise between desired levels of accuracy and precision, and practical aspects of foliage sample collection. Furthermore, it is these nutrients that are usually of the most interest to forest managers. Micronutrient concentrations (Cu, Zn, Fe, Mn, and B) are much more variable and between 20 and 60 samples would be required to attain the accuracy and precision stated above for macronutrients. These estimates for micronutrients are similar to those published by Ellis (1975) and are lower than many other studies.

3.5 CONCLUSIONS

1) The study revealed significant spatial and temporal variability of foliar nutrients in black cottonwood stands. Group 1 nutrients (N, P, K, S, SO_4, and possibly Mg and B) had significantly higher concentrations in the upper canopy at 2 sites, and were observed to fluctuate the most both seasonally, and from year to year. Group 1 nutrients are mostly macronutrients that are mobile within the tree, and thus their foliar concentrations may change unpredictably.

2) Foliar concentrations of several Group 1 nutrients was observed to increase in the third week of August which contradicts literature reports that foliar nutrient concentrations in broad-leaved trees are relatively stable at that time. Also, temporal fluctuations of individual foliar nutrients were often independent of other nutrients which was seen to alter the foliar nutrient ratios used to establish DRIS ratios. Observations of temporal variability in foliar nutrient concentrations reported here support those of other workers, and may seriously complicate the direct and simple interpretation of foliar nutrient concentrations.

3) Given poor knowledge of the physiological determinants of variable foliar concentrations in different areas of the canopy, it is recommended that foliar samples in black cottonwood be collected from the upper one third of canopy, according to the protocol described in the report. If this protocol is followed then the estimates of variability for the foliar nutrients studied will be valid.

4) Levels of variability and the required sampling effort in this study are similar to other studies, and support the established procedure of collecting 15 samples to capture spatial variability at a given moment in time. F ratios comparing variability among stands and within stands were highly significant for all nutrients and suggest the potential for establishing relationships between levels of foliar nutrient concentrations and black cottonwood site index.

CHAPTER 4

SPATIAL VARIABILITY OF SOIL NUTRIENTS IN BLACK COTTONWOOD STANDS

4.1 INTRODUCTION

The principal objective of soil nutrient sampling in forest productivity studies is to quantify levels of important soil nutrients within a given stand or other area of interest. The results of such sampling represent estimates of the quantities of nutrients available at a given time within the soil. These are often used as independent variables to investigate the relation to growth of a particular tree species over a range of sites (Broadfoot, 1969; Carmean, 1970, 1972; Carter and Klinka, 1990; Kabzems and Klinka, 1987b; Kayahara, 1991; Wang, 1992), or to quantify qualitative assessments of soil nutrient status (Courtin *et al.*, 1988; Kabzems and Klinka, 1987a; Klinka *et al.*, 1984). These objectives require an understanding of the spatial variability of the soil properties investigated to develop effective sampling strategies, and to determine statistical levels of accuracy and precision that can be associated with the estimates of mean values for the various nutrients.

If the objective of soil nutrient sampling is to correlate levels of soil nutrients with some productivity measure, such as the site index of a tree species, then the variability associated with a given nutrient within the site must be less than its variability among sites, if meaningful conclusions are to be drawn from the measurements (Ball and Williams, 1968; Carter and Lowe, 1986; Mader, 1963). For example, if spatial variability within sites is high, then significant relationships between soil nutrients and tree productivity may not be discernible at a given sampling intensity, even though these relationships do exist (Blyth and MacLeod, 1978). Many researchers have shown high spatial variability in soil nutrients within areas relatively uniform in soil and site properties, and, as a result, have recommended that an investigation of this variability should precede any attempts at correlating these assessments with measures of tree or

ecosystem productivity (Ball and Williams, 1968; Blyth and MacLeod, 1978; Carter and Lowe, 1986; Courtin *et al.*, 1983; Mader, 1963; Quesnel and Lavkulich, 1980; Troedsson and Tamm, 1969).

The work that has been carried out on spatial variation of soil nutrient values has focussed either on the forest floor under coniferous stands (Grier and McColl, 1971; Lowe, 1972; Mader, 1963; Mader and Lull, 1968; McFee and Stone, 1965; Quesnel and Lavkulich, 1980; Youngberg, 1965), or on the spatial variability of mineral soil properties (Blyth and MacLeod, 1978; Courtin *et al.* 1983; Drees and Wilding, 1973; Hart *et al.*, 1969; Lewis, 1976; McFee and Stone, 1965; Slavinsky, 1977; Troedsson and Tamm, 1969). None of these have been in hardwood stands with medium to very rich soil nutrient regimes, and Moder and Mull humus forms. Such a study was considered a necessary prerequisite to understanding the relationships between soil nutrient levels and black cottonwood site index.

Several workers have shown that the variability of soil nutrients is often very local in nature, i.e., as much as half of the spatial variability within a stand is contained in any square meter area of the stand, and that increasing plot size has little effect on sample variability (Beckett and Webster, 1971; McFee and Stone, 1965; Troedsson and Tamm, 1969). However, Robertson (1987), and Robertson *et al.* (1988) showed that, for mineralizable-N, samples within 20 m were highly correlated, and recommended that samples be placed at least 20 m apart to most efficiently capture site soil variability. The variability of soils in the vertical dimension, i.e., with depth, is in large part responsible for the large spatial variability over short horizontal distances, especially the continuity, depth, and character of soil organic horizons (Binkley and Hart, 1989). A number of factors create variability in surface organic layers: windthrown trees disturb the continuity of, and mix mineral soil into surface organic layers; understory and canopy species deposit leaf litter irregularly over the site, and each has litter that may have different properties for mineralization; large organic debris, such as branches, twigs and fallen trees, are distributed unevenly over the site; and, on alluvial sites, different parts of the stand will receive varying amounts and kinds of sediment deposition after flooding events. Mineral soil

layers are also subject to factors which affect the variability of soil nutrient concentrations: changes in soil texture affect the ability of a soil to hold nutrients; differences in physical conditions within the soil, such as the presence of soil water tables or poorly-aerated areas, can affect the rates at which minerals are weathered; differences in soil physical properties affect the total amount of nutrients available in the soil, e.g., the bulk density of the fine fraction and the percentage of coarse fragments, and both can vary considerably within the site. Soil samples collected to a given depth within any location within the stand will therefore incorporate both vertical and lateral spatial variability.

Temporal variability is seldom considered in studies of soil nutrients. Binkley and Hart (1989) stated that seasonal changes in nutrient concentrations in a given location are small, compared to spatial variability. However, Peterson and Rolfe (1982, 1985), and Peterson Hammer (1986) found significant seasonal differences of available N and P in a floodplain soil, and related these changes to the interactions of seasonal flooding and nutrient uptake. Important temporal changes in the levels of soil nutrients in other soils have also been documented (Haines and Cleveland, 1981; Harrison, 1979; Mollitor *et al.*, 1980; Weaver and Forcella, 1979). Seasonal variation in the availability of soil nutrients is not considered in this study.

This study investigates the spatial variability of soil nutrient concentrations and contents, and of some soil physical properties, both within a given soil pedon, and within and among sites, in 30 black cottonwood stands in south-coastal British Columbia. The within-pedon variability was assessed in an attempt to understand some of the factors that are responsible for the variability of nutrient determinations within study stands. Based on the analysis of 15 individual samples at 9 of the study sites, estimates of the numbers of soil samples required to attain various levels of accuracy and precision are presented. These variability estimates were compared to those from 21 sites where soil nutrient concentrations were estimated from composited samples. The results of the investigation are used to assess the sampling procedure used to quantify soil nutrient levels in black cottonwood ecosystems. Given the spatial

variability that exists, the usefulness of quantitative measures of soil nutrient concentrations and contents as independent variables to predict black cottonwood productivity is also discussed.

The specific objectives of the study were;

1) to analyze the sources and magnitudes of variability in soil nutrient concentrations and contents that occur within a soil pedon and contribute to overall variability in estimating soil properties for the site;

2) to quantify the level of variability in each of the soil nutrients measured within and among the 30 sites sampled;

3) to compare the effectiveness of the compositing technique used for sampling at 21 sites with the intensive sampling procedure used at 9 of the sites; and,

4) to evaluate the sampling procedures used, based on the variability observations and, if necessary, suggest improvements to the sampling methodology.

4.2 METHODS

4.2.1 Descriptions of Study Stands

Study stands used for the analysis of soil chemical variability were the same as those described in Chapter 2. Landforms, subzone, soil and humus form descriptions, and site association designations are given in Table 2.1. General properties of the soils are summarized in Table 2.2.

4.2.2 Soil Sampling

Soil sampling for chemical and physical properties was carried out at two levels of intensity. The intensive sampling, carried out at 9 sites, was used to evaluate within-site variability of soil nutrient concentrations and contents, and some other soil physical parameters.

Soil nutrient concentration is an estimate of the amount of a nutrient, expressed as a percentage, or as parts per million, of the dry mass of the soil fine fraction (< 2 mm diameter). Soil nutrient content attempts to estimate the total amount of a nutrient, and is expressed as kg/ha for a given soil depth. Estimates of soil nutrient concentrations and contents were made at a less-intensive level using compositing of soil samples at an additional 21 sites.

Each of the 9 black cottonwood stands sampled for the intensive analysis was divided into 15 approximately even-area plots, and a random process was used to select a soil pit location within each. For chemical analysis a 5 cm x 5 cm column of soil was excavated from the side of a pit, starting at the top of the mineral soil to a depth of 1 m. Estimates of main rooting depth, absolute rooting depth, depth of the Ah horizon, and changes in the texture of the various C horizons were carried out in each of the 15 pits used for the soil chemical sampling. Main rooting depth was defined as that depth of soil that is more or less completely occupied by roots. Absolute rooting depth was defined as that level beyond which no additional roots could be found. The accurate determination of absolute rooting depth was impractical given the deep nature of many of the soils studied. In many cases, absolute rooting depth was described simply as greater than the maximum depth of the soil pit excavated. Surface organic horizons (L, F, or H layers) were either absent or too thin to be included in the soil chemical sampling in all of the intensively sampled sites. At the Soowahlie and Carey I sites, 15 separate samples were collected from the Ah horizon, and from the underlying C horizons, to assess variability in nutrient concentrations with depth in the soil. At four of the sites, samples from individual C horizons were collected to evaluate changes in soil nutrient concentration with increasing depth below the Ah horizon.

In the 21 less intensively sampled study sites, each black cottonwood stand was divided into 4 equal areas, and a random procedure used to select a soil sampling location within each. In each quadrat a soil pit was excavated to a depth of at least 1 m (or to a restricting layer), and soil samples were removed from each of the 4 walls, using the same procedure described above for the intensively-sampled plots. These 4 samples were then placed in one sample bag to make

up a composite soil chemical sample. In some cases the less intensively sampled ecosystems had forest floors, and, in these cases, separate mineral soil and forest floor samples were collected in the following manner. At each of the 4 pits, 4 forest floor samples were cut with a knife so that the undisturbed dimensions of the rectangular section of forest floor removed could be measured and the volume calculated. Each forest floor sample was bagged separately for laboratory analysis, and later composited to get one sample for each of the 4 pits sampled.

Mineral soil bulk densities were measured in the field using two methods. In the first method a cylindrical hole was excavated to 30 cm soil depth and all material placed into a plastic bag and labelled. The volume of the hole was measured by inserting a thin, plastic bag into the hole, filling the bag with water to the soil surface, and then measuring the volume of water within the plastic bag in a graduated cylinder. This method was used to estimate soil bulk density at all 15 pits in the intensively sampled sites. The second method utilized a coring device in the side of the excavated soil pit where a 7 cm long cylinder of known volume was carefully pressed into the soil, after which the soil was removed and placed into a plastic bag. To coincide with the soil chemical sampling, this procedure was repeated until bulk density measures were made over the same soil depths as the soil chemical samples. Bulk densities in each of the 4 pits at the less-intensively sampled locations were made using the second method. Bulk density measurements at three to four soil pits at each of the intensively-sampled sites were also determined over the depth of soil nutrient sampling.

Coarse fragment content within the pits was evaluated by separating and weighing, in the field, all mineral fragments larger than 2.5 cm diameter, and by carefully excavating the soil pit to a known dimension so that the volume of the soil pit could be calculated. Using an average solid particle density conversion factor of 2.65, the total mass of coarse fragments >2.5 cm for the pit was converted to volume and expressed as a percentage of the soil volume. All mineral fragments greater than 2 mm diameter were removed by sieving soils in the laboratory, converted to a volume measure using the average solid particle density factor, and then added to the >2.5 cm coarse fragment fraction to get a total coarse fragment percentage.

4.2.3 Laboratory Analysis

Mineral soil samples were transported in plastic bags to the laboratory, where they were thoroughly mixed, air-dried, passed through a 2 mm sieve to remove coarse fragments, and then subsampled for analysis. Forest floor soil chemical samples were air-dried to constant mass, ground in a Wiley mill, and then composited for analysis. Mineral soil pH was measured with a pH meter using a 1:2 soil:0.01 M $CaCl_2$ suspension, as described by Peech (1965). Forest floor pH was measured with a pH meter using a 1:5 suspension in distilled water. Total carbon was determined using a Leco Induction Furnace (Bremner and Tabatabai, 1971). Total nitrogen was determined by semi-microKjeldahl digestion (Bremner and Mulvaney, 1982), followed by colorimetric analysis of ammonium using a Technicon Autoanalyzer (Anonymous, 1966). Mineralizable nitrogen was determined from incubated samples for 14 days at 30°C using the anaerobic incubation method of Wareing and Bremner (1964), as modified by Powers (1980), using a Technicon Autoanalyzer to measure released ammonium. The Mehlich extraction method (Mehlich, 1978) was used to measure extractable P, as suggested by Curran (1984). Available sulphate-sulphur was determined by ammonium acetate extraction (Bardsley and Lancaster, 1965), reduction to sulphide, followed by colorimetric determination of the reduced sulfide (Kowalenko and Lowe, 1972). Extractable K, Ca, and Mg were determined by extraction with Morgan's solution of sodium acetate with a pH of 4.8 (Grewelling and Peech, 1960), as recommended by Klinka *et al.* (1980). All soil nutrient measurements were expressed as percent or parts per million of soil dry mass.

Subsamples of the soil chemical samples were used to determine the percentage of clay, silt, and sand in the samples using the pipette method (Anonymous, 1974). Measurements of soil texture were carried out on samples composited over the entire depth used for the soil chemical sampling.

Coarse fragment free bulk densities were determined by measuring the mass of samples of known volume after oven-drying at 105°C to constant mass, and passing the samples through a 2 mm sieve to remove the coarse fragments. Mass of soil <2 mm in diameter was then divided

by the volume of soil <2 mm diameter (corrected for coarse fragments >2 mm using the average solid particle density factor) to arrive at coarse fragment free bulk density.

Soil nutrient measurements were expressed as concentrations (% or ppm) of soil dry mass based on the analytical procedures. Using soil nutrient concentration, coarse fragment free bulk density, and a measure of soil volume (coarse fragment corrections and main rooting depth/root restricting layer measurements), soil nutrients were expressed on a mass per unit area (kg/ha) basis.

4.2.4 Statistical Analyses

The SASCAL program (Marshall, 1987) was used to compute the numbers of samples required at several levels of accuracy and precision, using the procedures and approach outlined in Chapter 3. Analysis of variance was carried out using assumptions and methods of the multivariate general linear model (Cohen, 1968; Knapp, 1978), as outlined in Chapter 3. Relative sampling error (RSE) was calculated to compare the confidence intervals obtained from the composited samples with those from the intensively sampled sites using the following formula;

$$RSE = \frac{[\sqrt{s^2/n} \times t_{(n-1)}] \times 100}{\bar{x}}$$

where; s^2 = variance of the sample; n= number of soil samples analyzed; $t_{(n-1)}$= t value associated with the n of samples at the required accuracy; and x = mean of the sample

4.3 RESULTS AND DISCUSSION

4.3.1 Variability in Soil Properties within the Soil Pedon

Table 4.1 presents descriptions of two alluvial soil profiles (Carey I and Soowahlie) where sampling by depth was carried out. Ecto-organic surface horizons were largely absent from the soil profile in black cottonwood ecosystems, except in the fall after the period of annual litterfall. Litter materials are rapidly incorporated into the upper mineral soil forming an Ah horizon of varying depths, depending on the age of the stand and the nature of the flooding regime. The A horizons described in Table 4.1 are typical of the well-developed Ah horizons commonly found under black cottonwood stands. Soil colour in the Ah horizon was variable; dark brown and brown hues with values between 3 and 5 and chromas of 2 to 3 were common. Soil structure in the Ah horizon was distinctly granular, very loose and friable, and earthworms were common in most profiles observed in this study. Ah horizons under cottonwood stands had abundant roots of very fine to medium size. Characteristically, relatively large lateral roots spread out in the interface between the bottom of the Ah layer and the top of the mineral horizons below.

A region of darkly-stained mineral soil commonly underlaid the well-developed Ah horizon, and was designated as an Ah_2 horizon (Agriculture Canada, 1987). In alluvial soils, the organic-enriched A horizons on the surface usually overlaid mineral soils at depth that had been fluvially-deposited in distinct, sorted horizons. Structure in these horizons was single-grained (Luttmerding *et al.*, 1990) and coarse fragments were generally absent. The Borden site, located on a cobbly and bouldery alluvial surface along the high gradient portion of the Chilliwack River, was the only exception. The Carey 1 profile described in Table 4.1 is typical of many of the alluvial sites sampled; sandy loam at the surface overlaid layers of sand and loamy sand, which in turn overlaid channel gravels at depth. The coarse-textured loamy sand layer directly under the Ah horizon at Soowahlie pit 14 (Table 4.1) was relatively uncommon in the sites studied.

Table 4.1: Descriptions of two alluvial soil profiles from the Carey 1 and Soowahlie sample sites.

Carey I

Horizon	Depth (cm)	Horizon Description
LF	2-0	partially decomposed leaf and twig litter
Ah_1	0-12	dark brown (10 YR 4/3); loam; coarse, granular structure; roots very fine to medium, abundant; pH=6.3; earthworms
Ah_2	12-22	brown (10YR 5/3) sandy loam; single grained structure; roots very fine to coarse, abundant; pH=6.3
C_I	22-42	light brownish-gray (2.5Y 6/2) sandy loam; single-grained structure; roots fine to coarse, plentiful; pH=7.0
C_{II}	42-81	white (2.5Y 8/2) sand; single-grained structure; roots medium to coarse, very few; pH=6.3
C_{III}	81-144	pale yellow (2.5Y 7/4) loamy medium sand; single-grained structure; roots medium to coarse, plentiful; pH=7.9
C_{IV}	144-170+	yellow (2.5Y 7/6) coarse sand; single-grained structure; roots coarse, very few; pH=7.0

Soowahlie

Horizon	Depth (cm)	Horizon Description
LF	2-0	partially decomposed leaf and twig litter
Ah_1	0-10	dark grayish brown (10 YR 4/2) loamy sand; coarse, granular structure; roots fine to medium, abundant; pH=5.7; earthworms
C_I	10-34	pale yellow (2.5Y 7/4) sand; single-grained structure; roots coarse, few; pH=5.8
C_{II}	34-52	pale yellow (2.5Y 7/4) sandy loam; single-grained structure; small layers of pure, coarse sand; roots medium to coarse, plentiful; pH=6.0
C_{III}	52-65	light gray (2.5Y 7/2) sand; roots coarse, few; pH=5.6
C_{IV}	65-81	pale yellow (2.5Y 7/4) loamy fine sand; roots medium to coarse, few; pH=5.6
C_V	81-100+	light gray (2.5Y 7/2) sand; roots coarse, very few

At both sites, roots in the mineral soil were distributed according to the texture of the stratum, so that very coarse-textured soil horizons had very few roots, while loamy strata at greater depth had abundant roots of all sizes (Table 4.1). This pattern often made the meaningful determination of main rooting depth very difficult. At most sites, some roots were found throughout the profile down to, and into, the gravel layer, so that absolute rooting depth was also difficult to determine.

Bulk density data presented in Figure 4.1 are based on samples collected to a depth of 1 m in the soil pits from Carey I and Soowahlie shown in Table 4.1. Changes in bulk density within the soil profile paralleled soil morphology. Bulk density in the organic-enriched Ah horizon was about 0.95 mg/cm^3, and increased in the C horizons to between 1.1 and 1.4 mg/cm^3 (Figure 4.1) in both profiles. Coefficients of variation for mineral soil bulk density within a given profile ranged as high as 42% (Table 4.2), and show that vertical heterogeneity in soil texture and porosity add a significant component of variability to estimates of soil nutrient contents.

Figures 4.2 and 4.3 compare pH and mean concentrations of soil nutrients in 15 samples collected from the Ah horizon with 15 samples collected from the underlying C horizons (to a depth of 1 m) at the Carey 1 and Soowahlie sites. Nutrient concentrations were significantly higher in the Ah horizon for all nutrients except extractable-P at the Carey I site (Figure 4.2). At Soowahlie P concentrations were significantly higher in the Ah horizon. Soil pH changed little throughout the profile at both sites. The higher organic content of the Ah horizon resulted in higher concentrations of total-C, as well as total-N, mineralizable-N, and SO_4-S. Organic surfaces in the Ah horizon provide exchange sites for nutrient cations such as K, Ca, and Mg and may account for the higher concentrations of these cations. For most nutrients there were order-of-magnitude differences between concentrations in the Ah and C horizons within a given site.

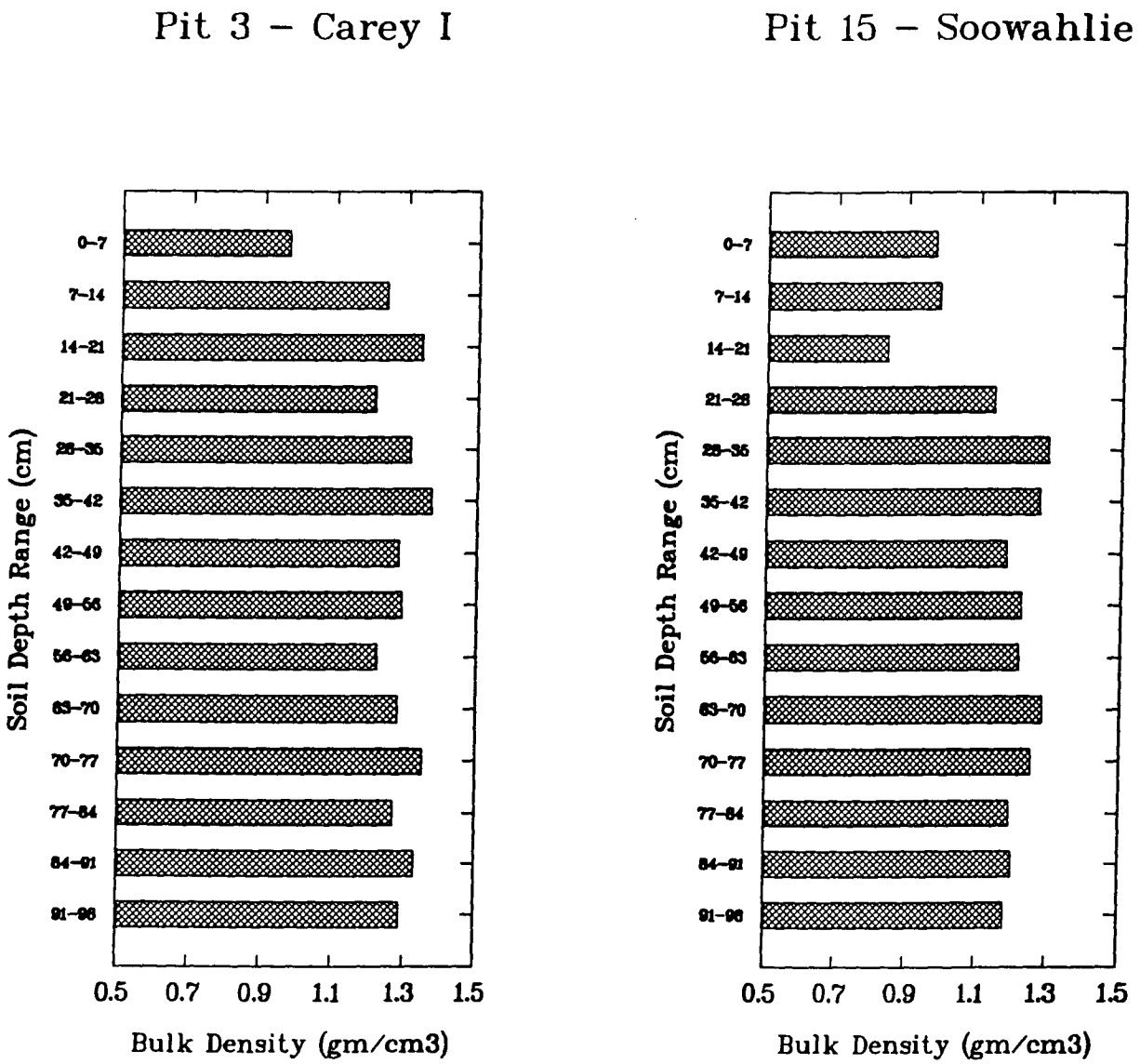
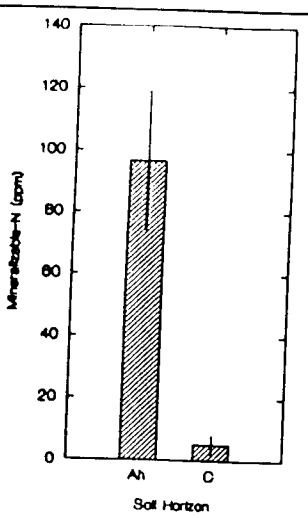
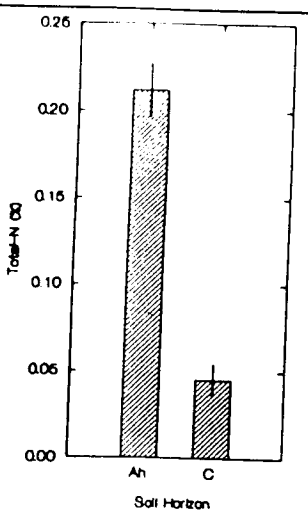
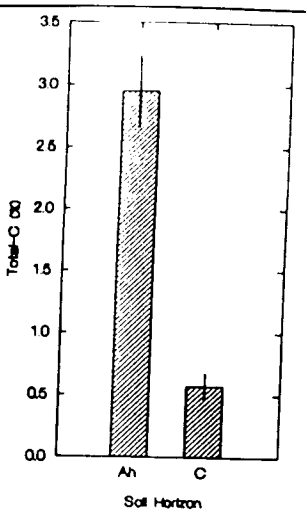


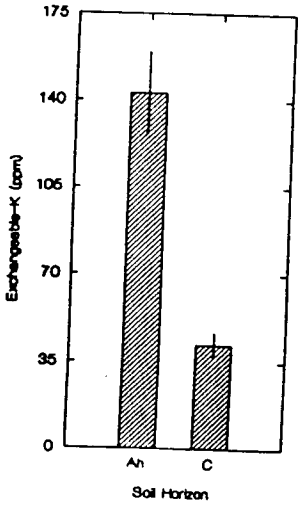
Figure 4.1: Changes in soil bulk density with depth in the soil profile at the Carey 1 and Soowahlie sample sites.

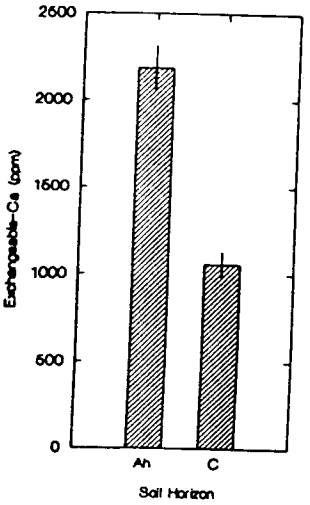
Figure 4.2: (Overleaf) Comparisons (lines represent 95% confidence intervals, n=15) between mean concentrations of soil nutrients in the Ah and C horizons (to a depth of 1 m) at the Carey 1 sample site.

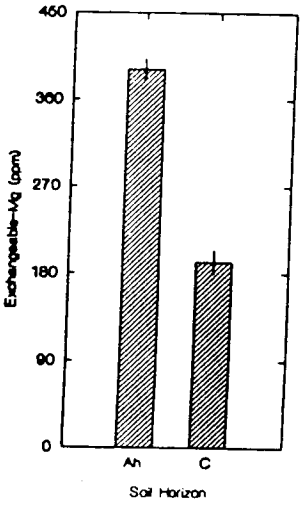

140
120
100
80
60
40
20
0
Ah
C
Soil Horizon

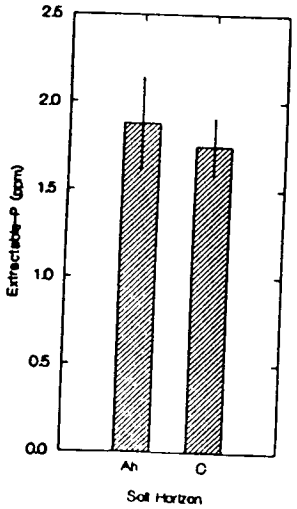

0.25
0.20
0.15
0.10
0.05
0.00
Ah
C
Soil Horizon

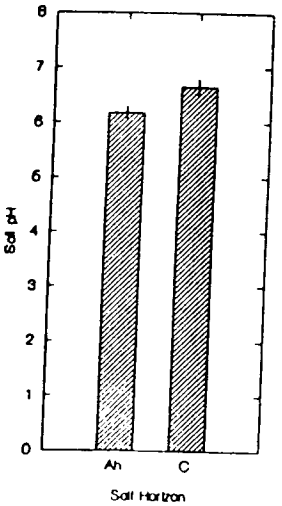

3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
Ah
C
Soil Horizon


175
140
105
70
35
0
Ah
C
Soil Horizon


2500
2000
1500
1000
500
0
Ah
C
Soil Horizon


450
360
270
180
90
0
Ah
C
Soil Horizon


2.5
2.0
1.5
1.0
0.5
0.0
Ah
C
Soil Horizon


8
7
6
5
4
3
2
1
0
Ah
C
Soil Horizon

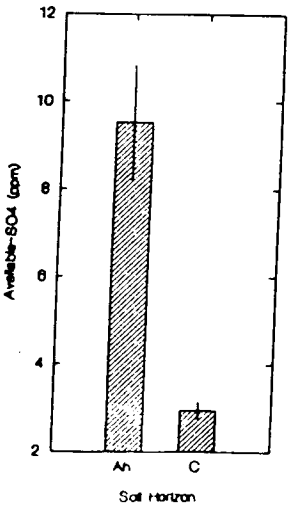
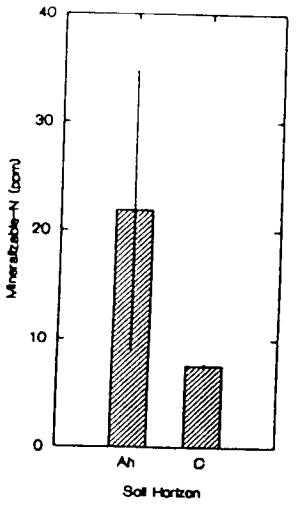
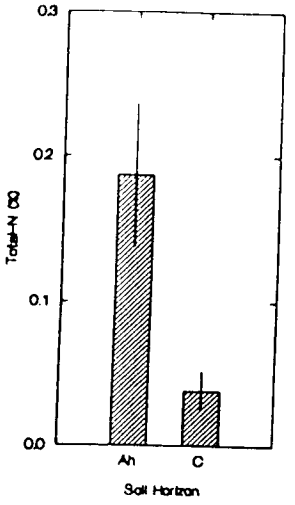
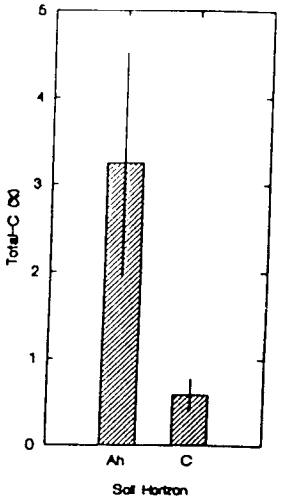
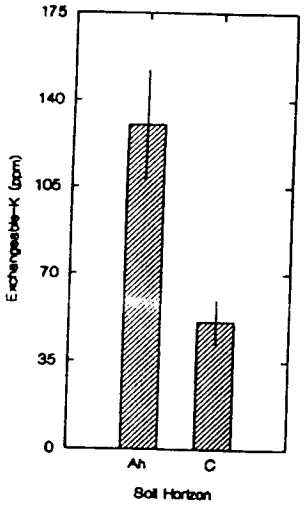

12
10
8
6
4
2
Ah
C
Soil Horizon

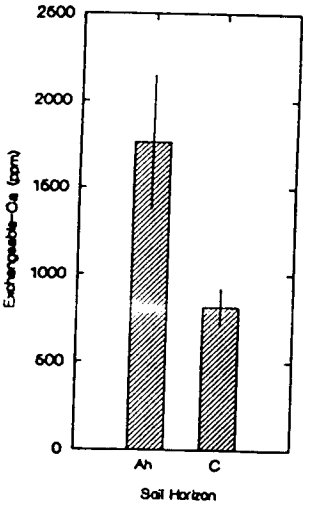
Figure 4.3: (Overleaf) Comparisons (lines represent 95% confidence intervals, n=15) between mean concentrations of soil nutrients in the Ah and C horizons (to a depth of 1 m) at the Soowahlie sample site.

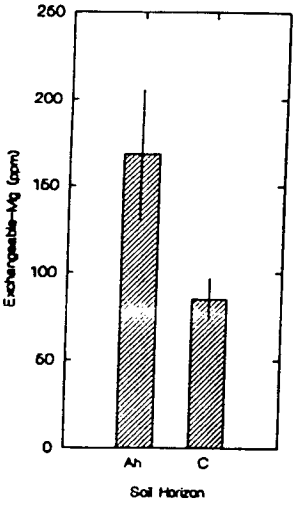

Mineralizable-N (ppm)
40
30
20
10
0
Ah
C
Soil Horizon

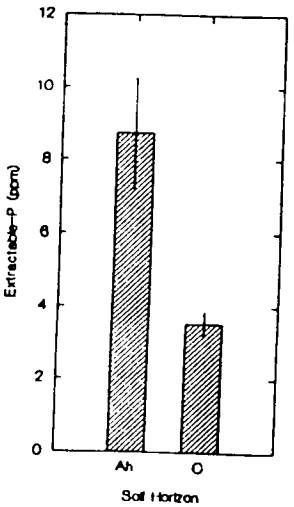

Total-N (%)
0.3
0.2
0.1
0.0
Ah
C
Soil Horizon

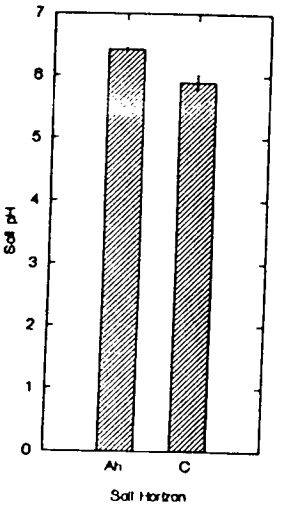

Total-C (%)
5
4
3
2
1
0
Ah
C
Soil Horizon


Exchangeable-K (ppm)
175
140
105
70
35
0
Ah
C
Soil Horizon


Exchangeable-Ca (ppm)
2600
2000
1600
1000
500
0
Ah
C
Soil Horizon


Exchangeable-Mg (ppm)
250
200
150
100
50
0
Ah
C
Soil Horizon


Extractable-P (ppm)
12
10
8
6
4
2
0
Ah
C
Soil Horizon


Soil pH
7
6
5
4
3
2
1
0
Ah
C
Soil Horizon

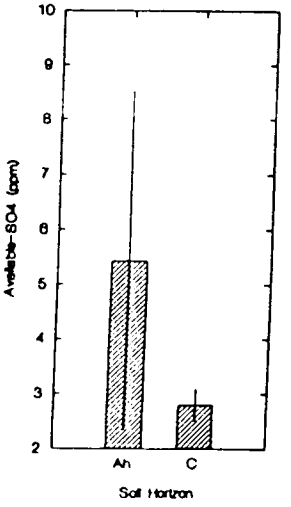

Available-SO4 (ppm)
10
9
8
7
6
5
4
3
2
Ah
C
Soil Horizon

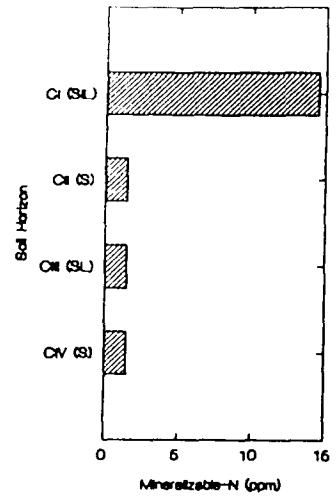
Table 4.2: Ranges of coefficients of variation in bulk density at the intensively sampled sites.

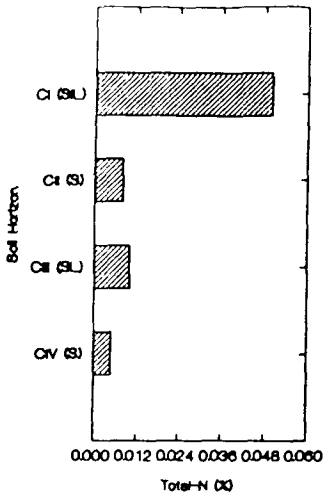
Site	No. of Pedons	C.V. Range
Soowahlie	3	13-23
Carey I	4	8-18
Squamish 23	3	11-16
Strawberry I	4	8-11
Chester	3	6-14
Squamish 38	3	11-21
Sumas	3	20-42
Salmon	3	22-29

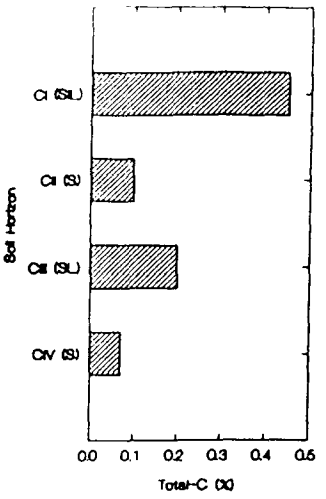
Significant differences in soil nutrient concentrations between the Ah and C horizons implies that the nutrient concentrations determined from samples collected over a 1 m depth will be affected to a large extent by the ratio of the depth of the Ah to the C horizon within a given sample. Table 4.3 presents means and CVs for the depth of the Ah horizon, and for main rooting depth in the intensively-sampled sites. CVs for Ah depth range from 17-51%. If samples were collected over the main rooting depth distinguished in the soil profile, then this would introduce another component of variability (CV range 15-53%) that would affect the estimation of both mean soil nutrient concentrations and contents.

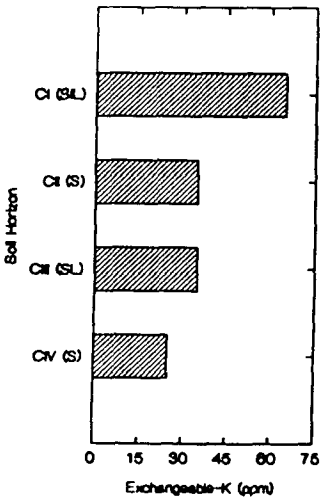
Concentrations of soil nutrient concentrations in the C_I to C_{IV} horizons at the Soowahlie and Carey I soil profiles described in Table 4.1, appear to be vary with the soil textures of the horizons, and observations of root abundance within the horizons (Figures 4.4 and 4.5).

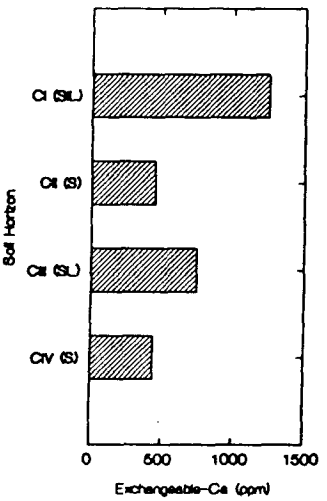
Figure 4.4: (Overleaf) Concentrations of soil nutrients by C horizon for the soil profiles shown in Table 4.1 at the Carey 1 sample site. Concentrations are based on a single sample for each horizon.

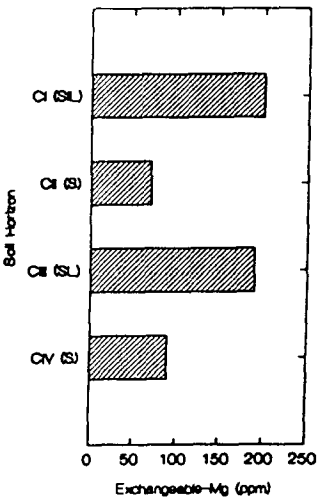

Soil Horizon
CI (SiL)
CII (S)
CIII (SL)
CIV (S)
0
5
10
15
Mineralizable-N (ppm)

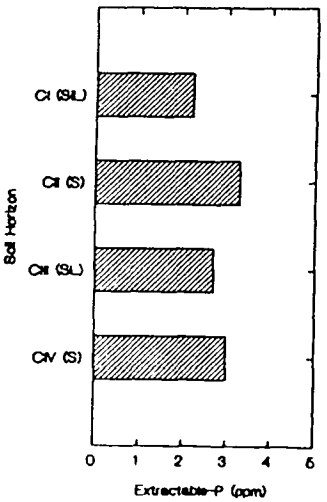

Soil Horizon
CI (SiL)
CII (S)
CIII (SL)
CIV (S)
0.000 0.012 0.024 0.036 0.048 0.060
Total-N (%)

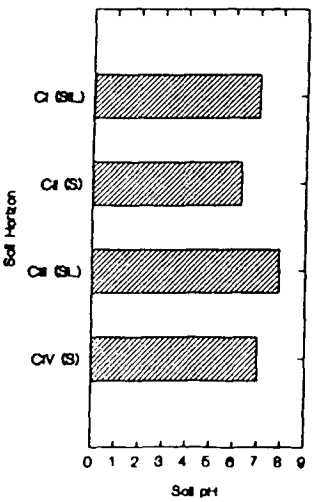

Soil Horizon
CI (SiL)
CII (S)
CIII (SL)
CIV (S)
0.0
0.1
0.2
0.3
0.4
0.5
Total-C (%)


Soil Horizon
CI (SiL)
CII (S)
CIII (SL)
CIV (S)
0
15
30
45
60
75
Exchangeable-K (ppm)


Soil Horizon
CI (SiL)
CII (S)
CIII (SL)
CIV (S)
0
500
1000
1500
Exchangeable-Ca (ppm)


Soil Horizon
CI (SiL)
CII (S)
CIII (SL)
CIV (S)
0
50
100
150
200
250
Exchangeable-Mg (ppm)


Soil Horizon
CI (SiL)
CII (S)
CIII (SL)
CIV (S)
0
1
2
3
4
5
Extractable-P (ppm)


Soil Horizon
CI (SiL)
CII (S)
CIII (SL)
CIV (S)
0
1
2
3
4
5
6
7
8
9
Soil pH

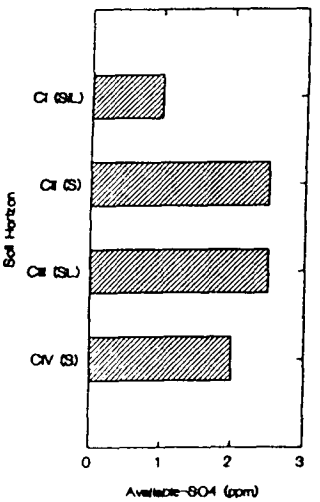
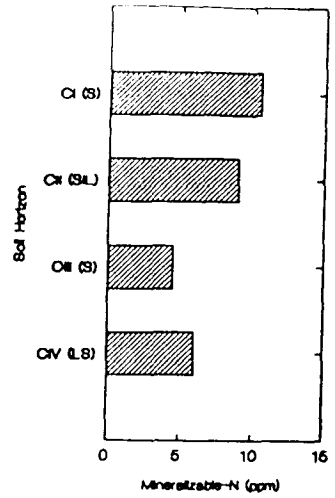
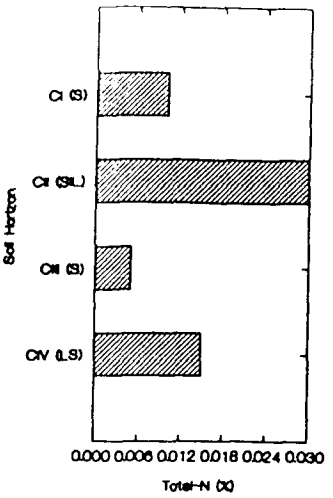
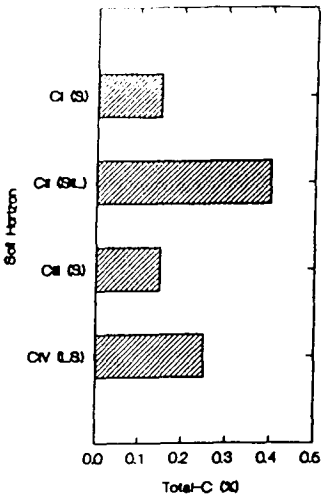
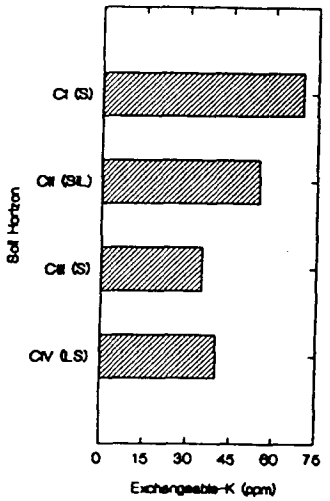

Soil Horizon
CI (SiL)
CII (S)
CIII (SL)
CIV (S)
0
1
2
3
Available-SO4 (ppm)

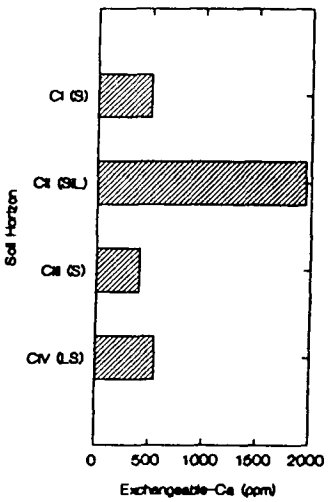
Figure 4.5: (Overleaf) Concentrations of soil nutrients by C horizon for the soil profiles shown in Table 4.1 at the Soowahlie sample site. Concentrations are based on a single sample for each horizon.

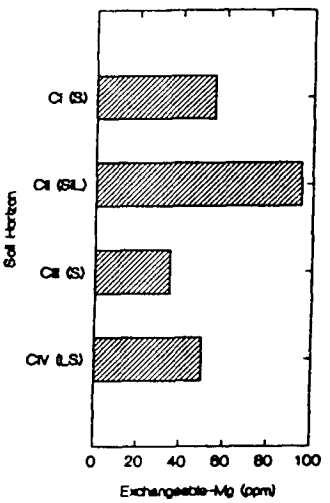

Ct (S)
Ct (SiL)
Cti (S)
Ctv (LS)
Soil Horizon
0
5
10
15
Mineralizable-N (ppm)

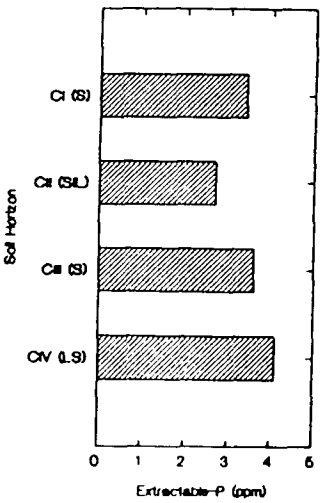

Ct (S)
Ct (SiL)
Cti (S)
Ctv (LS)
Soil Horizon
0.000 0.006 0.012 0.018 0.024 0.030
Total-N (%)

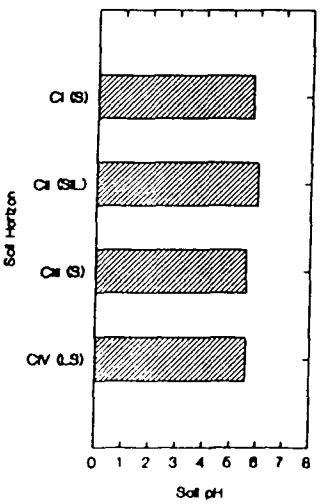

Ct (S)
Ct (SiL)
Cti (S)
Ctv (LS)
Soil Horizon
0.0
0.1
0.2
0.3
0.4
0.5
Total-C (%)


Ct (S)
Ct (SiL)
Cti (S)
Ctv (LS)
Soil Horizon
0
15
30
45
60
75
Exchangeable-K (ppm)


Ct (S)
Ct (SiL)
Cti (S)
Ctv (LS)
Soil Horizon
0
500
1000
1500
2000
Exchangeable-Ca (ppm)


Ct (S)
Ct (SiL)
Cti (S)
Ctv (LS)
Soil Horizon
0
20
40
60
80
100
Exchangeable-Mg (ppm)


Ct (S)
Ct (SiL)
Cti (S)
Ctv (LS)
Soil Horizon
0
1
2
3
4
5
Extractable-P (ppm)


Ct (S)
Ct (SiL)
Cti (S)
Ctv (LS)
Soil Horizon
0
1
2
3
4
5
6
7
8
Soil pH

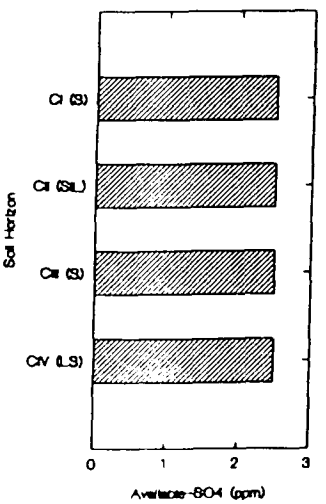

Ct (S)
Ct (SiL)
Cti (S)
Ctv (LS)
Soil Horizon
0
1
2
3
Available-SO4 (ppm)

Table 4.3: Variability in depth of the Ah horizon, and main rooting depth at the intensively sampled sites.

Site	Ah Depth Mean (m) / CV	Main Rooting Depth Mean (m) / CV
Soowahlie	0.13 / 38	0.62 / 38
Carey I	0.12 / 22	0.64 / 15
Squamish 23	0.12 / 28	1.01 /24
Strawberry I	0.03 / 28	0.55 / 27
Homathko	0.02 / 33	0.39 / 53
Chester	0.17 / 17	0.58 / 25
Squamish 38	0.06 / 51	0.49 / 20
Sumas	0.14 / 22	0.68 / 31
Salmon	0.10 / 23	0.83 / 23

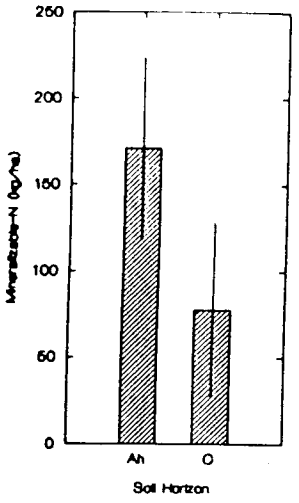
Concentrations shown in Figures 4.4 and 4.5 are based on only one sample for each horizon, so no statistical significance can be assigned to the differences between C horizons within a soil profile. Concentration values should be interpreted cautiously given the high variability of soil nutrient concentrations reported below. However, at both sites higher concentrations of total N, total C, and exchangeable Ca and Mg, occurred in the finer-textured horizons, and these horizons consistently had a higher abundance of roots (Table 4.1). Mineralizable N concentrations followed those of total N closely at the Carey I site but were less correlated at the Soowahlie site. Exchangeable K followed the same pattern as the other exchangeable cations at the Carey site, but not at the Soowahlie site. At the Soowahlie site the clay content decreased from 6.8% in the C_{II} (silt loam texture) to 1.2% in the C_{III} layer below (sand texture). Similarly, at the Carey 1 site, clay content of the soil decreased from 8.5% in the C_1 horizon (silt loam texture) to 1.6% in horizon C_{II}. (sand texture). Higher concentrations of exchangeable Ca and Mg in these layers may be the result of a greater surface area for cation exchange in soil horizons with higher clay contents, and to weathering of clay minerals in these layers. Also, the higher concentrations of total N and total C may be due to the decomposition of roots in these horizons. Differences between horizons were small for soil nutrients with very low concentrations, such as available P and SO_4-S.

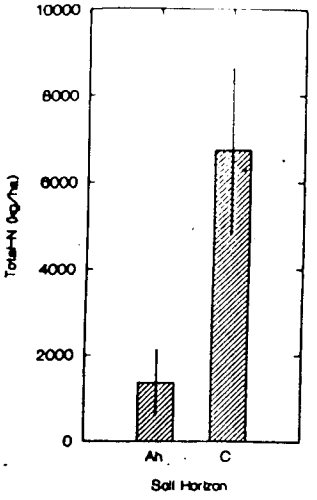
The pattern of having much higher nutrient concentrations in the Ah compared to the C horizons (Figures 4.2 and 4.3) is reversed when soil nutrient contents are compared (Figure 4.6 and 4.7). Except for mineralizable N at the Carey I site (Figure 4.6), soil nutrient contents were consistently much higher in the C horizons (over a depth of 1 m) than in the Ah horizon. The higher value for the content of mineralizable N in the Ah horizon at the Carey site results from the much higher concentration of mineralizable N in the Ah, compared to the C horizons at that site. Soil nutrient contents were based on a mean Ah depth of 0.12 m at the Carey I site and 0.13 m at the Soowahlie site. Thus C horizon soil contents were based on a depth of 0.88 m and 0.87 m respectively, and this factor, along with the higher bulk density for the C horizons, outweighed concentration differences and accounted for the reversal in the relationship between the two horizons. These comparisons show that, even though nutrient concentrations were much higher in the organic-rich A horizons in black cottonwood ecosystems, mineral subsoils also provided an important source of available nutrients.

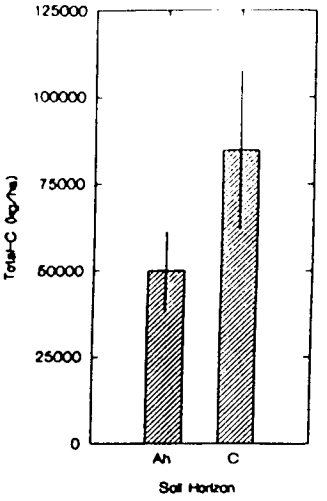
4.3.2 Within-Site and Among-Site Variability

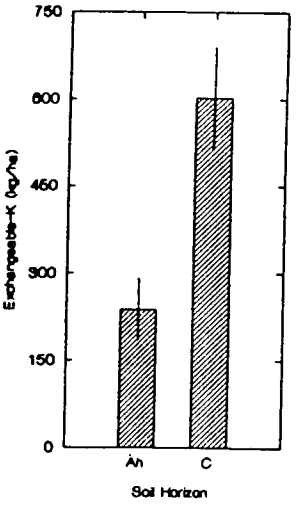
Coefficients of variation (CVs) for soil nutrient concentrations for 9 intensively sampled soils under cottonwood stands demonstrated high variability for concentrations of all soil nutrients within sites (Table 4.4). Mineralizable N (mean CV=52%) and available SO_4-S (mean CV=42%) had the highest, and exchangeable K (mean CV=25%) and available P (mean CV=26%) had the lowest mean within-site variabilities. The relatively higher within-site variability in the concentrations of mineralizable N and available SO_4-S is to be expected, since the availability of these nutrients is a function of microbiological activity, and will thus vary according to soil moisture, soil temperature, and other biotic factors that do not affect the concentrations of the other nutrients.

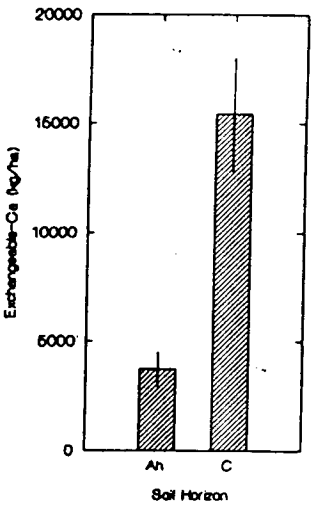
Figure 4.6 (Overleaf) Comparisons (lines represent 95% confidence intervals, n=15) between mean contents (kg/ha) of soil nutrients in the Ah and C horizons (to a depth of 1 m) at the Carey 1 sample site.

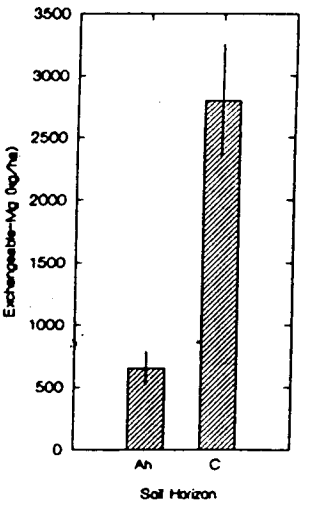

250
200
150
100
50
0
Ah
O
Soil Horizon

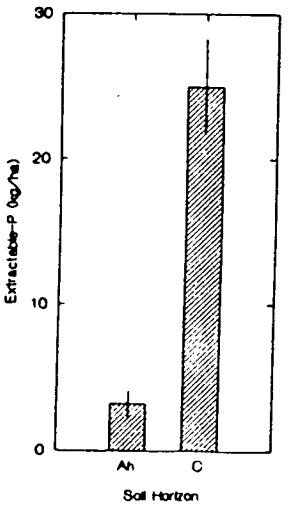

10000
8000
6000
4000
2000
0
Ah
C
Soil Horizon

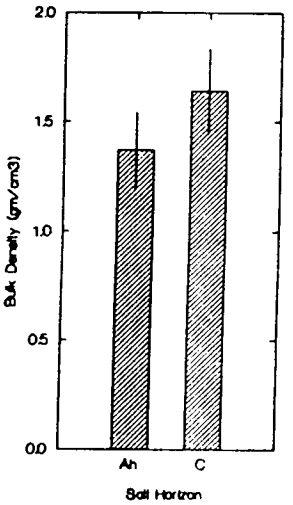

125000
100000
75000
50000
25000
0
Ah
C
Soil Horizon


750
600
450
300
150
0
Ah
C
Soil Horizon


20000
15000
10000
5000
0
Ah
C
Soil Horizon


3500
3000
2500
2000
1500
1000
500
0
Ah
C
Soil Horizon


30
20
10
0
Ah
C
Soil Horizon


2.0
1.5
1.0
0.5
0.0
Ah
C
Soil Horizon

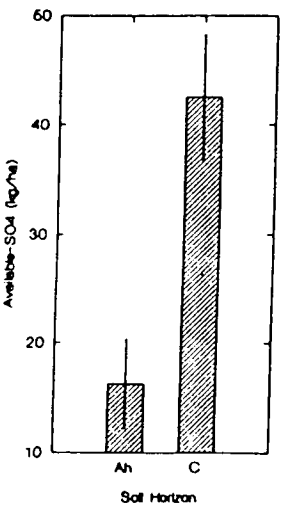
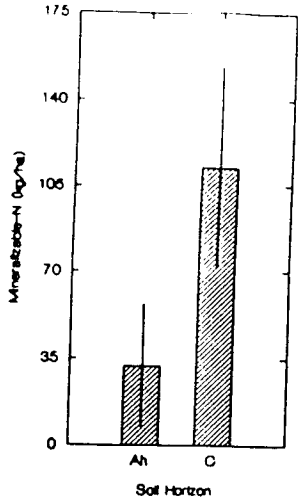
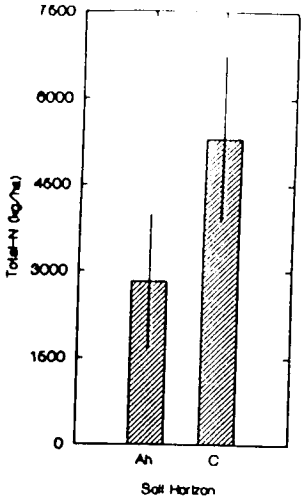
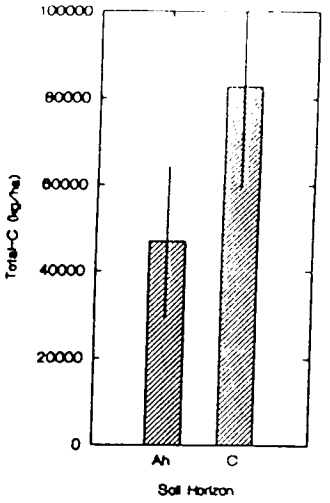
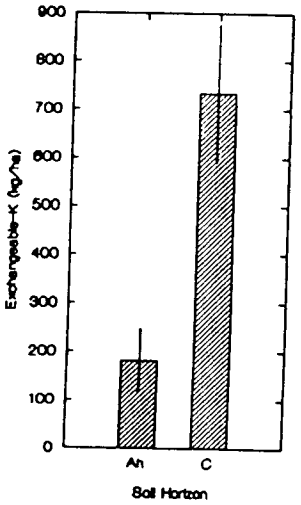

60
40
30
20
10
Ah
C
Soil Horizon

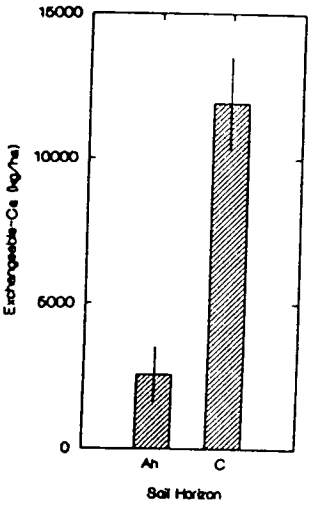
Figure 4.7: (Overleaf) Comparisons (lines represent 95% confidence intervals, n=15) between mean contents (kg/ha) of soil nutrients in the Ah and C horizons (to a depth of 1 m) at the Soowahlie sample site.

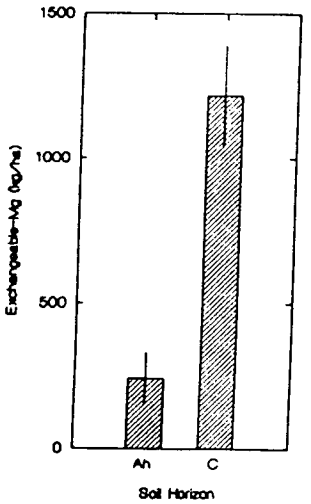

175
140
105
70
35
0
Mineralizable-N (kg/ha)
Ah
C
Soil Horizon

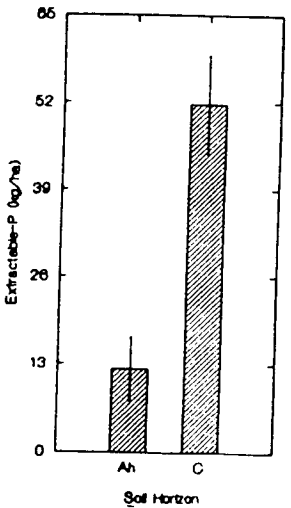

7600
6000
4500
3000
1500
0
Total-N (kg/ha)
Ah
C
Soil Horizon

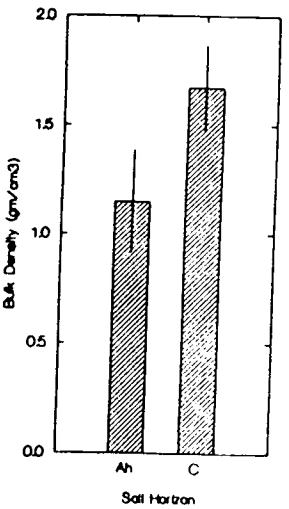

100000
80000
60000
40000
20000
0
Total-C (kg/ha)
Ah
C
Soil Horizon

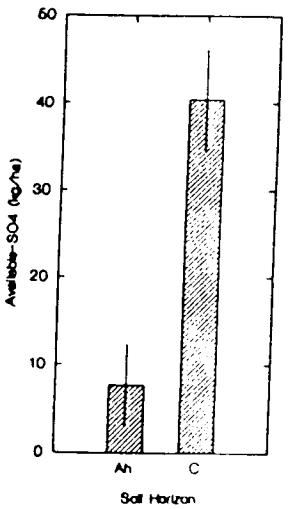

900
800
700
600
500
400
300
200
100
0
Exchangeable-K (kg/ha)
Ah
C
Soil Horizon


15000
10000
5000
0
Exchangeable-Ca (kg/ha)
Ah
C
Soil Horizon


1500
1000
500
0
Exchangeable-Mg (kg/ha)
Ah
C
Soil Horizon


65
52
39
26
13
0
Extractable-P (kg/ha)
Ah
C
Soil Horizon


2.0
1.5
1.0
0.5
0.0
Bulk Density (gm/cm3)
Ah
C
Soil Horizon


60
40
30
20
10
0
Available-SO4 (kg/ha)
Ah
C
Soil Horizon

The wide range of CVs for a given site show that the variability of soil nutrient concentrations was high and relatively unpredictable from site to site. This has important implications for the determination of the optimal sampling effort required for assessing soil nutrient concentrations within a given site, because the formula used to calculate the number of required samples at various levels of accuracy and precision is based on the mean CV values given in Table 4.4.

ANOVAs were carried out on the soil nutrient concentrations to compare variances within and among the 9 intensively sampled black cottonwood stands (Table 4.4). All F ratios were highly significant ($p < .001$) and show that, for the 9 intensively-sampled sites, the major variation is among, rather than within sites.

Table 4.4: Coefficients of variation (CVs), mean CVs, and F ratios comparing among-site to within-site variance for soil nutrient concentrations at the 9 intensively-sampled black cottonwood stands. CVs and ANOVAs are based on mean nutrient concentrations of 15 individual soil samples collected over the upper 1 m of soil.

Site	Total C (%)	Total N (%)	Min-N (%)	Av-P (%)	Ex-Ca (%)	Ex-Mg (%)	Ex-K (%)	SO_4-S (%)
Soowahlie	56	52	79	24	30	31	30	58
Carey I	24	23	68	20	11	8	20	18
Squamish 23	31	27	31	14	33	29	19	47
Strawberry I	34	15	65	19	17	17	8	13
Homathko	59	46	40	16	36	38	25	38
Chester	31	20	58	20	19	17	21	42
Squamish 38	48	56	61	25	73	64	35	56
Sumas	30	25	28	63	72	41	35	60
Salmon	22	20	43	29	23	26	28	47
Range of CVs	22-59	15-56	28-79	14-63	11-73	8-64	8-35	13-60
Mean CV	37	32	52	26	35	30	25	42
F Ratio	21.9	32.9	11.1	152	86.6	239	48.5	37.6

Patterns of relative sampling errors (RSEs) shown in Table 4.5 are similar to the variability data described for the 9 intensively sampled sites. The mean RSEs for SO_4-S and mineralizable N were the largest (+/- 36% and +/- 26% of the mean respectively at an alpha of

Table 4.5: Relative sampling errors (RSEs), ranges, and mean RSEs for soil nutrient concentrations at the 9 intensively-sampled black cottonwood ecosystems. RSEs are based on mean nutrient concentrations of 15 individual soil samples collected over the upper 1 m of soil.

Site	Total C (%)	Total N (%)	Min-N (%)	Av-P (%)	Ex-Ca (%)	Ex-Mg (%)	Ex-K (%)	SO_4-S (%)
Soowahlie	19	18	28	8	10	11	10	20
Carey I	8	9	24	7	4	3	7	6
Squamish 23	11	9	11	5	12	10	7	16
Strawberry I	12	5	23	7	6	6	3	5
Homathko	20	16	14	6	13	13	9	13
Chester	11	7	20	7	13	6	7	15
Squamish 38	17	20	21	9	25	22	12	19
Sumas	10	9	10	22	25	14	12	21
Salmon	8	7	15	10	8	9	10	16
Range of RSE	8-20	5-20	10-28	5-22	4-25	3-22	3-12	5-20
Mean RSE	13	11	18	9	13	10	9	15

0.90), and those of exchangeable K (+/- 17%) and Ca (+/- 18%) the smallest.

Calculation of RSE provided the opportunity to compare the relative variability of the intensively sampled sites with that of the composited sites (Table 4.6). Four of the 16 composited sites have been excluded from Table 4.6 because some of their mean nutrient concentrations had no variability. This occurred when concentrations of a nutrient were at the low end of the detection range for a given analytical procedure, so that all concentrations are given as the minimum detectable value. For all nutrients considered, the mean RSEs in the composited sites were approximately double that of the same nutrient in the intensively-sampled plots.

Table 4.6: Relative sampling errors (RSEs) at alpha=0.90, ranges, and mean RSEs for soil nutrient concentrations at 16 black cottonwood ecosystems where soil samples were composited into 4 samples at each site.

Site	Total C (%)	Total N (%)	Min-N (%)	Av-P (%)	Ex-Ca (%)	Ex-Mg (%)	Ex-K (%)	SO_4-S (%)
Borden	29	14	18	44	26	25	6	11
Chilliwack	28	28	25	28	20	21	27	25
Island 12	54	58	63	64	33	29	33	120
Mercer	8	13	31	16	9	7	15	18
Murphy high	6	13	20	20	19	14	12	36
Oyster	21	25	19	39	24	22	14	10
Squamish	28	26	21	11	8	19	4	19
Tamihi Fan	36	35	53	16	7	20	27	103
Ryder Lake	11	14	10	23	10	23	29	27
Chipmunk Creek	46	19	47	17	15	26	12	28
Pierce Creek	8	15	19	6	17	16	25	12
Elk3	17	21	8	44	21	25	12	31
Elk 1	35	28	36	21	48	55	28	55
Elk 2	18	21	26	17	15	15	21	44
Ashlu	20	1	12	25	5	12	4	8
Tamihi	16	13	13	8	11	25	8	26
Range of RSEs	6-54	1-58	8-63	6-64	5-48	7-48	4-33	8-120
Mean RSEs	24	22	26	25	18	22	17	36

Coefficients of variation for the 9 intensively sampled sites were consistently higher for soil contents (Table 4.7) than for concentrations (Table 4.4). The order of variability for the different nutrients was much the same; mineralizable N (mean CV=60%) and SO_4-S (mean CV=46%) had the highest variability, and exchangeable K (mean CV=34%) and available P (mean CV=34%) the lowest. The variability in nutrient contents for the intensively sampled sites was primarily a function of variability in bulk density (mean CV=23%) and nutrient concentrations from pit to pit. At all sites, a depth of 1 m, and not main rooting depth (see Table 4.3), was used to calculate the depth factor of the volume multiplier used to calculate soil contents, so this aspect of variability was not included in the estimates shown in Table 4.7.

Also, soils in the intensively sampled plots contained very few coarse fragments. Presumably, the variability would have been higher if soils in the intensively sampled plots had contained any coarse fragments. As for soil nutrient concentrations (Table 4.4), variation in soil nutrient contents from site to site was significantly higher than within-site variability, as shown by the highly significant F ratios for all nutrients (Table 4.7).

Table 4.7: Coefficients of variation (CVs), ranges of CVs, mean CVs and F ratios comparing among-site to within-site variance for soil nutrient contents (kg/ha) at the 9 intensively-sampled black cottonwood ecosystems. CVs are based on means of 15 individual samples.

Site	Bulk Density	Total C	Total N	Min-N	Av-P	Ex-Ca	Ex-Mg	Ex-K	SO_4-S
Soowahlie	21	49	47	63	25	32	25	34	25
Carey I	21	46	49	112	22	29	28	25	24
Squamish 23	18	36	31	36	28	37	41	30	65
Strawberry I	24	48	30	61	26	34	35	24	26
Homathko	30	82	52	44	36	29	56	41	48
Chester	26	42	32	67	36	31	30	35	45
Squamish 38	9	47	55	59	23	74	64	35	54
Sumas	24	43	38	41	65	78	47	39	65
Salmon	30	42	29	58	42	39	37	46	60
Range of CVs	9-30	36-82	29-55	36-112	22-65	29-78	28-64	24-46	24-65
Mean CV	23	48	41	60	34	43	40	34	46
F Ratio	10.2	66.9	87.0	14.1	125	81.8	230	28.6	24.6

Table 4.9 shows the numbers of samples required for the determination of soil nutrient concentrations at the sites for this study, at different levels of accuracy and precision. The order of sample requirements for the nutrients measured are similar to the patterns of variability shown in Table 4.4; mineralizable N and available SO_4-S would require the largest sampling effort, and exchangeable K the smallest, at a given level of accuracy and precision. However, for all nutrients, very intensive soil sampling would be required to obtain highly accurate and precise estimates of soil nutrient concentrations. For example, at an alpha and gamma level of 0.95%

with an error of 10%, the most variable nutrient, mineralizable-N, would require 186 individual samples, and the least variable nutrient, exchangeable K, would require 52 individual samples.

Table 4.8: CVs for coarse fragment content for 6 study sites with a significant component of coarse fragments.

Site	CV of Coarse Fragment Volume
Polygon 19	14
Ryder	52
Tamihi Fan	48
Oyster River	83
Chipmunk Creek	35
Borden Creek	57

Table 4.9: Numbers of soil samples required to estimated soil nutrient concentrations in black cottonwood ecosystems at different levels of alpha, gamma and percentage error.

	Alpha	0.95	0.95	0.90	0.90	0.95	0.95	0.90	0.90
	Gamma	0.50	0.50	0.50	0.50	0.95	0.95	0.80	0.80
Nutrient	Error	10%	20%	10%	20%	10%	20%	10%	20%
pH		3	3	3	3	5	3	3	3
Total C (%)		52	15	37	11	111	31	55	15
Total N (%)		37	11	26	8	79	23	39	12
Mineralizable N (ppm)		87	24	62	17	186	50	91	25
Available P (ppm)		30	9	22	7	65	19	32	10
Exchangeable Ca (ppm)		61	17	43	12	130	36	64	18
Exchangeable Mg (ppm)		44	13	31	9	94	27	47	14
Exchangeable K (ppm)		25	7	17	6	52	16	26	8
Extractable SO_4 (ppm)		73	20	52	14	157	43	77	21

Numbers of samples required for the same levels of accuracy and precision were, for most nutrients, close to twice as high for the determination of soil contents (Table 4.10) as for soil concentrations (Table 4.9). This is to be expected given the extra variability involved in the estimation of soil nutrient contents, as discussed above for Table 4.7.

Table 4.10: Numbers of soil samples required to estimate bulk densities and soil nutrient contents in soils within black cottonwood stands at different levels of alpha, gamma and percentage error.

	Alpha	0.95	0.95	0.90	0.90	0.95	0.95	0.90	0.90
	Gamma	0.50	0.50	0.50	0.50	0.95	0.95	0.80	0.80
Nutrient	Error	10%	20%	10%	20%	10%	20%	10%	20%
Bulk Density (gm/cm^3)		22	7	16	5	54	17	23	8
Total C (%)		92	25	65	18	229	61	96	26
Total N (%)		68	19	48	13	170	46	72	20
Mineralizable N (ppm)		141	37	100	26	352	92	148	39
Available P (ppm)		46	13	33	10	114	32	48	14
Exchangeable Ca (ppm)		72	20	51	14	180	49	76	21
Exchangeable Mg (ppm)		65	18	46	13	161	44	68	19
Exchangeable K (ppm)		48	14	34	10	118	33	50	15
Extractable SO_4 (ppm)		83	23	59	16	207	56	87	24

4.4 DISCUSSION

The magnitude of variability for soil nutrient concentrations sampled in this study was high for all measures except soil pH, and is thus comparable to results from similar studies of mineral soils (Ball and Williams, 1968, 1971; Binkley and Hart, 1989; Courtin *et. al.*, 1983; Mader, 1963). Mean CVs ranged from 25% for exchangeable K to 52% for mineralizable N, and, for any nutrient, there was a wide range of CVs among the different study stands. This range in variability has also been observed in other studies (Blyth and MacLeod, 1978; Courtin *et al.*, 1983).

High variability in nutrient concentrations within a site has been attributed to changes in nutrient concentration with depth in the soil profile (Binkley and Hart, 1989). In this study, nutrient concentrations in the Ah horizon were higher than underlying C horizons by an order of magnitude for most nutrients. There is also some evidence to suggest that soil nutrient concentrations varied as a function of soil texture within the C horizons of the alluvial soils

sampled. These observations suggest that, within a given pedon, soil nutrient concentrations will vary as a function of the nature (texture, organic matter content, aeration) and depth of the various soil horizons, relative to the depth of sampling.

Variability in the estimation of soil nutrient contents in this study was consistently higher than that for soil concentrations, and was of the same magnitude as that found by Courtin *et al.* (1983). Variability in soil nutrient contents is higher than soil nutrient concentrations because, in addition to the variability introduced by soil nutrient concentrations, the calculation of soil nutrient content requires multiplication by factors that are themselves subject to considerable variation. Variation in soil bulk density, coarse fragment content, and rooting depth all contributed considerable variability to the accurate estimation of soil nutrient contents.

To develop the most meaningful relationships between measures of black cottonwood site index and soil nutrients, the optimal depth of soil nutrient sampling should be, within practical limits, that depth over which black cottonwood collects the majority of its nutrients. Most absorption of soil nutrients is through the fine roots (Bowen, 1984) and concentrations of fine roots are well correlated with soil mineral nutrient concentrations within the soil profile (Kimmins and Hawkes, 1978; Powers, 1984). The results of this study were consistent with this pattern in that fine root concentrations were highest in the upper soil layers, and these layers were seen to have significantly higher concentrations of almost all soil nutrients. Given this information, one sampling approach would be to restrict sampling to the main rooting depth, since the majority of fine roots were located within that depth (Kayahara, 1991). Compared to sampling over a fixed depth such as a meter, this approach has the advantage of requiring considerably less sampling effort in each pedon. However, in the alluvial soils sampled in this study, determination of the main rooting depth often proved problematic because the distribution of roots in the soil profile varied with soil texture. In some cases, sandy mineral soil layers near the surface had very few roots, after which more fine-textured layers at depth were completely occupied by roots. Also, in this study, fine-textured subsurface horizons appeared to have higher concentrations of nutrients than coarse-textured layers near the surface. White and Wood

(1958) showed that fine-textured, subsurface layers were important sources of K in K-limited red pine systems in New York. Also, although subsurface layers had lower concentrations of soil nutrients, their greater depth and bulk density resulted in much higher nutrient contents, and they thus represented an important source of nutrients within the soil profile. Other arguments against sampling over the main rooting depth are; - 1) the main rooting depth varies from pedon to pedon and thus becomes another source of variability that reduces the accuracy and precision of determinations of soil contents, and - 2) some of the soils in the study had root restricting layers that reduced rooting volume, so that, if samples had been collected over the main rooting depth, the effects of reduced soil volume would not be expressed in the estimates of soil contents. This would provide inaccurate comparisons of soil nutrient contents available for black cottonwood growth at different sites. Given the presence of nutrients at considerable depth in the soil profile, the presence of roots to utilize these nutrients, the variability and difficulty of accurately determining the main rooting depth, and the potential for including the effects of restricted rooting depth, it was concluded that the 1 m depth of sampling utilized in this study represents the most practical and meaningful method for estimating soil nutrients available to black cottonwood.

The order of variability of the different nutrients found in this study differs from those reported by Courtin *et al.*, (1983), Ike and Clutter (1968), Lewis (1976), and Slavinsky (1977) (Table 4.11). Blyth and MacLeod (1978) studied several soils in which the order of variability also varied significantly from area to area. These differences in the order of nutrient variability, and the observed high range in variability from site to site for all nutrients, means that variability estimates obtained from previous soil studies have limited value as pilot studies. As stated by a number of workers (Ball and Williams, 1968; Blyth and MacLeod, 1978; Carter and Lowe, 1976; Courtin *et al.* 1983), serious studies of the relationships between soil nutrients and tree productivity or other variables, should be preceded by variability studies that provide information specific to the soils being sampled.

Table 4.11: Relative order of variability in nutrient concentration in this study compared to other studies.

Study	Relative Order of Variability
This study	Min-N, SO_4-S > %C, Ca, %N, Mg > P > K > pH
Slavinsky (1977)	Ca > Mg > %N, %C, K > pH
Lewis (1976)	Ca, Mg> K > %C, %N> pH
Courtin *et. al* (1983)	P, SO_4, Ca> Min-N, K > Mg > %C, %N > pH
Ike and Clutter (1968)	Ca > P, K, Mg

The high variability inherent in soil nutrient concentrations and contents in forest soils means that precise estimates based on individual samples, even for areas that appear to have relatively uniform soils, will be too expensive to obtain (Courtin *et al.*, 1983; Mader, 1963). To increase the efficiency and decrease the cost of soil nutrient sampling, a compositing procedure was utilized for 21 of the 30 sites sampled. Other studies (Carter and Lowe, 1986; Mader, 1963; Slavinsky, 1976) have shown that soil nutrient values obtained from composited samples fall within the confidence interval established for intensively-sampled estimates of the mean for the same site, and have recommended a compositing procedure to increase sampling efficiency. Ball and Williams (1968) however, showed that for the level of sampling employed, the values obtained from composited samples fell outside the confidence interval of the mean for some nutrients. In this study, a direct comparison of the relative efficiencies of the two methods was not possible, because the two sampling approaches were never carried out at the same site. However, comparisons of the relative sampling errors for the intensive and compositing procedures for each of the nutrients measured, showed that the confidence intervals for the composited sites were consistently higher than those for the intensively sampled sites, for all nutrients considered. This result means that the compositing sampling procedure used was considerably less successful than the intensive sampling procedure in capturing soil variability within a given site.

The rationale for collecting four samples from each of four pedons in the composited soil samples in this study is based on the idea that up to one-half of the variability in soil nutrient concentration for a given site is included in any square meter of the site (Beckett and Webster, 1971; Troedsson and Tamm, 1969). Given this, four samples collected from each of the four walls of a meter square soil pedon, and then thoroughly mixed, should incorporate up to one half of the variability of the site. If soil nutrient concentrations within each soil pedon were independent of each other, then the four composite samples should account for the same amount of variability as 16 individual samples, and the resulting mean should have about the same precision as the mean estimated by 15 individual samples. However, the fact that the confidence interval provided by the compositing sampling procedure was close to double that of the intensive sampling procedure, suggests that the samples collected from a single soil pedon were highly correlated. In retrospect, this correlation is to be expected given the observed uniformity of soil strata within a sample pedon. This result supports the observations of Robertson (1987), who showed a high degree of correlation in soil samples collected over a small area, and recommended that sampling locations be separated by at least 20 m to provide the most efficient sampling design. In this study, the intensive sampling procedure, where soil pits were always at least 40 m apart, estimated soil nutrient concentrations with almost twice the precision of the composited approach. For these reasons it is argued that the compositing sampling procedure used in the study should be altered so that fewer samples are collected from within each pedon, and that more soil pits, located at least 20m apart, should be excavated.

Although levels of within-site variability of concentrations and contents were high for all nutrients, F ratios comparing variances among- to within-sites were all highly significant ($p<.001$). This suggests that, given the sampling intensity employed, it may be possible to correlate changes in black cottonwood site index with changes in soil nutrients. It can be expected, however, that, high within-site variability will tend to obscure these relationships. Also, because variability differs among the nutrients measured, correlations between soil nutrient levels and black cottonwood site index will be more discernible for some nutrients than for others.

4.5 CONCLUSIONS

1. For two Humic Regosol soils typical of the study sites sampled, concentrations of soil nutrients were higher by an order of magnitude in the Ah horizon, than in to the underlying C horizons. As a result, variation in soil nutrient concentrations was due principally to variability in the depth of the Ah layer, relative to the overall depth of the sample.

2. For the same two soils, soil nutrient contents (kg/ha) were significantly higher for all nutrients in the C horizons than the overlying the Ah horizon. Higher soil content in the C horizon was a function of their higher bulk density, and much greater volume. Variability of soil nutrient content was consistently higher than concentration variability. This was attributed to variability in factors such as bulk density, and coarse fragment content, that, in addition to soil nutrient concentration, are used to calculate soil nutrient contents. For the nine soils sampled intensively and used for estimating coefficients of variations in this study, coarse fragment content was very low, and soils were sampled to a depth of 1 m. Variability estimates for soil nutrient contents can be expected to increase where sampling is carried out over the main rooting depth, or in soils with high and variable coarse fragment contents.

3. Coefficients of variation for soil nutrient concentrations and contents in this study were high, and were similar to other studies for each of the nutrients. Mineralizable N and SO_4-S were the most variable, and exchangeable K and available P the least. Between 25 and 87 samples would be required to estimate soil nutrient concentrations at an alpha of 0.95 with 10 percent error. For nutrient contents the required number of samples would be 46 to 141 for the same accuracy and precision. At the intensively sampled sites, where 15, well-spaced samples were collected, an alpha of 0.90 with 20 percent error was achieved for mineralizable N, the most variable nutrient. Despite high within-site variability, variability was higher among than within sites, and this makes it possible to correlate changes in soil nutrient levels with black cottonwood site index.

4. Compared to the intensive sampling procedure, the compositing procedure used in this study resulted in much higher within-site variation for all nutrients. This was attributed to the high correlations of four samples from within the same soil pit. It was suggested that the use of more widely-spaced sample pits, with fewer subsamples from each, would more effectively capture within-site variability. It was also argued that the 1 m sampling depth used in the study was the most effective sampling depth for estimating nutrient availability for black cottonwood in the sites sampled.

CHAPTER 5

RELATIONSHIPS BETWEEN BLACK COTTONWOOD SITE INDEX, FOLIAR AND SOIL NUTRIENTS, UNDERSTORY VEGETATION, AND SITE UNITS

5.1 INTRODUCTION

Research that has attempted to correlate ecological variables with the site index of tree species within a given geographic area has been summarized into 'factorial' and 'holistic' (Jones, 1969) approaches. The objective of the factorial approach has been to measure and identify ecological (principally physiographic and soil) factors that limit the productivity of the species, usually through the use of multivariate models (Carmean, 1954, 1965; Cox *et al.* 1960; Eis, 1962; Schmidt and Carmean, 1988; Wilde, 1970). The approach has been widely applied in the United States, and studies have been reviewed by Carmean (1975), Hagglund (1981), Spurr and Barnes (1980), and Coile (1952). In general, the percentage of variance explained by the linear models developed through the factorial approach seldom exceeds 60% (Covell and McClurkin, 1967; Hagglund, 1981; Jones, 1969), unless the sampling universe is stratified, as in the studies of Myers and van Deusen (1960) and Carmean (1965). In British Columbia the factorial approach has been used to correlate environmental variables such as potential evapotranspiration, average water balance as derived from energy-driven models (Spittlehouse and Black, 1981), and soil nutrient contents, with site index of Douglas-fir (Carter and Klinka, 1990), lodgepole pine (Wang, 1992), and western hemlock (Kayahara, 1991). Wang (1992) for example, was able to explain more than 80% of the variation in lodgepole pine site index using a combination of soil nutrient and soil moisture measures.

Holistic or integrative ecological approaches are based on correlating site index with taxonomic units such as those derived from classification of soils (Agriculture Canada Expert Committee on Soil Survey, 1980; Soil Survey Staff, 1975) or sites (Pojar *et al.*, 1987; Pfister *et al.* 1977). By correlating site index of tree species with the taxonomic units of a land classification system, an estimate of the productivity of the species on the site can be generated, even if the species is not occupying the site. Also, the units are generally used for more general management purposes, so that species' productivities can be related to other aspects of forest management. Attempts to correlate soil taxonomic units with measures of species productivity have been largely unsuccessful, and this has been principally attributed to the wide range of ecological conditions that are included within a single soil taxon (Carmean, 1970,1975; Jones, 1969). Correlations with site units have met with higher success (Green *et al.*, 1989; Kayahara, 1992; Klinka *et al.*, 1989a; Klinka and Carter, 1990; Monserud, 1984; Wang, 1992). Monserud (1984) found differences in site index of Douglas-fir, and different height growth patterns among habitat types. Green *et al.* (1989) explained 86% of the variation in Douglas-fir site index using site units of the biogeoclimatic ecosystem classification (Pojar *et al.*, 1987). Using similar site units Kayahara (1991) explained 71% of the variation in western hemlock site index, and Wang (1992) explained 81% of the variation in lodgepole pine site index. These results suggest that site units can be very effective in differentiating ecologically-significant segments of regional edatopic gradients, as measured by the site index of the species examined. The problem with utilizing the holistic approach alone to predict the productivity of a species is that the correlation does not provide functional explanations for the growth of a particular species on a given site unit.

No studies employing either a factorial or a holistic approach have been carried out on black cottonwood, although considerable work has been done on the eastern cottonwood (*P. deltoides*) by Broadfoot (1960), and Baker and Broadfoot (1976, 1979). Broadfoot (1969) criticized the factorial approach for it's difficulty in establishing and measuring site and soil properties that can be reliably correlated with site index of the species in question, and for the inapplicability of the results outside of the restricted geographic area or climate-landform

conditions in which the study was carried out. On the other hand, he felt that subjective systems, such as those provided by assessment of indicator plants or landform-soil classes, did not provide a sufficiently accurate assessment of site index (Baker and Broadfoot, 1976). The approach taken by Baker and Broadfoot (1976, 1979) combines both subjective and objective approaches by using quantitative measures of site properties to define the characteristics of 4 subjectively-derived factors important for cottonwood growth on all sites - soil physical condition, moisture availability, nutrient availability, and soil aeration. Harrington (1986) used a similar approach employing stepwise linear regression to identify major environmental factors affecting site index of red alder in western Washington and Oregon.

The approach taken in this study combines elements of the holistic and factorial approaches by establishing inter-relationships between black cottonwood site index, qualitative measures of ecological site quality as assessed using biogeoclimatic ecosystem classification, and quantitative estimates of soil nutrient contents and foliar nutrient concentrations. Correlations of black cottonwood site index with subzone, soil nutrient regime, and site association are used as a starting point for assessing the factors that determine black cottonwood productivity in the present study. Qualitative estimates of soil nutrient regime describe nutrient availability for a site in general terms, but cannot account for the fact that the availability of soil nutrients for a particular species will differ from other species because of different physiological adaptations and nutrient requirements (Chapin *et al.* 1986). By establishing relationships between black cottonwood site index, quantities of soil-available nutrients (soil nutrient contents), and measures of nutrients taken up by the target trees (foliar nutrient concentrations), the particular nutrient or nutrients that are limiting can be identified (Attiwill, 1986; Chapin *et al.* 1986; White and Carter, 1970a,b). Relationships within groups, such as soil nutrient interactions, and between soil and foliar nutrient levels, can also aid in the interpretation of the measurements as they may affect the productivity of black cottonwood. The determination of foliar nutrient status also permits the application of analytical methods such as critical nutrient levels (Ballard and Carter, 1986; Lavender, 1970; Weetman and Wells, 1990), and assessments of nutrient balance through the determination of DRIS indices (Beaufils, 1973; Leech and Kim,

1979, 1981; Schutz and de Villiers, 1986), that are based on foliar nutrient concentrations. By summarizing soil and foliar nutrient measures over black cottonwood site index classes, the optimal amounts of nutrients can be assessed, and these can be compared to nutrient measures in each of the site associations. This will provide quantitative information for interpreting the nature of black cottonwood nutrient limitation within the site associations, and will express the results of the analysis in a format that has operational application.

The success of vegetation classification as a method of assessing ecological site quality is based on the fact that certain species have relatively narrow ecological amplitudes along climate, soil moisture, and soil nutrient gradients (Daubenmire, 1976; Klinka *et al.*, 1989b; Mueller-Dombois and Ellenberg, 1974). In British Columbia the indicative value of many plant species has been summarized by Klinka *et al.* (1989b), and several workers have attempted to use either individual species, or indicator species classes as predictive variables to evaluate site productivity, and to predict site index of tree species (Kayahara, 1991; Klinka *et al.*, 1989a; Klinka and Carter, 1990; Klinka and Krajina, 1987; Wang, 1992). The usefulness of understory vegetation in predicting site index of black cottonwood is assessed in the present study, using estimates of cover of understory vegetation species within the sample plots, and total cover of all species in several indicator species groups.

The rate of height growth of black cottonwood in the 29 sites used for the study shows a greater than three-fold increase from 8.5 m/15 yrs in a low bench alluvial site to 30.8 m/15 yrs on an upland loess soil with seepage (see Table 2.1). This range in site index implies that there is a range of ecological conditions that parallels the increase in height growth. The general objective of this study was to begin to understand the changes in nutrient availability that occur as ecological factors change along this range of black cottonwood height growth in coastal British Columbia. The specific objectives of the study were:

1) to correlate black cottonwood site index with taxa of the biogeoclimatic ecosystem classification (Pojar *et al*, 1987) - especially site association, subzone, and soil nutrient regime;

2) to assess the usefulness of understory vegetation in assessing black cottonwood site index;

3) to characterize black cottonwood site index classes, and site association in terms of soil and foliar nutrient quantities;

4) to establish relationships among foliar nutrients, soil nutrients, and black cottonwood site index so that limiting nutrients and optimal foliar ratios can be established; and,

5) to use foliar nutrient levels, DRIS indices, and soil contents to interpret the potential cause of nutrient limitation or sufficiency in the different site units.

5.2 METHODS

5.2.1 Ecosystem Description and Classification

A summary of ecological characteristics for the 29 sites used in the study has been provided in Chapter 2 and in Tables 2.2 and 2.3.

5.2.2 Soil and Foliar Nutrient Sampling and Analysis

Sampling protocols and analytical methods for foliar nutrients are described in Chapter 3, and for soil nutrients in Chapter 4.

5.2.3 Stem Analysis and Site Index

The stem analysis procedure used to estimate black cottonwood site index is described in Chapter 2. Details of stand age and composition are summarized in Table 2.1. The sites were ranked from low to high site index in Table 2.1, and divided into 3 site index classes: Low=8.5-14.5 m/15 yrs; Medium=15.0-21.9 m/15 yrs; and High=23.0 to 30.8 m/15 yrs. These classes were used as grouping variables in this study to correlate black cottonwood site index with site units and ecological variables.

5.2.4 Statistical Methods

Box diagrams (Titus, 1987; Tukey, 1977; Velleman and Hoaglin, 1981) were used in this study to show the general distribution of the soil nutrient and foliar nutrient data within the different qualitative classes. The central line of each box is the median of ordered values, and the ends of the box ('hinges') split each half of the data again. The 'Hspread' is the absolute value of the length of the box, and the 'whiskers' (the lines extending from either end of the box) show the range of data within 1.5 Hspreads of the hinges. 'Outside' values (asterisks) are those greater than 1.5 Hspreads from the hinge, and 'far outside' values (open circles) are greater than 3 Hspreads from the hinge.

Approaches and procedures for testing the assumptions of ANOVA and regression analysis are described in Chapter 3. Ecological variables used to predict black cottonwood site index are seldom independent and thus violate a major assumption of linear regression (Chatterjee and Price, 1977). For this reason a series of univariate regressions were used to demonstrate relationships between dependent and independent variables, and were combined into complete multiple regression models only for variables where intercorrelations were not significant. Where intercorrelations between predictive variables were significant, only the percentage of variance explained was used to evaluate the models.

5.3 RESULTS

5.3.1 Correlations of Black Cottonwood Site Index with CWH Subzones, Site Associations and Soil Nutrient Regime

The relatively low influence of stand location within the 3 CWH subzones on black cottonwood site index is shown by the Box diagrams in Figure 5.1. The ANOVA comparing means for the 3 groups (Table 5.1) was not significant (p=.593) and suggests that the limited range of climates in which study sites were located had no significant effect on the height growth of black cottonwood.

As shown in the Box diagrams and ANOVAs (Figure 5.1; Table 5.1), black cottonwood site index in the 6 site associations sampled falls into two main groups - a group with significantly lower site index that includes study sites within the Ac-Willow, 'Gleyed' (Cw-Salmonberry/Cw-Black twinberry), and Cw-Swordfern site associations, and a second group, with significantly higher site index, that includes the Ac-Red osier dogwood, Ss-Salmonberry, and Cw-Foamflower site associations. Because of the small number in each class and similar black cottonwood site index, study sites within the Cw-Salmonberry/Cw-Black twinberry site associations were considered together as the 'Gleyed' s,a.'s in this study. The ANOVA on site associations was highly significant ($p < .001$) and explained 87% of the variance in black cottonwood site index (Table 5.1).

Black cottonwood site index increased in a linear fashion along a gradient of increasing soil nutrient availability, as shown by the Box diagrams (Figure 5.1) and the ANOVA results (Table 5.1). The results of the ANOVAs show that black cottonwood site index within the medium and rich SNR groups was not significantly different, but were significantly less than black cottonwood site

Table 5.1: Means and results of ANOVAs for black cottonwood site index (m/15 yrs) in 3 subzones, 3 soil nutrient regime groups, and 5 site associations. Values with the same letter are not significantly different at $p < 0.05$.

Group/Subgroup	n	Black cottonwood Site Index (m/15 yrs)
SUBZONE		
CWHdm	17	19.3a
CWHds	6	21.8a
CWHxm	6	18.1a
Significance[1]		**NS**
SOIL NUTRIENT REGIME		
Medium	3	11.7 a
Rich	15	18.3 a
Very Rich	11	23.6 b
Significance[1]		**
SITE ASSOCIATION		
Ac-Willow	6	11.5 a
'Gleyed'	4	14.7 a
Ac-Red osier dogwood	5	21.6 b
Ss-Salmonberry	7	25.4 b
Cw-Foamflower	6	23.5 b
Significance[1]		***

[1] Statistical significance of the ANOVA; NS = $p > 0.05$; * = $0.05 > p > 0.01$; ** = $0.01 > p > 0.001$; *** = $p < 0.001$

index in the very rich SNR group. As for site associations, the ANOVA on SNR groups was highly significant (p=.003), but the SNR ANOVA explained only 36% of the variance in black cottonwood site index.

The ANOVAs of black cottonwood site index within site association or soil nutrient regime did not isolate the effect of soil moisture or soil nutrients because the site association groupings included medium to rich soil nutrient regimes, and the soil nutrient classes encompassed the range of flooding regimes and soil moisture conditions. The ANOVA of black cottonwood site index by soil nutrient regime within site associations explained 88% of the

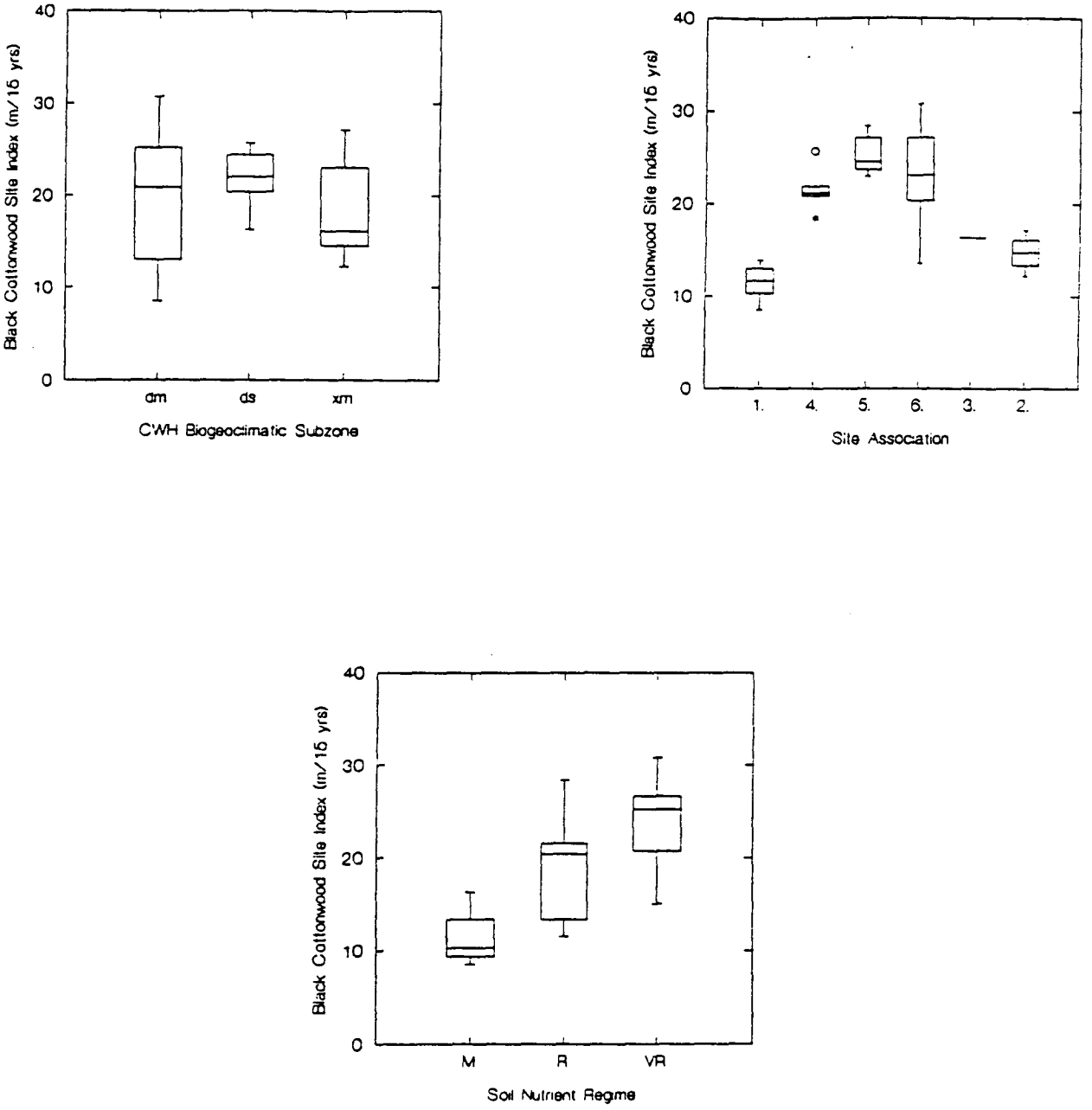


Figure 5.1: Box diagrams showing distributions of black cottonwood site index in biogeoclimatic subzone, soil nutrient regime (M=medium; R=rich; VR=very rich), and site association (1=Ac-Willow; 2="Gleyed" sa's; 3=Cw-Swordfern; 4=Ac-Red osier dogwood; 5=Ss-Salmonberry; 6=Cw-Foamflower) groups.

variance within the rich class, and 74% of the variance within the very rich class. Because of the small numbers in each group it was not possible to assess the effect of nutrient regime within site association.

5.3.2 Principal Component Analysis of Vegetation, Soil Nutrients, and Foliar Nutrients

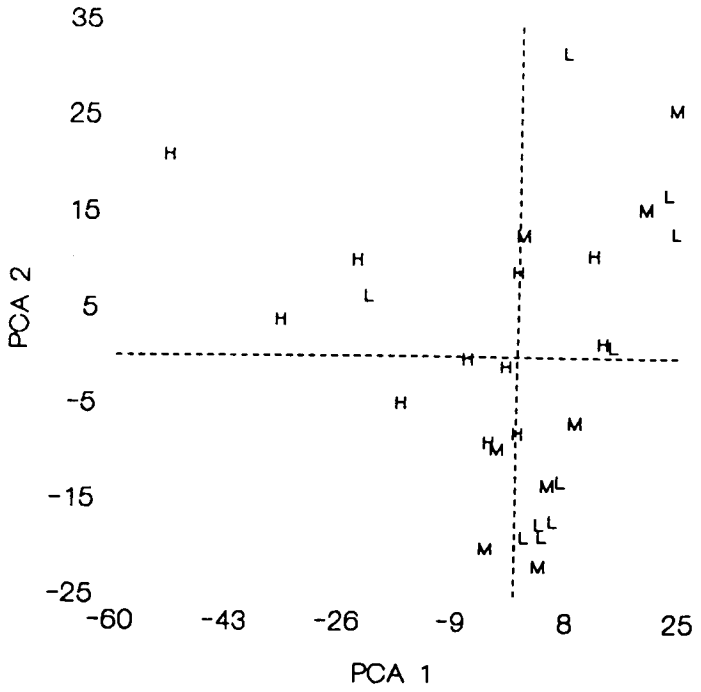
The first six axes of the PCA of 85 understory species in the 29 study sites explained 85% of the variation in the vegetation cover data (Table 5.2). The first two PCA axes accounted for 53.1% of the variation in the vegetation data, and an ordination of plot locations of these two axes is shown in Figure 5.2. To show inter-relationships among the groupings, study sites in the ordination are labelled by site index class, and site association (s.a.). Those species significantly correlated with the first two PCA axes are given in Table 5.3, and their SNR and SMR indicator status are also given in that table to assist with the interpretation of the ordination in Figure 5.2. Species positively correlated with PCA axis 1 (*Equisetum arvense* group) are common on flooded sites, both on the alluvial Ac-Red osier dogwood and Ac-Willow s.a.'s, and on the 'Gleyed' s.a.'s. Species negatively correlated with PCA axis 1 included a group of species common in the

Table 5.2: Eigenvalues (variance explained), percentage of total variance explained, and total cumulative variance explained for PCA axes 1 - 6 of the PCA of 85 understory species (presence class > II) in 29 black cottonwood study sites.

Axis	Eigenvalues	Percent of Total Variance Explained	Total Cumulative Variance Explained
PCA 1	441.58	29.8	29.8
PCA 2	343.80	23.3	53.1
PCA 3	180.58	12.2	65.3
PCA 4	147.97	10.0	75.3
PCA 5	88.22	5.96	80.0
PCA 6	69.78	4.72	85.0

Figure 5.2: (Overleaf) PCA ordination of 85 plant species with presence class > II in 29 black cottonwood stands. Study sites are labelled by site index class (L=low; M=medium; H=high) and site association (1=Ac-Willow; 2="Gleyed" sa's; 3=Cw-Swordfern; 4=Ac-Red osier dogwood; 5=Ss-Salmonberry; 6=Cw-Foamflower).

(a) Site Index Class



(b) Site Association

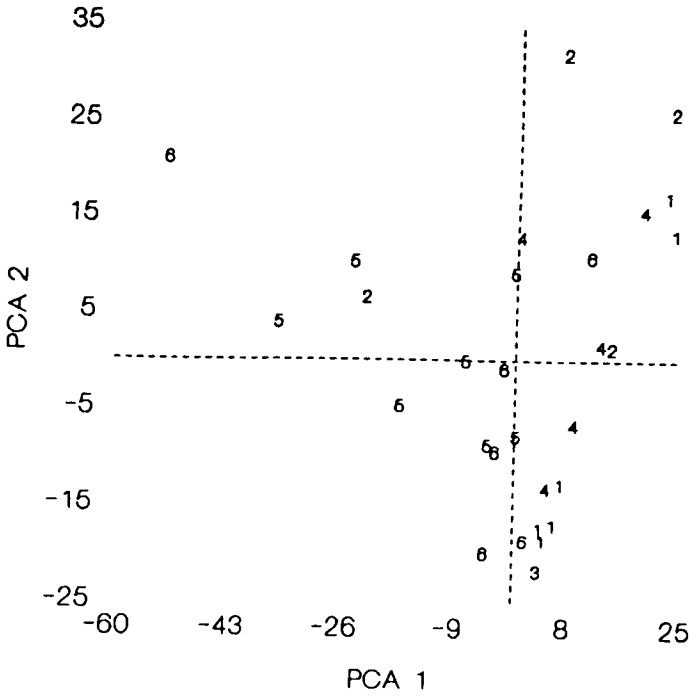


Table 5.3: List of species significantly ($p < .10$) correlated with the first and second PCA axes that have soil moisture and/or soil nutrient regime indicator status (Klinka and Krajina, 1986). The first group for each axis is negatively correlated with the axis.

Species	r^2 (PCA 1)	SNR[1]	SMR[1]
Rubus spectabilis	0.887	R	VM-W
Athyrium felix-femina	0.710	R	VMW
Sambucus racemosa	0.701	R	F-VM
Ribes bracteosum	0.490	R	VM-W
Polystichum munitum	0.446	R	
Tellima grandiflora	0.425	R	F-VM
Geum macrophyllum	0.378	R	F-VM
Plagiomnium insigne	0.363	R	VM-W
Carex deweyana	0.320	R	F-VM
Equisetum arvense	0.310	M	
Crataegus douglasii	0.325	R	VM-W
Cornus sericea	0.332	R	VM-W
Symphoricarpos albus	0.398	R	
Lonicera involucrata	0.553	R	VM-W

Species	r^2 (PCA 2)	SNR[1]	SMR[1]
Fragaria virginiana	0.440	M	
Adenocaulon bicolor	0.408	R	MD-F
Clintonia uniflora	0.392	P	MD-F
Acer circinatum	0.381	R	F-VM
Rhytidiadelphus triquetrus	0.370	M	
Hylocomium splendens	0.368	P	
Smilacina stellata	0.318	R	
Asarum caudatum	0.315	R	F-VM
Angelica genuflexa	0.335	R	W-VW
Stachys cooleyae	0.379	R	VM-W
Rubus spectabilis	0.401	R	VM-W
Achlys triphylla	0.409	R	
Carex obnupta	0.429	R	W-VW
Symphoricarpos albus	0.462	R	
Cornus sericea	0.591	R	VM-W
Rubus parviflorus	0.612	R	
Lonicera involucrata	0.627	R	VM-W

[1] SMR and SNR codes are as shown in Table 2.2

Cw-Foamflower and Ss-Salmonberry s.a.'s, and indicate a gradient along the axis from sites regularly flooded, to those sites where flooding is either infrequent, as in the Ss-Salmonberry s.a., or sites within the Cw-Foamflower s.a. that do not experience flooding. A gradient of increasing black cottonwood productivity is evident from right to left along PCA axis 1 - all low (except one) and medium (except two) site index plots occur at the positive end of the axis. On the second PCA axis, species positively correlated species had very moist to wet (VMW) and wet to very wet (WVW) SMR indicator status, and rich SNR status (Table 5.3), and were common on gleyed upland sites (Table 2.5). This group can be contrasted with species negatively correlated with PCA axis 2, which had moderately dry to fresh, and fresh to very moist, SMR status, and poor to rich SNR indicative values (Table 5.3). A gradient from nutrient poorer and drier sites, to those with very moist to wet soil moisture regimes is also demonstrated by the distribution of site associations along the axis. All Gleyed s.a.'s occurred at the positive end, and the Cw-Swordfern, the driest of the s.a.'s sampled in the study, is situated at the negative extreme of PCA axis 2. Also, all sites with medium SNR status are located at the extreme negative end of PCA axis 2, and are associated with a group of sites with low black cottonwood site index. The PCA of vegetation indicates that vegetation within study sites is affected by combined flooding and soil nutrient gradients, although the effects of flooding are more evident. The site index of black cottonwood is weakly associated with gradients of soil moisture and nutrients, as indicated by the vegetation on the sites.

The first three axes of the PCA of soil pH and soil nutrient contents for 29 black cottonwood ecosystems explained a cumulative total of 80% of the variation in the data (Table 5.4, Figure 5.3). PCA 1 explained 33.8% of the variance in the data, and presents a gradient from sites with relatively high organic matter (total N, total C, mineralizable N), to those with low organic content and high pH. PCA 2 explained 28.5% of the variance and represents a gradient from sites with high pH and high levels of exchangeable Ca, to those with relatively higher levels of mineralizable N, total N, and available P. The third PCA axis explained 17.6% of the variance in the data and contrasts sites with high available P and exchangeable K, with

Table 5.4: Correlations of pH and soil nutrient contents (kg/ha) with the first three principal component axes, eigenvalues, and percentage and cumulative percentage variance explained by the PCA axes in 29 black cottonwood ecosystems. Bolding indicates significance of the correlations at $p < 0.05$.

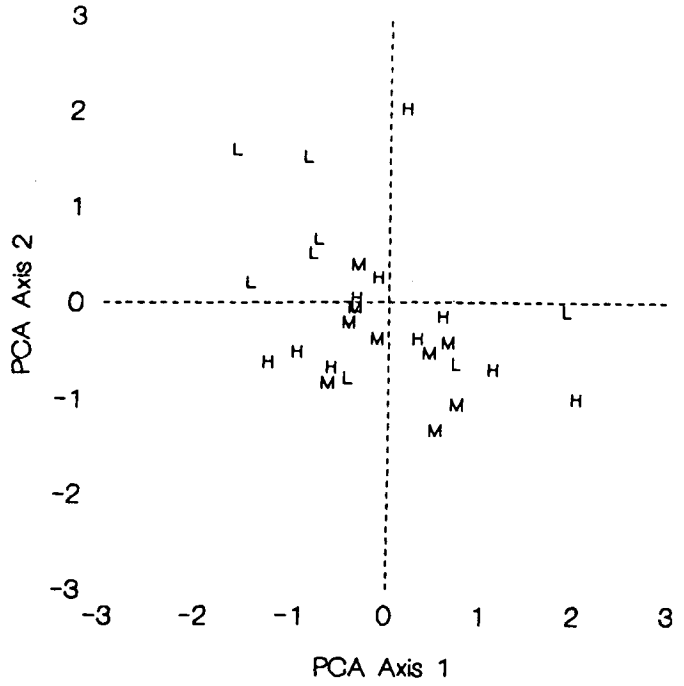
Nutrient	PCA 1	PCA 2	PCA 3
Total N	**0.969**	-0.068	0.079
Mineralizable N	**0.560**	-0.230	0.087
Total C	**0.927**	0.197	0.000
Exchangeable Ca	0.250	**0.915**	0.019
Exchangeable K	0.106	0.238	**0.577**
Available P	0.041	-0.132	**0.968**
Available SO_4-S	-0.026	0.207	0.010
Exchangeable Mg	-0.050	0.243	-0.188
pH	-0.328	**0.766**	-0.251
Eigenvalue	3.04	2.57	1.58
% of Variance Explained	33.8	28.5	17.6
Cumulative % of Variance Explained	33.8	62.3	79.9

those that have higher pH and exchangeable Mg. The general trend of variation summarized in the three PCA axes is to contrast sites with a high organic matter content, available P, and exchangeable K, with sites with high pH and contents of exchangeable Ca and Mg.

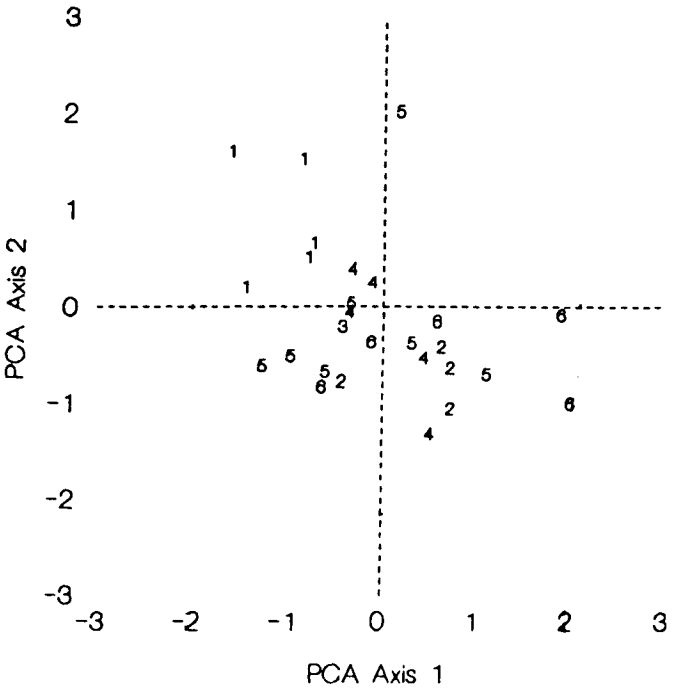
Figure 5.3 uses labels for black cottonwood site index class and site association to compare characteristics of the sites on PCA axes 1 and 2 of the soil nutrient-pH ordination. The upper left quadrant of the ordination includes mostly Ac-Willow (and 2 Ac-Red osier dogwood) sites that have low black cottonwood site index, and medium to rich soil nutrient regimes. Given the correlations shown in Table 5.4, this distribution suggests that Ac-Willow and Ac-Red osier dogwood sites with high pH and exchangeable Ca levels were relatively poor sites for black cottonwood growth. These sites are contrasted with those in the lower right quadrant of the ordination, which includes most of the sites with very rich soil nutrient regimes, mostly

Figure 5.3: (Overleaf) PCA ordination of pH and 8 soil nutrient content properties in 29 black cottonwood stands. Study sites are labelled by site index class (L=low; M=medium; H=high) and site association (1=Ac-Willow; 2="Gleyed" sa's; 3=Cw-Swordfern; 4=Ac-Red osier dogwood; 5=Ss-Salmonberry; 6=Cw-Foamflower).

(a) Site Index Class



(b) Site Association



medium to high black cottonwood site index, and which were included in a variety of site associations. This quadrant includes sites with relatively high organic matter content and available P, and correspondingly low pH and exchangeable Ca (Table 5.4). This comparison suggests that, in general, sites with high organic matter and available P, and lower pH and exchangeable Ca contents, were relatively good sites for black cottonwood growth. The inclusion of a few sites with low black cottonwood site index in the lower right quadrant (Figure 5.3) shows that this generalization does not apply to all sites. Both of the sites with low black cottonwood site index in the lower right quadrant of the ordination have gleyed horizons within the rooting zone, so that uptake of nutrients that would otherwise be available may be impeded by poor soil aeration. A weak gradient of increasing flooding frequency from right to left along PCA axis 1 is discernible in the ordination (Figure 5.3). Two Cw-Foamflower sites occur at the extreme right end of the axis, and lower bench alluvial floodplain site associations increase, from right to left along the axis.

The first three PCA axes of 13 foliar nutrients in 26 black cottonwood ecosystems accounted for about 64% of the variance in the foliar nutrient data matrix (Table 5.5). PCA axis 1 accounted for about 35% of the variability in the foliar nutrient data, and contrasts sites where black cottonwood foliage had relatively high foliar concentrations of N, K, Cu, B, S, S-SO_4, and active-Fe, with those with relatively higher concentrations of Ca, Mg, and Mn. The gradient along PCA axis 1 is correlated with decreasing black cottonwood site index, and a change from sites representing the Cw-Foamflower and Ss-Salmonberry s.a.'s, to those representing the Ac-Willow and Gleyed s.a.'s (Figure 5.4). This gradient can be interpreted as one of increasing rooting zone flooding associated with a reduction in black cottonwood site index. PCA axes 2 and 3 each accounted for about 14% of the variation in the foliar data, and demonstrate gradients from foliage high in N, Mg, and Mn, to that high in Zn, and from foliage high in Zn and B, to that high in P, Fe, and active -Fe, respectively.

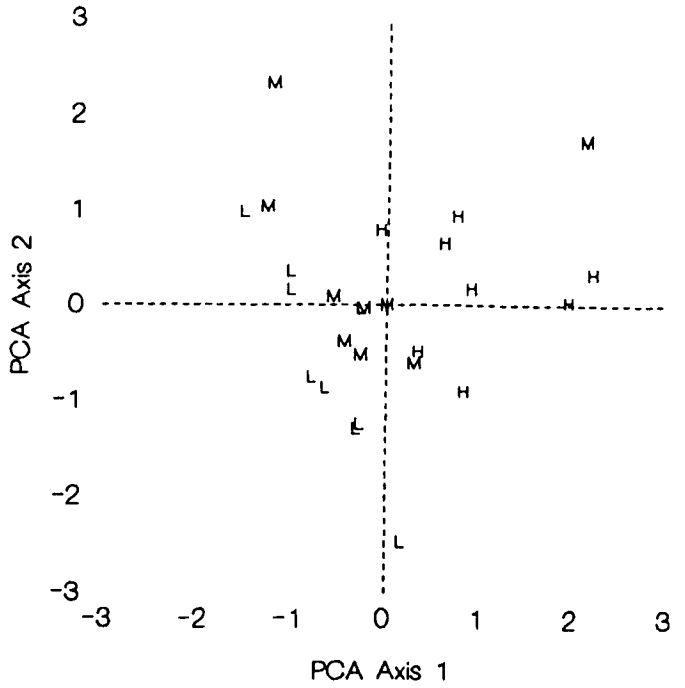
Table 5.5: Correlations of foliar nutrient concentrations with the first three principal component axes, eigenvalues, and percentage and cumulative percentage variance explained by the PCA axes in 26 black cottonwood stands. Bolding indicates significance of the correlations at $p < 0.05$.

Foliar Nutrient	PCA 1	PCA 2	PCA 3
N (%)	**.617**	**.608**	-.026
P (%)	.111	.113	**-.420**
K (%)	**.837**	-.094	-.320
Ca (%)	**-.540**	.214	.142
Mg (%)	**-.384**	**.682**	.140
Cu (ppm)	**.820**	.337	.155
Zn (ppm)	.223	**-.396**	**.481**
Fe (ppm)	.313	-.346	**-.527**
Mn (ppm)	**-.495**	**.594**	-.143
B (ppm)	**.490**	-.294	**.639**
S (%)	**.879**	.381	.145
SO_4 (ppm)	**.837**	.146	.243
active-Fe (ppm)	**.466**	-.065	**-.693**
Eigenvalue	4.528	1.903	1.843
% of Variance Explained	34.8	14.6	14.2
Cumulative % of Variance Explained	34.8	49.4	63.6

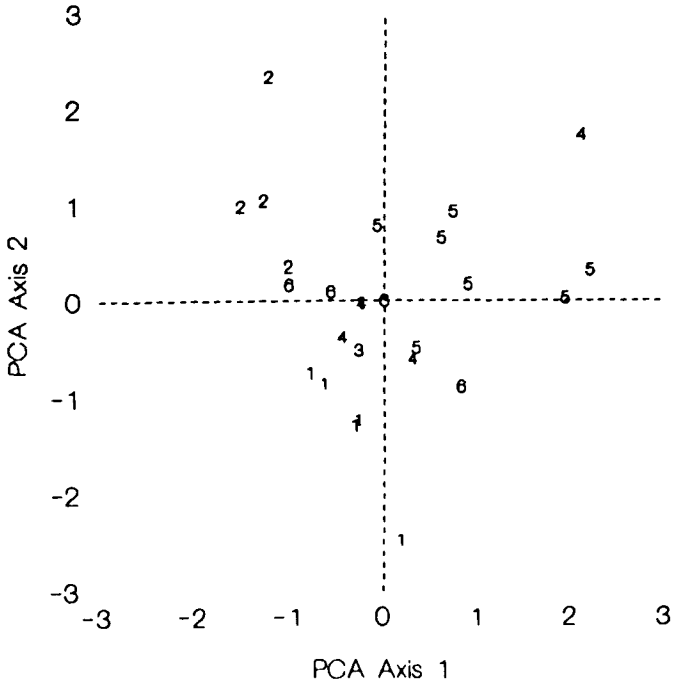
The contrast along PCA 1 of the foliar ordination between sites with high concentrations of foliar N and K, and those with high foliar Ca and Mg concentrations, is similar to PCA 1 of the soil nutrient ordination - sites with high soil contents of mineralizable N are contrasted with sites of relatively higher exchangeable Ca and Mg. In both the soil and foliar nutrient ordinations, black cottonwood site index decreased along this gradient.

Figure 5.4: (Overleaf) PCA ordination of 13 foliar nutrient concentrations in 29 black cottonwood stands. Study sites are labelled by site index class (L=low; M=medium; H=high) and site association (1=Ac-Willow; 2="Gleyed" sa's; 3=Cw-Swordfern; 4=Ac-Red osier dogwood; 5=Ss-Salmonberry; 6=Cw-Foamflower).

(a) Site Index



(b) Site Association



5.3.3 ANOVAs of Soil and Foliar Nutrients in Black Cottonwood Site Index Classes, Soil Nutrient Regimes, and Site Associations

ANOVAs comparing the statistical significance of the differences in mean soil nutrient content in 3 site index classes, 3 soil nutrient regime classes and 5 site associations are presented in Table 5.6. Only mineralizable N and total N demonstrated significant ($p < 0.05$) changes among site index classes. Mineralizable N, total N, total C, available P, and exchangeable K all increased with black cottonwood site index. Exchangeable Ca and Mg decreased with increasing black cottonwood site index. This pattern of soil content of exchangeable Ca and Mg being negatively related to black cottonwood site index, and opposite in trend to the other soil nutrients was observed in the PCA for soil nutrient contents shown in Figure 5.3. Sulphate S showed no trend with regard to site index class.

Only total N and total C had significant differences in soil contents among soil nutrient regime classes (Table 5.6). Soil nutrient contents increased from medium to rich to very rich soil nutrient regimes mineralizable N, total N, and total C. Considering that the differentiation of soil nutrient regime classes in this study was based to a large extent on the depth and development of the Ah layer, it is to be expected that nutrients associated primarily with the mineralization of organic matter are higher in the rich and very rich classes. For exchangeable Mg and K, and for available P, soil contents decreased from nutrient rich to very rich soil nutrient regimes, although the decreases were not statistically significant (Table 5.6).

Significant ($p < .05$) differences among 5 site associations were demonstrated for all soil nutrients (Table 5.6). For total N, total C, mineralizable N, and available P, the significance of the ANOVAs was the result of much lower soil nutrient contents in the Ac-Willow s.a. Soil nutrient contents for mineralizable N, total C, exchangeable K, and available P all increased along a gradient of decreasing flooding frequency, from Ac-Willow to Ss-Salmonberry s.a.'s. Exchangeable Ca and Mg (and pH - not shown) decreased along the same gradient. High total N and total C contents in upland s.a.'s (Cw-Foamflower, 'Gleyed') are the result of the presence of Moder humus forms, unique to those sites.

Table 5.6: ANOVAs of soil nutrient contents (kg/ha), for 29 black cottonwood ecosystems in 3 index classes, 3 soil nutrient regime classes, and 5 site associations. The Cw-Swordfern site association had only one site and was not included in the ANOVAs. For a given nutrient, in a given class, values with the same letter are not significantly different ($p < 0.05$).

SITE INDEX CLASS	n	Total N	Total C	Min-N	Av-P	Ex-Ca	Ex-Mg	Ex-K	SO_4-S
Low	9	5,506a	95,001a	94a	34a	12,912a	1,769a	453a	20a
Medium	9	9,964ab	135,998a	155ab	46a	8,257a	1,506a	705a	18a
High	11	11,019b	145,364a	187b	60a	7,666a	768a	755a	23a
Significance[1]		*	NS	*	NS[2]	NS	NS[2]	NS[2]	NS[2]
SOIL NUTRIENT REGIME	n	Total N	Total C	Min-N	Av-P	Ex-Ca	Ex-Mg	Ex-K	SO_4-S
Medium	3	3,859a	71,648a	90a	16a	11,277a	723a	573a	21a
Rich	15	8,124b	108,961b	144a	57a	10,106a	1,605a	674a	22a
Very Rich	11	11,784c	169,724c	177a	43a	8,231a	1,091a	568a	20a
Significance[1]		**	**	NS	NS	NS	NS	NS	NS[2]
SITE ASSOCIATION	n	Total N	Total C	Min-N	Av-P	Ex-Ca	Ex-Mg	Ex-K	SO_4-S
Ac-Willow	6	4,177a	72,282a	58a	16a	15,907a	2,084a	448ab	25ab
Ac-Red osier dogwood	5	10,216ab	114,947ab	126b	34ab	14,412a	3,025a	815c	42b
Ss-Salmonberry	7	8,673ab	122,603ab	146b	66ab	6,263b	754b	789c	22ab
'Gleyed'	4	11,017b	181,362b	180b	38ab	2,985b	674b	221a	6.5a
Cw-Foamflower	6	14,227b	201,903b	220b	84b	6,675b	849b	719bc	17ab
Significance[1]		**	**	**	*[2]	***[2]	***	***[2]	*[2]

[1] statistical significance of the ANOVA; NS = $p > 0.05$; * = $0.05 > p > 0.01$; ** = $0.01 > p > 0.001$; *** = $p < 0.001$

[2] variables transformed to natural logarithms to satisfy model requirements for homogeneity of variance or normality.

ANOVAs comparing the statistical significance of group differences in 13 foliar nutrients are presented in Table 5.7. Foliar concentrations of N, P, K, S, Cu, SO_4, and active Fe all increased with increasing black cottonwood site index. The increases were statistically significant for all of these nutrients except P (Table 5.7), and the recurrent pattern was for foliar concentrations in the high site index class to be significantly higher than concentrations in both the low and medium site index classes. Differences in foliar N concentrations were significant for all site index classes. The nutrients demonstrating this trend of increase as black cottonwood site index increases, are part of a group of nutrients positively correlated with the first axis of the

PCA of foliar nutrient data, where there occurrence was correlated with the high site index class (Figure 5.4).

Relationships between foliar nutrient concentrations and site associations were more complex than for site index class, and many of the differences were statistically significant (Table 5.7). Foliar concentrations of N, K, and S demonstrated similar relationships within site associations - they all increased with increasing bench height on alluvial floodplains, followed by concentration decreases in upland site associations. Foliar P concentrations showed the same trend of increasing with increasing bench height on alluvial floodplains, but maintained high concentrations in upland site associations. Concentrations of foliar Ca, Mg, B, Mn, and SO_4, demonstrated irregular differences among site associations, that appeared to be unrelated to

Table 5.7: ANOVAs of foliar nutrient concentrations of 29 black cottonwood stands in 3 site index classes, and 5 site associations. The Cw-Swordfern site association has only one site and was not included in the ANOVAs. For a given nutrient, in a given class, values with the same letter are not significantly different at $p < 0.05$. The number of study stands in each group is given in Table 5.6.

SITE INDEX CLASS	N (%)	P (%)	K (%)	Ca (%)	Mg (%)	Cu (ppm)	Zn (ppm)	Fe (ppm)	Mn (ppm)	B (ppm)	S (%)	SO4 (ppm)	act-Fe (ppm)
Low	1.81a	0.21a	1.10a	1.30a	0.28a	6.8a	93a	91a	47a	26a	0.19a	411a	68a
Medium	2.05b	0.21a	1.28a	1.38a	0.27a	7.8a	81a	97a	56a	28a	0.21a	420a	69a
High	2.45c	0.24a	1.76b	1.21a	0.21a	10.9b	99a	91a	34a	26a	0.27b	679b	71a
Significance[1]	***	NS	**	NS	NS	***	NS	NS	NS	NS	***	**[2]	NS

SITE ASSOCIATION	N (%)	P (%)	K (%)	Ca (%)	Mg (%)	Cu (ppm)	Zn (ppm)	Fe (ppm)	Mn (ppm)	B (ppm)	S (%)	SO4 (ppm)	act-Fe (ppm)
Ac-Willow	1.71a	0.19a	1.18a,b	1.16a	0.24a	7.3a,b	94a	100a	41a,b	32b	0.20a,b	476a	71a
Ac-Red osier dogwood	2.02b	0.19a	1.31b,c	1.19a,b	0.31a	10b,c	96a	100a	45a,b	38b	0.21a,b	445a	69a
Ss-Salmonberry	2.55c	0.26b	1.90d	1.12a	0.21a	11c	99a	82a	37a	24a,b	0.27b	646b	66a
Cw-Foamflower	2.04b	0.28b	1.50b,c,d	1.42a,b	0.21a	6.8a	97a	102a	66a,b	23a,b	0.23b	566a,b	77a
'Gleyed'	2.11b	0.21a	0.82a	1.75b	0.43b	6.8a	76a	99a	66b	13a	0.20a	234a	74a
Significance[1]	***	***	***	*	***	***	NS	NS	*	**	**	*[2]	NS

[1] statistical significance of the ANOVA; NS = $p > 0.05$; * = $0.05 > p > 0.01$; ** = $0.01 > p > 0.001$; *** = $p < 0.001$

[2] variables transformed to natural logarithms to satisfy model requirements for homogeneity of variance or normality

black cottonwood site index. Foliar Fe, active Fe, and Zn showed slight changes among site associations and no significant differences were found (Table 5.7).

5.3.4 Linear Regressions of Vegetation on Site Index

The linear model fit by forward stepwise regression analysis using the first 10 axes of the vegetation PCA utilized the first 4 PCA axes, and accounted for 51% of the variation in site index (Equation 1 - Table 5.8). PCA axis 2 had the highest partial F value, and the coefficient was positive, and reflected the clustering of sites in the low site index class at the negative end of the axis (Figure 5.2). Similarly, PCA axis 1 had the second highest partial F value, had a negative regression coefficient, and had a preponderance of sites in the high site index class at the negative end of the axis in the vegetation ordination (Figure 5.2). The regression suggests that about half of the variation in black cottonwood site index can be explained by the presence or absence of the different understory species growing in association with black cottonwood on the study sites.

Table 5.8: Models, probabilities, coefficients of determination (R^2), and standard error of the estimate (SEE) for vegetation variables on site index in 29 black cottonwood stands.

MODEL	p	R^2	SEE (m)
(1) SI_{Ac} = 19.597 + 0.096 (PCA2) - 0.201 (PCA1) - 0.158 (PCA4) - 0.139 (PCA3)	.001	0.51	4.73
(2) SI_{Ac} = 15.835 - 0.152 (M) + 0.044 (R)	.007	0.32	5.35
(3) SI_{Ac} = 11.214 - 0.126 (FVM) + 0.067 (VMW)	.003	0.36	5.20
(4) SI_{Ac} = 19.603 - 0.114 (PCA2) + 0.043 (PCA1)	.002	0.39	5.07

The regression of the frequency of species in three soil nitrogen indicator species groups (N-poor, N-medium, and N-rich) on black cottonwood site index was less successful than the species themselves, and explained 32% of the variation (Equation 2 - Table 5.8). N-medium species had a negative regression coefficient, and N-rich sites had a positive regression

coefficient, and showed the respective negative and positive correlations of these species indicator groups with black cottonwood site index. The regression of soil moisture indicator species groups on black cottonwood site index explained a slightly higher amount of variation (36%) than the soil nitrogen indicator species groups (Equation 3 - Table 5.8). The negative regression coefficient of the fresh to very moist indicator species group showed the reduced site index on sites supplied with relatively lower amounts of soil moisture, and can be compared to the positive effect of moister sites with a preponderance of species with very moist to wet SMR indicator status.

Given the high intercorrelations of soil moisture and soil nitrogen indicator species groups, a stepwise linear regression analysis combining both indicator groups was not carried out. The forward stepwise regression on the first 5 axes (which explained 85% of the total variation in the PCA) of the PCA using soil moisture and nitrogen indicator species group data identified PCA axes 1 and 2 as the most important variables correlated with black cottonwood site index, and explained 39% of the variation in the model (Equation 4 - Table 5.8).

5.3.5 Linear Regressions of Soil Nutrient Contents on Site Index

The results of univariate regressions for each of the soil nutrients on site index (Table 5.9) followed the same trends as those discussed for Table 5.6. Log-transformed variables are listed where their regressions explained a higher percentage of the variance in the model. Log total N (ltotN), log total C (ltotC), log mineralizable N (lminN), log available P (lavP), and log exchangeable K (lexK) all had significant linear relationships with black cottonwood site index for the 29 study sites. The percentage of variance explained by the univariate regressions ranged from 42% for log total N and 37% for log mineralizable N, to 16% for log exchangeable K (Table 5.9). The standard error of the estimate for the models was large and varied from 4.76 m for log total N to 5.91 m for log exchangeable K. The univariate models suggested that a total N/mineralizable N/total C group were the most important nutrients determining the height

growth of black cottonwood across all 29 study sites. Available P and exchangeable K were also important but appeared to play a secondary role.

Table 5.9: Models, probability, coefficients of determination (R^2), and standard error of the estimate (SEE) for univariate regressions of soil nutrient contents on black cottonwood site index in 29 black cottonwood stands. Only soil nutrients with significant ($p < 0.05$) regressions are shown.

MODEL	p	R^2	SEE (m)
(1) SI_{Ac} = -42.64 + 6.900 (ltotN)	.000	0.42	4.76 m
(2) SI_{Ac} = -38.11 + 4.956 (ltotC)	.043	0.15	5.90 m
(3) SI_{Ac} = -3.67 + 4.192 (lminN)	.001	0.37	5.13 m
(4) SI_{Ac} = 8.56 + 3.156 (lavP)	.027	0.18	5.91 m
(5) SI_{Ac} = -8.84 + 4.478 (lexK)	.033	0.16	5.91 m

The correlation matrix of variables that had significant linear regressions on black cottonwood site index (Table 5.10) shows that the significant soil nutrients fell into 2 correlated groups - total N (totN), total C (totC), and mineralizable N (minN) were significantly correlated with each other, as were available P (avP) and exchangeable K (exK). In the multiple regressions shown in Table 5.11, mineralizable N was used as the measure of nitrogen availability, because it was highly correlated with both total N and total C. Exchangeable K and available P were also used in the multiple regressions, both individually, and together with mineralizable N. Equations 1 and 2 in Table 5.11 included all 3 soil nutrients and explained 60% of the variance in site index for the log-transformed variables, and 58% for the untransformed measures of soil nutrient contents. Substituting total N for mineralizable N (Equation 3 - Table 5.11), and including soil pH (Equation 4 - Table 5.11) did not increase the explanatory power of the multiple linear regression of soil nutrients on black cottonwood site index. Forward stepwise analysis of log transformed soil nutrient variables resulted in a model that included only mineralizable N and available P, and accounted for 53% of the variation in the model (Equation 5 - Table 5.11). The same procedure for untransformed variables resulted

in Equation 6 in Table 5.11, and accounted for 42% of the variation in the model. Models 5 and 6 in Table 5.11 are presented as the 'best' complete equations relating soil nutrient contents to black cottonwood site index for the 29 study sites.

Table 5.10: Correlation matrices for soil nutrient variables with significant univariate linear regressions on black cottonwood site index. Bolding indicates significant ($p < 0.05$) correlations.

	minN	exK	avP	totC
exK	.045			
avP	.228	**.447**		
totC	**.695**	-.221	-.098	
totN	**.640**	.074	.014	**.859**

	lminN	lexK	lavP	ltotC
lexK	.194			
lavP	.299	**.418**		
ltotC	**.845**	-.046	.062	
ltotN	**.838**	.167	.195	**.916**

Table 5.11: Probability (p), coefficients of determination (R^2), and standard error of the estimate (SEE) for multiple regressions of soil nutrients on black cottonwood site index, using variables with significant univariate regressions on black cottonwood site index.

SOIL NUTRIENTS	p	R^2	SEE (m)
(1) lminN, lavP, lexK	.000	.60	4.60 m
(2) minN, avP, exK	.001	.58	4.71 m
(3) totN, avP, exK	.005	.49	5.01 m
(4) pH, minN, avP, exK	.002	.59	4.79 m
MODEL	**p**	**R^2**	**SEE (m)**
(5) SI_{Ac} = -10.24 + 4.41 lminN + 2.15 lavP	.000	.53	4.75 m
(6) SI_{Ac} = 9.23 + 0.041 minN + 0.007 exK	.002	.42	5.12 m

Parameters and summary statistics for univariate regressions of soil nutrients on site index for a reduced data set that includes only those stands where cottonwood predominated are shown in Table 5.12. In sites deleted from the full data set, black cottonwood occurred as

Table 5.12: Probability (p), coefficients of determination (R^2), and standard error of the estimate (SEE) for univariate regressions of soil nutrient contents on black cottonwood site index in the reduced data set (n=22). Only soil nutrients with significant ($p < 0.05$) regressions are shown.

MODEL	p	R^2	SEE (m)
(1) SI_{Ac} = 11.58 + 0.001 (totN)	.000	0.52	4.64
(2) SI_{Ac} = -93.19 + 9.810 (ltotC)	.000	0.57	4.45
(3) SI_{Ac} = -8.14 + 6.16 (lminN)	.000	0.62	4.12
(4) SI_{Ac} = 6.12 + 4.198 (lavP)	.009	0.31	5.68
(5) SI_{Ac} = 26.62 - 0.003 (exCa)	.013	0.30	5.76
(6) SI_{Ac} = 24.88 - 0.001 (lexMg)	.030	0.22	5.99

as scattered individuals among other deciduous and coniferous species (see Table 2.1). The 22 sites included in the reduced data set provided the opportunity to examine soil nutrient - black cottonwood site index relationships in more uniform soil conditions that were typical of well-stocked black cottonwood stands. Univariate regressions of soil nutrient contents on black cottonwood site index for the reduced data set were similar to those shown for the full data set, except that exchangeable K was not significant, and exchangeable Ca and Mg demonstrated significant and negative linear relationships. For all nutrients except exchangeable K, the variance explained by the linear models was about twice as high for the reduced data set, compared to the complete data set. The stronger relationships demonstrated for soil nutrients in the reduced data set were due primarily to the reduction in humus form variability, and in the deletion of upland sites where soil drainage was impeded, so that uptake of nutrients present within the soil was impaired. As for the complete data sets, coefficients for exchangeable Ca and Mg in the reduced data set were negative, and show that increasing amounts of these nutrients were significantly correlated with decreasing site index.

Correlation matrices for both the log-transformed and the non-transformed values of soil nutrients in the reduced data set in Table 5.13 showed the same pattern as the full data set (Table

5.10). Total N, total C and mineralizable N formed a significantly, positively correlated group, as did exchangeable Ca and Mg. Available P had a significant negative correlation with both exchangeable Ca and Mg.

Table 5.13: Correlation matrices for soil nutrient variables with significant univariate linear regressions on black cottonwood site index for the reduced data set. Bolding indicates significant ($p < 0.05$) correlations.

	totN	totC	minN	avP	exCa
totC	**0.870**				
minN	**0.662**	**0.728**			
avP	0.070	-0.070	0.350		
exCa	-0.407	-0.396	-0.471	**-0.600**	
exMg	-0.118	-0.174	-0.278	**-0.527**	**0.745**

	ltotN	ltotC	lminN	lavP	lexCa
ltotC	**0.920**				
lminN	**0.850**	**0.865**			
lavP	0.226	0.057	**0.407**		
lexCa	-0.294	-0.279	-0.389	**-0.473**	
lexMg	0.046	0.009	-0.119	**-0.416**	**0.881**

Multiple regression models of soil nutrients significantly correlated with site index (Model 1 - Table 5.14) explained about 80% of the variance in site index for the reduced data set. Complete models with regression coefficients are not given because of significant correlations among the explanatory variables with significant univariate probabilities (Table 5.12). As for the full data set, mineralizable N was used to represent soil nitrogen availability. Given the high positive correlation of exchangeable Ca and Mg, a new variable was created (ex Ca+Mg) that summed the 2 values. Using this variable did not increase the explanatory power of the models (Model 2 - Table 5.14). Dropping exchangeable Mg from the model did not reduce the percentage of variance explained (Model 3 - Table 5.14), although, when exchangeable Ca was omitted, the percentage of variance explained dropped to 69% (Model 4 - Table 5.14). The model using the log transformed values explained about the same percentage of variance as the non-transformed soil nutrient values (Model 5 - Table 5.14).

Table 5.14: Probability (p), coefficients of determination (R^2), and standard error of the estimate (SEE) for multiple regressions of soil nutrients on black cottonwood site index, using variables with significant univariate regressions on black cottonwood site index in the reduced data set (n=22).

Soil Nutrients	p	R^2	SEE
(1) minN, avP, exCa, exMg	.000	.79	3.59
(2) minN, avP, ex (Ca+Mg)	.000	.79	3.38
(3) minN, avP, ex Ca	.000	.80	3.34
(4) minN, avP, ex Mg	.000	.69	4.08
(5) lminN, lavP, lex(Ca+Mg)	.000	.80	3.46

5.3.6 Interaction of Available-P, Exchangeable Ca, and pH.

The solubility and availability of soil P is determined to a large extent by soil pH and the concentrations of Ca available to fix P as calcium phosphate concretions (Boishot *et al.*, 1950; Cole *et al.*, 1953; Griffin and Jurinak, 1973; Russell, 1974). The significant ($p < 0.05$) negative relationship between available P and exchangeable Ca (Table 5.13) in the reduced data suggests that this effect may be responsible for the low amounts of available P in study site soils with high exchangeable Ca contents. This relationship is well demonstrated for the 22 sites in the reduced data set (Figure 5.5). In Figure 5.5, available P is much lower when pH is in excess of 6.5, and when exchangeable Ca contents increase over about 15,000 kg/ha (see hatched lines in Figure 5.5). Data labels in Figure 5.5 refer to high, medium, and low site index classes, and the trend is for high site index class sites to have high amounts of available P, relatively low amounts of exchangeable Ca, and relatively low pH. Although an indication of total P in these soils is required to confirm it, one explanation for this relationship is that soil contents of available P are fixed and thus made unavailable in black cottonwood stands with high pH and exchangeable Ca contents.

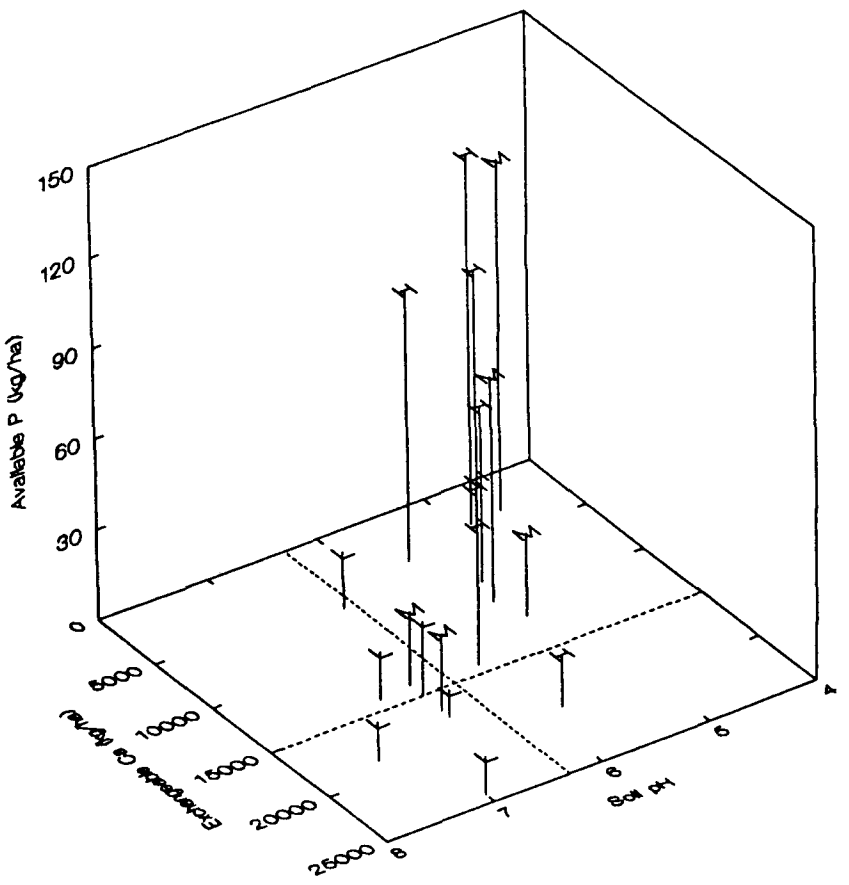


Figure 5.5: Three dimensional scattergram showing the effect of increasing soil pH and content of soil exchangeable Ca on content of soil available P for the reduced data set (n=22). Study sites are labeled by their black cottonwood site index class (L=low; M=medium; H=high).

5.3.7 Linear Regressions of Foliar Nutrient Concentrations on Site Index

Foliar nutrients with significant univariate linear regressions on site index (Table 5.15), were the same as those with significant ANOVAs among site index classes in Table 5.7. The regressions of foliar N, K, S, SO_4, and Cu were all highly significant. The percentage of variance in site index explained by the regressions ranged from about 70% for foliar S to 20% for foliar SO_4. Standard errors of the estimate ranged from 3.23 to 5.34 m.

Table 5.15: Univariate models, probabilities (p), coefficients of determination (R^2), and standard errors of the estimate (SEE) for regressions of foliar nutrients on site index in 26 black cottonwood stands. Only foliar nutrients with significant ($p < 0.05$) regressions are shown.

MODEL	p	R^2	SEE (m)
(1) SI_{Ac} = 13.325 + 132.68 (folS)	.000	.695	3.232
(2) SI_{Ac} = -8.834 + 12.788 (folN)	.000	.630	3.481
(3) SI_{Ac} = 5.552 + 9.576 (folK)	.000	.462	4.372
(4) SI_{Ac} = 4.58 + 1.640 (folCu)	.000	.455	4.398
(5) SI_{Ac} = 14.703 + 0.007 (folSO$_4$)	.023	.198	5.337

Almost all of the foliar nutrients that had significant regressions on site index were highly correlated (Table 5.16). As for soil nutrients, this creates problems of collinearity when constructing multiple regression models of the foliar nutrients on site index. Various combinations of those foliar nutrients with significant univariate regressions on black cottonwood site index are shown in Table 5.17, where the percentage of variance explained ranged from 58 to 77%, and the standard errors of the estimate ranged from 3.0 to 3.6 m. Model 1 in Table 5.17 includes all five foliar nutrients with significant univariate regressions, and has the highest R^2 (0.77) of all models. Model 2 excludes foliar S, and assumes that S is not limiting growth, but rather is taken up in proportion to the amount of N taken up. The very high

correlation between foliar S and N shown in Table 5.16 supports this interpretation. Model 2 explains 73% of the variation in black cottonwood site index with a standard error of the estimate of 3.12 m. Combining highly correlated variables into one variable that was

Table 5.16: Correlation matrix for foliar nutrient variables with significant univariate linear regressions on black cottonwood site index. Bolding indicates significant ($p < 0.05$) correlations.

	Cu	SO_4	S	N
SO_4	.320			
S	**.714**	**.669**		
N	**.712**	.263	**.814**	
K	.484	**.680**	**.696**	.451

the sum of the concentrations of all of the nutrients (N+Cu+S and N+Cu+S+K) did not significantly increase the explanatory power of the models (Models 3 and 4 - Table 5.17). Forward stepwise regression analysis of all significant nutrients identified foliar N and SO_4 as the most important nutrients (Model 5 - Table 5.17), although the percentage of variance explained was lower than for Models 1 and 2 in the same table. Using just foliar N, K, and Cu (Model 6), forward stepwise regression identified foliar N and K as the most important in determining site index. The percentage of variance explained for this model was about the same as Model 2, where all three variables are included.

Table 5.18 presents model parameters for foliar nutrients with significant regressions on black cottonwood site index for the reduced data set (n=20) described above for the soil nutrient regressions. The list of nutrients was essentially the same as for the complete data set, except that the regression with foliar P was significant, and that for SO_4 was not. In general, the percentage of variance explained was higher (32-70%) for the reduced data set, and the standard errors of the estimate about the same. Foliar N alone accounted for about 70% of the variation in site index, followed by foliar K, Cu, P and S, in decreasing order of variance explained.

Table 5.17: Probabilities (p), coefficients of determination (R^2), and standard errors of the estimate (SEE) for multiple regression models of foliar nutrients on black cottonwood site index, using variables with significant univariate regressions.

Foliar Nutrients	p	R^2	SEE
(1) N, K, S, SO_4, Cu	.000	.774	2.967
(2) N,K,Cu	.000	.730	3.115
(3) (N+Cu+S), K	.000	.642	3.425
(4) (N+Cu+S+K)	.000	.584	3.598
(5) forward stepwise (N, K, S, SO_4, Cu) - N, SO_4	.000	.635	3.536
(6) forward stepwise (N, K, Cu) - N, K	.000	.729	3.048

Table 5.18: Probabilities (p), coefficients of determination (R^2), and standard errors of the estimate (SEE) for univariate regressions of foliar nutrients on black cottonwood site index in 20 black cottonwood ecosystems (reduced data set). Only foliar nutrients with significant ($p<0.05$) regressions are shown.

Foliar Nutrient	p	R^2	SEE (m)
(1) SI_{Ac} = -7.937 + 12.767 (folN)	.000	.701	3.362
(2) SI_{Ac} = 2.772 + 11.506 (folK)	.001	.458	4.660
(3) SI_{Ac} = 274.66 + 446.19 (folCu)	.004	.381	4.979
(4) SI_{Ac} = 2.550 + 80.442 (folP)	.010	.315	4.762
(5) SI_{Ac} = 4.903 + 61.107 (folS)	.010	.315	5.237

As for the complete data set, the correlation matrix presented in Table 5.19 shows a high degree of intercorrelation among foliar nutrients that have significant regressions on site index. The multiple regression model that included all foliar nutrient variables with significant univariate regressions on black cottonwood site index (Model 1 - Table 5.20) had the highest explanatory power with an R^2 of about 80%. Model 2, which excluded S, had a slightly lower

R^2, as did Model 3, which included only foliar N, P, and K. Forward stepwise regression that began with all foliar variables with significant univariate regressions identified foliar N and P as the most important nutrients determining site index in the reduced data set (Model 4). This model explained 78% of the variation in black cottonwood site index, an had a standard error of the estimate of 3.07 m.

Table 5.19: Correlation matrix for foliar nutrient variables with significant univariate linear regressions on black cottonwood site index in the reduced data set. Bolding indicates significant ($p < 0.05$) correlations.

	N	P	K	S
P	**.573**			
K	**.817**	**.687**		
S	**.824**	.272	**.648**	
Cu	**.823**	.287	**.650**	**.804**

Table 5.20: Probabilities (p), coefficients of determination (R^2), and standard errors of the estimate (SEE) for multiple regressions of foliar nutrients on black cottonwood site index in the reduced data set (n=20).

Foliar Nutrients	p	R^2	SEE
(1) N,P,K,S,Cu	.001	.795	3.28
(2) N,P,K,Cu	.000	.788	3.20
(3) N,P,K	.000	.779	3.24
(4) Forward stepwise (N,P,K,S,Cu) - N,P	.000	.775	3.07

5.3.8 Relationships Between Foliar and Soil Nutrients

Univariate regressions (Table 5.21) show that concentrations of P, N, K, and Mg in black cottonwood foliage were well correlated with measures of soils contents (kg/ha) for the same nutrients. Scattergrams for all nutrients listed in Table 5.21 are shown in Figure 5.6, where best-fit lines are shown. Regressions and scattergrams are based on the reduced data used for analysis in both the soil and foliar nutrient analyses above. Measures of soil available P, as measured by the new Mehlich method, accounted for 83% of the variation in foliage concentration of black cottonwood trees on those sites, and had a standard error of the estimate of .018% dry mass. Increases in foliar P were also associated with increasing black cottonwood site index, as shown by the site index class labels for the sites (Figure 5.6).

Table 5.21: Univariate models, probabilities (p), coefficients of determination (R^2), and standard errors of the estimate (SEE) for regressions of foliar nutrients on soil nutrient content of the same nutrient (reduced data set; n=20).

MODEL	p	R^2	SEE
1) Foliar P = 0.175 + .001 (Soil Available P)	**.000**	.831	.018
2) Foliar N = 1.642 + .004 (Soil Mineralizable N)	**.001**	.497	.282
3) Foliar Mg = 0.190 + .00002 (Soil Exchangeable Mg)	**.011**	.323	.042
4) Foliar K = 1.042 + .004 (Soil Exchangeable K)	**.018**	.272	.317
5) Foliar S = 0.210 + .0005 (Soil Available SO_4)	.365	.051	.035
6) Foliar Ca= -1.197 + .0004 (Soil Exchangeable Ca)	.922	.001	.293

Although the percentage of variance explained was not as high (Table 5.21), similar relationships existed for foliar N and foliar K concentrations (Figure 5.6). The increasing concentrations of foliar Mg were significantly correlated with measures of soil exchangeable Mg contents, but the increase was not associated with increases in site index (Figure 5.6). Most sites in the high site index class had relatively low foliar Mg concentrations and soil Mg contents. Regressions for foliar S and Ca on measures of soil SO_4 and Ca contents were not significant,

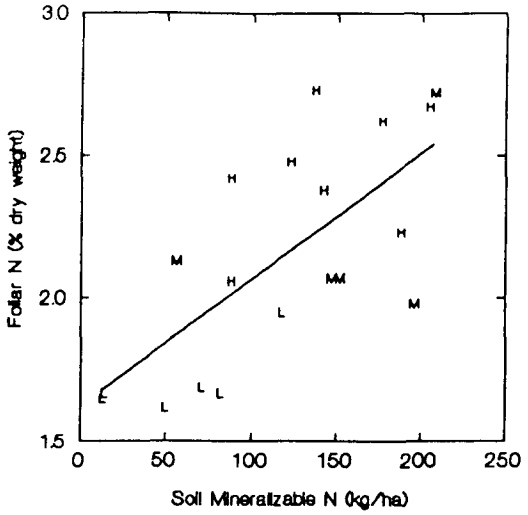
and suggested that soil contents of these nutrients were sufficient and did not limit their uptake in the sites studied.

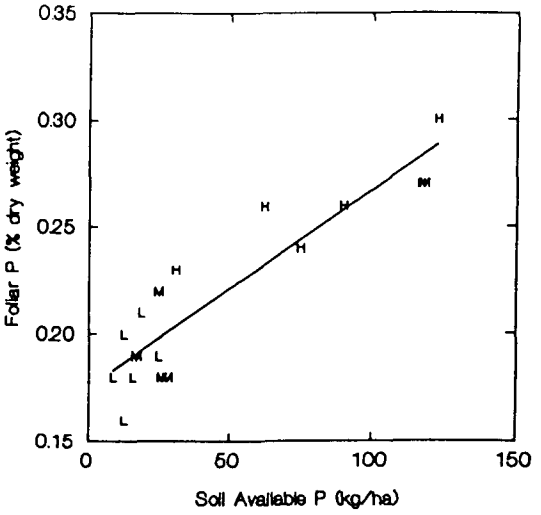
The results of the regressions shown in Table 5.21 and illustrated in Figure 5.6 support a trend that is evident from analysis of both the soil and foliar nutrient data for the stands studied. The availability of N, P, and K in soils within the study sites were the principle nutrient factors that determined black cottonwood site index. Foliar S was associated with increases in site index, but was not considered to be causative. This conclusion is supported by the regressions shown in Figure 5.6, where increases in foliar S are unrelated to the availability of SO_4 in study area soils. As suggested by several authors (Dijkshoorn and van Wijk, 1967; Kelly and Lambert, 1972; Turner *et al.*, 1977), S is present in proportion to the uptake of N, and in a ratio required for the synthesis of plant proteins.

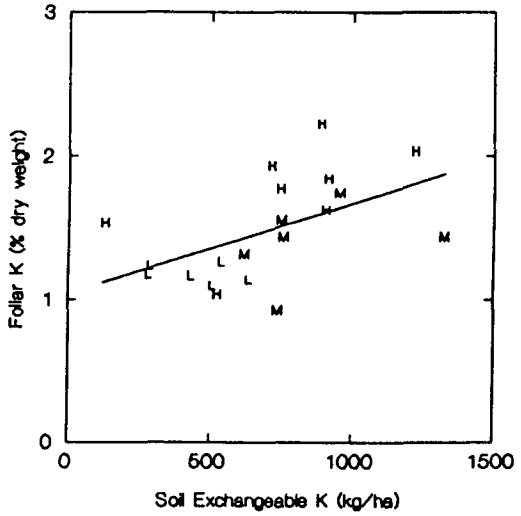
5.3.9 Identification of Optimal Nutrient Levels for Black Cottonwood

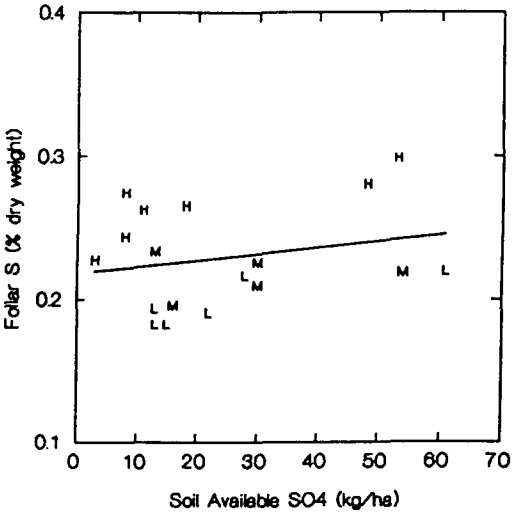
Scattergrams relating foliar concentrations of N, P, K, and Cu to site index are shown in Figure 5.7. Mean values for foliar nutrient concentrations for the high site index class (Table 5.7) are shown as vertical dashed lines in Figure 5.7, and are included for reference. A distance-weighted least squares smoothing algorithm (McLain, 1974) has been used to fit a second order polynomial line through the data points to show the general trend of the data. For foliar N, P, and Cu the trend is for site index to increase through the low and medium site index classes, as the concentrations of the foliar nutrients increase, and then to taper off in the high site index class as foliar concentrations increase. These trends can be interpreted as a 'deficiency to sufficiency, or critical levels curves (Ballard and Carter, 1986; Chapin *et al.*, 1986; Leyton, 1948; Lavender, 1970; Weetman and Wells, 1990). The trend for foliar K differs from the other three nutrients in that no levelling of the curve is apparent, and the relationship is more or less linear. This may mean that, given the concentrations of the other nutrients, the K sufficiency level has not been reached, and thus that higher levels of foliar K

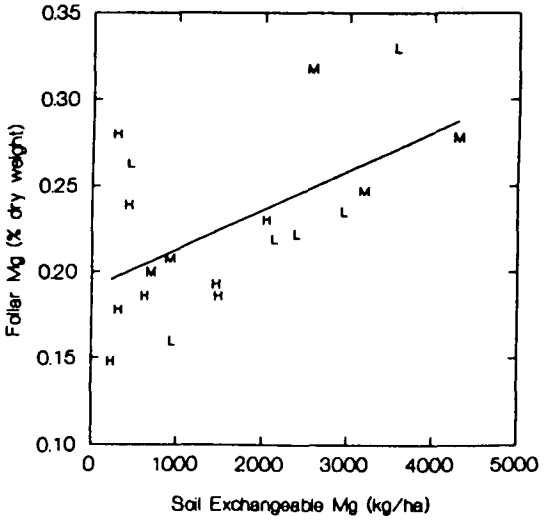
Figure 5.6: (Overleaf) Regressions of foliar nutrient concentrations on their soil nutrient contents. Study sites are labeled by their black cottonwood site index class (L=low; M=medium; H=high). Linear best-fit lines are shown to demonstrate trends of the different regressions.


Foliar N (% dry weight)
3.0
2.5
2.0
1.5
0
50
100
150
200
250
Soil Mineralizable N (kg/ha)


Foliar P (% dry weight)
0.35
0.30
0.25
0.20
0.15
0
50
100
150
Soil Available P (kg/ha)


Foliar K (% dry weight)
3
2
1
0
500
1000
1500
Soil Exchangeable K (kg/ha)


Foliar S (% dry weight)
0.4
0.3
0.2
0.1
0
10
20
30
40
50
60
70
Soil Available SO4 (kg/ha)


Foliar Mg (% dry weight)
0.35
0.30
0.25
0.20
0.15
0.10
0
1000
2000
3000
4000
5000
Soil Exchangeable Mg (kg/ha)

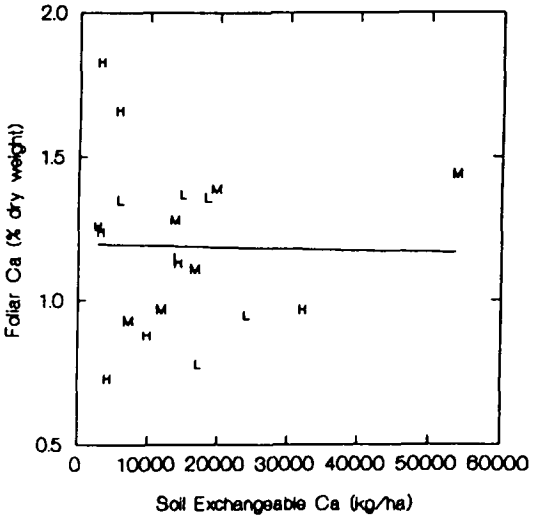
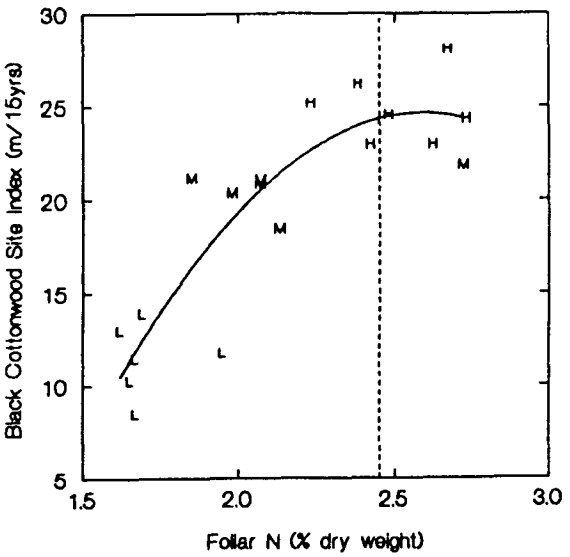
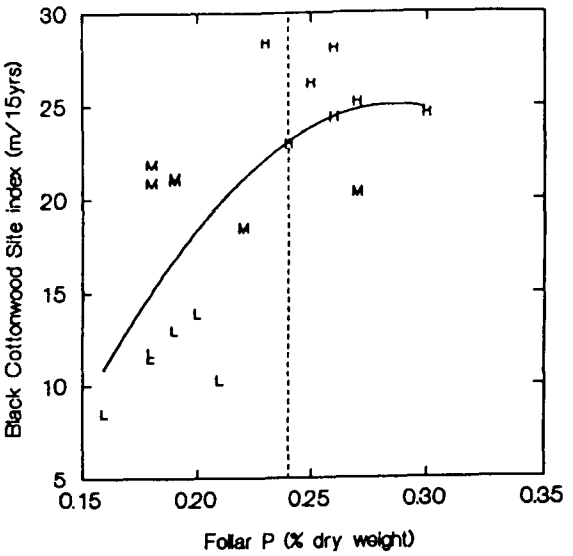
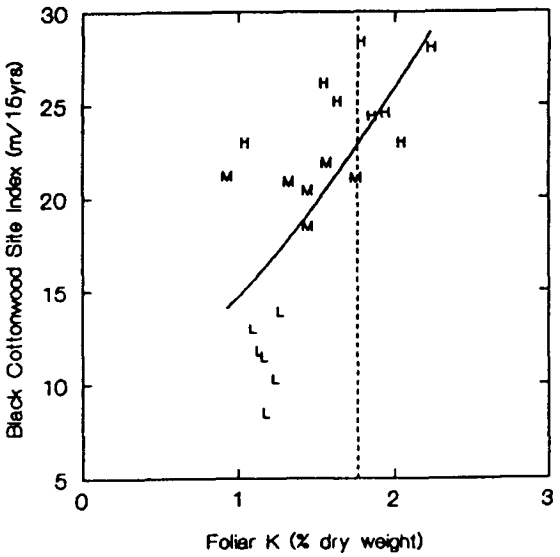
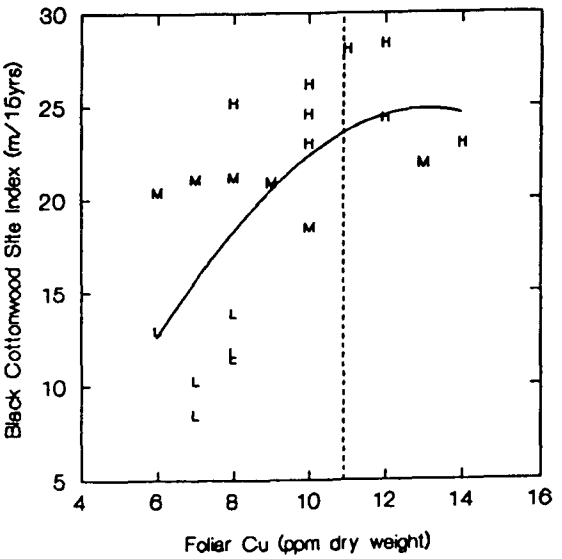

Foliar Ca (% dry weight)
2.0
1.5
1.0
0.5
0
10000
20000
30000
40000
50000
60000
Soil Exchangeable Ca (kg/ha)

Figure 5.7: (Overleaf) Scattergrams of black cottonwood site index and selected foliar nutrients. Study sites are labeled by their black cottonwood site index class (L=low; M=medium; H=high). Best fit second order polynomial lines have been drawn using a distance-weighted least squares smoothing algorithm (McLain, 1974).


Black Cottonwood Site Index (m/15yrs)
30
25
20
15
10
5
1.5
2.0
2.5
3.0
Foliar N (% dry weight)


Black Cottonwood Site Index (m/15yrs)
30
25
20
15
10
5
0.15
0.20
0.25
0.30
0.35
Foliar P (% dry weight)


Black Cottonwood Site Index (m/15yrs)
30
25
20
15
10
5
0
1
2
3
Foliar K (% dry weight)


Black Cottonwood Site Index (m/15yrs)
30
25
20
15
10
5
4
6
8
10
12
14
16
Foliar Cu (ppm dry weight)

will result in higher black cottonwood site index. Although foliar Cu concentrations followed an almost identical trend to foliar N and P, it was difficult to attach a critical level to it, since requirements for Cu are normally very low (Ballard and Carter, 1986). The increase in foliar Cu concentration may reflect higher uptake of the element, as more rapid growth occurs in cottonwoods on sites well supplied with other limiting nutrients such as P, N, and K.

Table 5.22 presents published critical foliar nutrient concentrations for black cottonwood and other *Populus* species. Mean foliar concentrations for the high black cottonwood site index class (Table 5.7) are included in the table to compare foliar levels in this study. Compared to a study of similar-aged *P. deltoides* in natural stands in Mississippi (White and Carter, 1970a), foliar concentrations in the fastest-growing trees in this study are higher for all nutrients except Ca and Mg. Foliage concentrations of N and P in young hybrid poplars grown in greenhouse culture are much higher than those for older, native trees in this study. The value of 2.5% for foliar N, as reported by Heilman (1985) is for a 6 year-old plantation of black cottonwood and was very close to the value of 2.45 % measured in this study. For all 5 nutrients considered, foliage concentrations measured for the high site index class in this study were most similar to those reported by Leech and Kim (1981) for plantations of hybrid poplars in Ontario. No critical values have been published for the other macro- and micro-nutrients measured in this study. Given the paucity of other data for black cottonwood, and the relatively good correlations with the data for other *Populus* species and hybrids that are available, the mean foliar concentrations measured in the 11 stands in the high site index class (site index > 22 m/15 years), were considered to be optimal foliage levels for the species, and were used in the calculation of DRIS ratios for comparing the nutrient status of the different site associations.

Table 5.22: Published foliar nutrient critical levels (% dry mass) for *Populus* spp. and hybrids.

Foliar Nutrient	1	2	3	4	5	6	This Study
N	2.00	2.20	3.00	2.50	3.78	2.45	2.45
P	0.17	-	0.30	-	0.57	0.24	0.24
K	1.30	1.40	1.20	-	2.64	1.40	1.76
Ca	2.30	-	-	-	1.21	0.68	1.21
Mg	0.18	0.20	-	-	0.26	0.15	0.21

1. White and Carter (1970a) for *P. deltoides*
2. van der Meiden (1960) for *Populus* spp.(cited in White and Carter, 1970a
3. Bonner and Broadfoot (1967) for *P. deltoides* in greenhouse culture
4. Heilman (1985) for *P. trichocarpa*
5. Leech and Kim (1981) for *P deltoides* clone D38 in greenhouse culture
6. Leech and Kim (1981) for *P deltoides* clone D38 in field plantation

5.3.10 Diagnosis of Nutrient Limitations in the Site Associations

DRIS (Beaufils, 1973; Leech and Kim, 1981) ratios for the 6 site associations sampled in this study are presented in Table 5.23, and utilized foliar nutrient concentrations in the high site index class (Table 5.7) as norms for comparison among the site associations. The DRIS process

Table 5.23: Comparisons of DRIS ratios in 6 site associations sampled in the study. Norms for the establishment of the ratios are based on mean foliar concentrations from stands in the high site index class (see Table 5.7).

SITE ASSOCIATION	n	N (%)	P (%)	K (%)	Ca (%)	Mg (%)	Cu (ppm)	Zn (ppm)	Fe (ppm)	Mn (ppm)	B (ppm)	S (%)
Ss-Salmonberry	7	1	3	3	-3	0	0	0	-4	3	-3	0
Ac-Red osier dogwood	5	-8	-10	-10	-1	17	-4	-2	4	12	17	-11
Ac-Willow	6	-11	-5	-5	3	10	-13	2	8	13	13	-8
Cw-Foamflower	6	-8	6	-7	6	0	-22	-1	5	34	-5	-1
'Gleyed'	4	-4	-3	-41	24	49	-21	-10	8	45	-35	-10
Cw-Swordfern	1	-2	5	-1	18	-7	-23	-8	-20	9	34	-8

assumes that not only are the concentrations of foliar nutrients optimal for natural stands, but also that the relative concentrations among species in the high site index class represent a condition of nutrient balance (Shear *et al.*, 1946; 1948).

The Ss-Salmonberry s.a. came closest to representing optimal nutrient intensity and balance for black cottonwood growth, as shown by very low DRIS indices (Table 5.23). This is to be expected because it was principally Ss-Salmonberry sites that made up the high site index class (see Table 2.1) and thus were used to calculate the norms.

Sites in the Ac-Red osier dogwood s.a. were diagnosed as deficient in the order S > P = K > N > Cu > Zn. It was concluded from the regression of foliar S on soil S, that S was not limiting, but was likely taken up in proportion to N (see Section 5.3.9). DRIS indices for Cu and Zn were very low and thus not considered critical. From this analysis, site index in Ac-Red osier dogwood sites appears to be limited principally by P and K, and to a lesser degree N.

According to the DRIS indices given in Table 5.23, Ac-Willow sites are limited in the order Cu > N > P = K. Foliar Cu concentrations were never below 6.8 ppm in any of the site associations, and Ballard and Carter (1986) suggest that, in conifers, Cu deficiencies do not occur until at least 4 ppm. Thus for Ac-Willow sites, it is assumed that N is the most limiting nutrient, followed by P and K, which are about equally deficient.

DRIS indices for the Cw-Foamflower s.a. indicate deficiency in the order Cu > N > K. Using the same reasoning for Cu deficiency level, it can be argued that N, and then K limit black cottonwood growth in this site association.

Gleyed s.a.'s demonstrated a more complex pattern of nutrient deficiency, and are diagnosed as nutrient-limited in the order K > B > Cu > Zn = S > N > P. The highly negative K DRIS index is considered to be very important in limiting black cottonwood growth on these site associations. The mean foliar concentration of 0.82% for the Gleyed s.a.'s was well below all critical levels listed in Table 5.20 for this nutrient. The mean B concentration for the gleyed group of site associations was 13 ppm, which is diagnosed as 'possibly deficient' by Ballard and

Carter (1986) based on observations of conifers. It is possible therefore that black cottonwood on sites within the gleyed group are also limited by low B levels. As discussed above for Cu, Zn concentrations are well above deficient levels proposed by Ballard and Carter (1986) for conifers, and are not considered to be limiting. Thus, black cottonwood growth on the gleyed sites is considered to be limited principally by K and possibly B, and only slightly by P and N.

The Cw-Swordfern was represented by only one study site, which was diagnosed as limited in the order Cu > Fe > S > Mg > N > K. As discussed above, Cu and S at the foliar concentrations measured are not considered to be limiting. Fe and active-Fe concentrations were 53 and 38 ppm respectively, neither of which was considered limiting in conifers by Ballard and Carter (1986). The foliar concentration of Mg was 0.16 % which was considerably lower than those of the other site associations, and was below the critical level proposed by van der Meiden (1960; cited in White and Carter, 1970a) for hybrid poplars, and by White and Carter (1970a) for *P. deltoides* (see Table 5.20). Based on this reasoning, this site is interpreted as having a moderate Mg deficiency, and a slight N and P deficiency.

5.4 DISCUSSION

5.4.1 Nutrient Availability and Site Index - General Trends

In the study, inter-relationships among black cottonwood site index, classes of the biogeoclimatic ecosystem classification, soil nutrient contents, and foliar nutrient concentrations were consistent in the PCAs, ANOVAs and linear regression analyses. In the PCA of soil contents, sites with low soil organic matter (total N, total C, and mineralizable N), high pH, high soil contents of exchangeable Ca and Mg, and low site index were correlated with one another, and were contrasted with sites with high soil organic matter, lower pH, relatively high contents of available P and exchangeable K, and overall higher site index. The PCA of foliar nutrients contrasted trees with high foliar N, P, and K on sites in the high site index class, to trees with high Ca and Mg, on sites with low site index. In both the soil and foliar PCAs, a gradient of

increasing flooding severity was associated with the low site index group of sites, both in the upland and alluvial site associations. In the ANOVAs of black cottonwood site index classes, and linear regressions of soil and foliar nutrients on black cottonwood site index, measures of soil and foliar N, P, and K were consistently associated with increasing black cottonwood site index, while pH, and foliar soil measures of Ca and Mg had negative relationships.

The high concentration of Ca, high pH, and low P contents found in this study have been reported by Peterson and Rolfe (1982, 1985, 1986) in alluvial soils subjected to periodic annual flooding. They observed a decrease in soil P concentrations and an increase in pH and Ca content following flooding in 2 years of measurements, and attributed the increase in Ca concentration and pH to soil reducing conditions. In that study, the pH increased above 6.5, after which solubility of P decreased rapidly, and a higher concentration of Ca resulted in the precipitation of P as insoluble calcium phosphates (Peterson and Rolfe, 1982). In this study it has been demonstrated that high pH and high soil Ca content were negatively correlated with soil P content, and with site index. If soils on the frequently flooded sites sampled in this study do become anaerobic, then the mechanism suggested by Peterson and Rolfe (1982) may be responsible.

Analysis of soil nutrient - foliar regressions, and black cottonwood site index class provided the opportunity to identify levels of foliar nutrients that are considered to be optimal for black cottonwood growing in unmanaged stands in coastal British Columbia. The levels are similar to critical levels published by other workers for *Populus* spp. growing in plantations or natural stands. The mean foliar concentrations were used as DRIS norms for comparing nutrient deficiencies among the different site associations. Interpretations of black cottonwood site index in the context of the ecological processes operative within the various site associations are described below.

Nutrient limitations within the different site associations sampled were compared to those found in the high site index class, since, under unmanaged conditions, these were observed to be growing the most rapidly. However, black cottonwood stands in the high site index class

may also be nutrient-limited. DRIS norms generated in Chapter 6 from the 25 fastest-growing, fertilized trees at the Squamish 23 site can be used to assess nutrient limitation in the high site index class. Trees used to develop the norms were fertilized with a balanced fertilizer which included all macro- and micro-nutrients. Using DRIS, nutrient deficiencies for trees in the high site index class were identified as B (-24) > K (-18) > P (-13) > S (-6). The role of B in limiting growth of black cottonwood growth is difficult to assess (Carter and Brockley, 1990), and the foliar concentrations of trees in the high site index class were well above that required for conifers (Ballard and Carter, 1986). Also, B deficiency should be expressed in apical areas of the trees (Carter and Brockley, 1990), and there was no indication of B deficiency symptoms in the fast-growing population of cottonwood studied. It was apparent from regressions of foliar S on soil S that sufficient soil S was available, but was not taken up by the trees. For this reason it is assumed that S is not limiting to black cottonwood in the stands studied. The regression of foliar K on soil K was the only relationship that was more or less linear, and it was suggested that increasing the uptake of K may result in growth increase for rapidly-growing black cottonwood stands. The high negative K index from the DRIS analysis supports this conclusion. Based on the DRIS analysis, and the data presented in this study, it is concluded that, in unmanaged stands, the fastest-growing black cottonwoods are limited by the uptake of K, and then P.

5.4.2 Interpretations of Black Cottonwood Growth in the Site Associations

Ac-Willow Site Association (Low Bench)

The Ac-Willow s.a. represents sites located on the lowest elevations of alluvial floodplains, and thus are the most frequently flooded. The data collected in this study indicates that these site units are flooded more or less annually for 2 to 3 weeks above the surface during the growing season. Ac-Willow sites had considerably lower soil contents of total C, total N, mineralizable N, and available P, and higher exchangeable Ca, than all ecosystems studied.

Only the gleyed sa's had lower levels of soil exchangeable K. Comparisons of foliar concentrations from black cottonwoods on these sites with those in the high site index class suggested serious limitation by the availability of N, P, and K, in that order.

It appears that growth of black cottonwood on sites representing the Ac-Willow sa. is limited by low availability of soil nutrients, and possible impedance of uptake of those nutrients that are available, due to frequent and prolonged inundation during the growing season. Frequent inundation erodes surfaces and disrupts decomposer communities and reduces mineralization of soil organic matter. Nitrogen will be leached from the soil if flooding is prolonged enough to create reducing conditions. Soil P may be less available because of flooding-related interactions with high soil pH and content of soil Ca. Low soil K may be the result of leaching, where soils have high Ca concentrations so that K is displaced from the exchange complex. All of these factors may reduce nutrient availability and uptake and severely limit black cottonwood growth on Ac-Willow sites.

Ac-Red osier dogwood Site Association (Middle Bench)

Sites classified within the Ac-Red osier dogwood s.a. occur in the middle of the flooding gradient on active alluvial floodplain surfaces, and are inundated above the surface during the growing season about once every 5 years, for a period of about 2 weeks. Soil contents on Ac-Red osier dogwood sites reflect the intermediate flooding position in that, compared to Ac-Willow sites, they have much higher levels of organic matter (total C, total N, and mineralizable N), and exchangeable K, but have comparable soil contents of exchangeable Ca and Mg. Available P is almost double that of Ac-Willow sites, but is half that of Ss-Salmonberry sites, located on the highest areas of alluvial floodplains. According to the DRIS analysis, Middle Bench ecosystems were limited mainly by P and K, and to a lesser extent N.

Black cottonwood site index on sites of the Ac-Red osier dogwood s.a. is mostly in the upper half of the medium site index class. This significant increase in productivity over Ac-

Willow sites is attributed primarily to the reduced flooding frequency and reduced physical and soil chemical effects of flooding. The reduced flooding permits more active decomposition, and thus promotes nutrient cycling and the availability of N, and other important nutrients that have been correlated with black cottonwood growth in this study. The infrequent flooding that does occur has a relatively long duration (about 2 weeks) which may impede the uptake of nutrients during the warmest part of the growing season. The flooding may also limit the development of humus layers, and, given the high soil Ca and Mg contents and relatively low available P, may also limit the availability of P and K, as discussed above for Ac-Willow sites.

Ss-Salmonberry Site Association (High Bench)

Sites located within the Ss-Salmonberry s.a. are inundated less frequently, and for a shorter duration, than all other site units on alluvial floodplains. It is estimated that these sites are flooded about as frequently as sites of the Ac-Red osier dogwood s.a, but for a much shorter duration. Whereas Ac-Red osier dogwood sites can be expected to flood for 2-3 weeks, Ss-Salmonberry sites are inundated above the surface, during the growing season, for several days at the most. Compared to the Ac-Red osier dogwood, Ss-Salmonberry sites have approximately equal amounts of total C, total N, mineralizable N, and exchangeable K, much lower contents of soil Ca and Mg, and about twice the available P. Based on the DRIS analysis, the nutrient status of this site association is optimal, and, relative to stands growing on sites representing other site associations, no nutrients are limiting growth.

The mean site index for the Ss-Salmonberry sites was 25.4 m/15 yrs, and was higher than all other site units. All study sites for this site association fell within the high site index class. The high productivity of these sites is attributed to reduced flooding effects, especially flooding duration during the growing season, which permits the development of a deep Mull humus that is a dynamic centre for cycling of nutrients within the ecosystem. Because flooding is of short duration the main effect is to recharge soil water and provide optimal conditions for nutrient uptake and black cottonwood growth. Higher availability of soil P may be related to lower

levels of soil Ca. Although soil K is higher in Ac-Red osier dogwood sites, foliar K is considerably higher in Ss-Salmonberry sites, and this may also be a result of shorter duration of flooding.

'Gleyed' Site Associations

The 4 sites considered together as the 'gleyed' group are comprised of 2 sites belonging to the Cw-Black twinberry s.a., and 2 sites classified within the Cw-Salmonberry s.a. All 4 sites were located in landscape depressions, where relatively well-drained marine sands overlay compact, gleyed marine silt and clay at various depths. The depth to the underlying compact layer is the basis for site differentiation, so that sites classified within the Cw-Salmonberry sa. had at least 35 cm above the gleyed horizon, and the Cw-Black twinberry between 15 and 35 cm (Banner *et al.*, 1990). A third site association, the Cw-Slough sedge is defined where the gleyed layer is less than 15 cm from the soil surface, and the Elk 2 site is transitional to this unit. Soil moisture in these ecosystems fluctuates seasonally, so that in the winter there may be standing water to various depths (wet and very wet SMRs), while in the summer, the most elevated site unit (Cw-Salmonberry s.a.) may achieve a fresh SMR, which implies that there is no soil moisture in excess of that required for uptake (Pojar *et al.*, 1987). Soil contents of total C, total N, mineralizable N and available P were comparable, but contents of exchangeable Ca, Mg, and K were lower than all other sites. The 'Gleyed' site associations were diagnosed as having serious B and K deficiencies, with slight deficiencies of P and N.

Black cottonwood site index in the gleyed group of site associations was in the low, or low half of the middle site index class, and ranged from 12.2 m/15 years at the Oyster site to 17.2 m/15 years at Elk 2. This poor growth is interpreted to be a function of reduced volume above compact, gleyed horizons, and to nutrient deficiencies particular to the marine soils on which the sites were located. The reduced rooting depth decreased the volume of soil available for supplying nutrients and probably impeded uptake where soils are anaerobic. The deficiencies of K can be related to very low soil K contents, and may be a result of the type of

mineral present for weathering in the marine soils in which all of the sites occur. Although no data on soil B was collected, B deficiencies have been diagnosed in coastal British Columbia on sorted sandy soils (Carter and Brockley, 1990), such as those that occur over the compact deposits in the soils sampled.

Cw-Foamflower Site Association

Sites in the Cw-Foamflower s.a. had a moist to very moist soil moisture regime, which means that available soil moisture ranges from soil water being in excess of that which can be utilized, to soils where a water table is present at greater than 30 cm depth (Pojar *et al.*, 1987). As a result soil moisture is available for nutrient uptake over the entire growing season. For black cottonwood, an important differentiation of sites with very moist SMRs is whether subsurface water is freely-flowing and oxygenated, as in the case of seepage sites, or whether water is slow-moving and anaerobic conditions develop, as evidenced by gleyed soil horizons. In this study seepage sites were sampled on alluvial fans (Tamihi Fan, Squamish 38) and where deep loess blankets overlie impermeable basal till (Ryder, Sumas). Gleyed sites were sampled in level terrain, where fine-textured glaciofluvial materials have been deposited over compact layers at depth (Chilliwack, Pierce) so that soil drainage is impeded. Soils sampled in the Cw-Foamflower sa. had the highest total N, total C, mineralizable N, and available P contents of all of the site associations sampled. Levels of exchangeable Ca, Mg, and Ca were comparable to sites of the Ss-Salmonberry s.a. As a group, sites within this site association were diagnosed as deficient in N and then K, using DRIS analysis.

Productivity of black cottonwood in the Cw-Foamflower s.a. must be broken down in to the seepage and gleyed types described above to assess the range of site index that this site unit encompasses. Black cottonwood site index on one of the two seepage sites sampled for this study was the highest of all study stands (Ryder - 30.8 m/15 years), and the other was the fourth highest (Sumas - 27.1 m/15 years). Both of these sites had Ah horizons in excess of 10 cm, silty loess soils, and permanent seepage - all features which are interpreted as providing optimal

growth conditions for black cottonwood. The Tamihi fan (25.2 m/15 years) and Squamish 38 (21.1 m/15 years) sites were located on alluvial fan landforms where seepage is present throughout the year, but soils were considerably coarser, and Ah horizons thinner. Under these conditions mineralization processes were probably somewhat reduced (although foliar N was high at both sites) and the surface area for cation exchange and nutrient retention considerably lower. Given the coarse soil textures and thin humus layers, the high productivity of alluvial fan sites is somewhat anomalous, and requires further investigation. Two of the 6 sites in the Cw-Foamflower were gleyed within 60 cm of the surface, and thus the sites experience anaerobic conditions within the rooting zone. The Pierce site (20.4 m/15 years) had a permanent water table at a depth of about a meter, with gleyed horizons beginning at a depth of 65 cm. The Chilliwack site (13.6 m/15 years) had a compact silty soil with pronounced mottles and gleying that start at 10 cm and increases with depth. The negative influence of soil gleying on black cottonwood site index is suggested by this comparison, and by the low site index of the gleyed group of site associations described above.

Cw-Swordfern Site Association

Only 1 study site was sampled in the Cw-Swordfern sa., so few general conclusions can be drawn about the productivity of black cottonwood within the unit. On the site sampled, black cottonwood had a site index of 16.3 m/15 years, and was located on relatively coarse glaciofluvial materials, with a Moder humus form. The site was diagnosed as having a moderate Mg deficiency, and slight N and P deficiencies. The medium productivity of the species is attributed to a relatively short moisture deficit, relatively slower mineralization rate, and soil mineralogy that is somewhat deficient in content of soil Mg.

5.5 CONCLUSIONS

1) Site index differed insignificantly among the 3 subzones sampled, and it was concluded that the limited climatic range of study sites was insufficient to significantly affect growth of black cottonwood. Membership in site association and soil nutrient regime classes explained 87% and 36% of the variation in black cottonwood site index, respectively. This showed that black cottonwood site index was highly predictable, if the site association was known, and much less predictable, based on soil nutrient regime alone. Much of the poor predictive capability of soil nutrient regime can be attributed to the fact that the three soil nutrient regime classes incorporated a range of soil moisture regime classes and flooding regimes. Soil nutrient regime explained 88% of the variance in site index when stratified within site association, which can be used as a surrogate for soil moisture regime class. Also, it was demonstrated in the study that soil nutrient regime was principally a gradient of increasing N availability, and that the availability of other important nutrients, such as P and K, did not increase along this same gradient in the stands studied. P and K were diagnosed as limiting nutrients on some sites, especially in the high site index class, and this may also help explain the poorer predictive power of soil nutrient regime.

2) In general, about 50% of the variation in site index was accounted for by the understory vegetation growing in the sample stands. Many understory species have ecological amplitudes that covered a range of soil moisture and/or soil nutrient regime classes, and it was observed that black cottonwood site index changed significantly along these ecological gradients. For example, salmonberry indicates a very moist to wet soil moisture regime range, which meant that it was abundant on sites belonging to both the Ss-Salmonberry s.a., where site index was high, and to the 'Gleyed' s.a.'s, where site index was much lower. Also, sample stands represented juvenile stages of forest succession following different types of disturbance, and the

presence of many 'weedy' species that reflected disturbance rather than ecological conditions reduced the predictive capacity of the vegetation models.

3) All methods of analysis revealed consistent relationships between measures of site nutrient status and site index. Sample stands with high pH, high levels of exchangeable Ca and Mg, and low levels of soil N, P, and K, had foliar concentrations of N, P, and K diagnosed as limiting to black cottonwood growth, and had the lowest site index. High site index was recorded in stands with more or less opposite soil and foliar properties.

4) Site index was seen to decrease in site units with increasing flooding frequency and duration on alluvial floodplains. The decrease was attributed to the negative impact of flooding on the rate of organic matter mineralization, on nutrient uptake, and on the negative effect of high levels of soil Ca and high soil pH on the availability of soil P. On upland sites, soil gleying and prolonged rooting zone flooding during the growing season were correlated with low site index.

5) Optimal foliar levels for 13 foliar nutrients based on mean foliar concentrations from the high site index class were used as a 'field standard' (Leech and Kim, 1981) for DRIS interpretations of black cottonwood nutrient status. Using DRIS norms from the fastest-growing, fertilized trees in Chapter 6, it was concluded that black cottonwood stands in the high site index class are limited by K, and then P.

CHAPTER 6

GROWTH RESPONSE OF THREE BLACK COTTONWOOD STANDS TO FERTILIZATION BASED ON DRIS DIAGNOSIS

6.1 INTRODUCTION

The impressive response of many *Populus* species and hybrids to nutrient additions has been demonstrated in North America (Aird 1962; Bowersox and Ward, 1976 a,b; Cannell and Smith, 1980; Crist and Dawson, 1975; Dawson *et al.*, 1976; Ek and Dawson, 1976; Isebrands *et al.*, 1983; Palmer, 1991; Switzer *et al.* 1976) and Europe (Anderson and Zsuffa, 1975; Cannell, 1980; FAO, 1958; Kolster and van der Meiden, 1979). Much of this fertilization work has been carried out on hybrid poplars under intensive silvicultural regimes that optimized growth conditions so that the full growth potential of the trees could be realized (Cannell and Smith, 1980). In Washington, the productivity of black cottonwood and its hybrids in short-rotation intensive culture has been examined both alone (Heilman *et al.* 1972; Heilman and Peabody, 1981; Heilman and Stettler, 1985b; Stettler *et al.*, 1988), and in association with *Alnus rubra* (DeBell and Radwan, 1979; Harrington and DeBell, 1984; Heilman and Stettler, 1983; Heilman and Stettler, 1985a; Radwan and DeBell, 1988). Overall, it has been shown that young stands and plantations of *Populus* species and hybrids respond to fertilization with increased growth, even in temperate climates, if nutrient balance is maintained (Leech and Kim, 1979, 1981; Schutz and deVilliers, 1986) and site conditions are optimal.

Little fertilization work has been carried out in unmanaged *Populus* stands, although fertilization of unmanaged stands of other hardwood species has been carried out (Auchmoody and Filip, 1973; Czapowskyj and Safford, 1979; Ellis and von Althen, 1973; Safford and Filip, 1974; van Cleve, 1973; von Althen, 1973). In addition to examining how much growth response can be expected, the addition of nutrients also provides an opportunity to test hypotheses of nutrient limitation (Chapin *et al.*, 1986; Timmer and Ray, 1988; White and Carter, 1970a), to

establish optimal or critical foliar nutrient levels for a species (Leech and Kim, 1981), and to test the effectiveness of several techniques of foliar diagnosis.

The objective of the diagnosis of stand nutrient status is to determine what nutrients are limiting growth, and has been based primarily on an analysis of nutrient concentrations in foliage (Ballard and Carter, 1986; Lavender, 1970; Morrison, 1974), although other plant tissues, such as xylem (Barnes, 1962, 1963) or phloem (White *et al.*, 1972; Will, 1965), have also been used. It has been generally accepted that, of all of the alternatives (soil analysis, bioassays, analysis of different plant tissues) foliar diagnosis, combined with a knowledge of soil nutrient levels and site factors, provides the most practical approach for evaluating the nutrient status of forest trees (Ballard and Carter, 1986; Leaf, 1973; Morrison 1974; Weetman and Wells, 1990). Foliage samples are collected according to an established protocol for the species, analyzed for concentrations of plant nutrients and compared to established critical levels for the species to determine the relative sufficiency of the various nutrients. The critical level for a given nutrient is the foliar concentration above which little growth response is obtained if the supply of the nutrient is increased (Ballard and Carter, 1986; van den Driessche, 1974). The critical level is often associated with a second order polynomial curve in which growth response is linear until the critical value is reached, levels off as the requirement for that nutrient is satisfied, and then declines, because of a 'toxic' effect (Everard, 1973; Leyton, 1958; Richards and Bevege, 1972).

Simple interpretations of critical foliar nutrient levels are complicated by observations that foliar nutrient concentrations can be effected by climate, season, aspect, altitude, genetic variation, competition, stress, plant part sampled, age of tissue, moisture content, position on the plant, and time of day, as reviewed by Schutz and de Villiers (1986). Although many of these factors can be controlled by standardizing sampling procedures and local interpretations (Ballard and Carter, 1986), additional problems, such as dilution effects and nutrient balance considerations, limit the general usefulness of the critical levels approach. The critical levels

approach has been most successful when one nutrient has severely limited the growth of forest stands (Ballard and Carter, 1986; Morrison, 1974a,b).

Given the problems associated with utilizing critical levels of individual nutrients, foliar diagnosis methodologies that compare ratios of nutrients are commonly used (Ballard and Carter, 1986; Schutz and de Villiers, 1986; van den Driessche, 1972; Weetman and Wells, 1990). The use of nutrient ratios recognizes that nutrients required for the metabolism of plant tissue must be available in the correct proportions (Ingestad, 1962; Leech and Kim, 1981; Shear *et al*, 1946, 1948), and thus acknowledges the importance of nutrient balance. Ballard and Carter (1986) present interpretations of important nutrient ratios for conifers of western North America. Ingestad (1962) has used fertilization methods to develop optimal ratios between foliar nitrogen and other nutrients, and has shown that these ratios are very consistent among conifer species for macronutrient concentrations (reviewed by van den Driessche, 1974; and Weetman and Wells, 1990).

A diagnostic procedure that uses the ratios of all nutrients simultaneously is the Diagnosis and Recommendation Integrated System (DRIS), originally used by Beaufils (1973), and later by many others (Beverly *et al.*, 1984, 1986; Leech and Kim, 1979a,b, 1981; Letzsch and Sumner, 1983; Sumner 1977a, 1977b, 1978, 1979). Using the DRIS method, a series of equations, based on ratios of all pairs of nutrients measured in the analysis, are used to compute indices that compare the nutrient balance within the stand being assessed to DRIS 'norms' - nutrient concentration levels from rapidly-growing populations of the species being tested. For agricultural crops, DRIS norms have been based on very large data sets from a wide geographic sample (Sumner, 1977b). The DRIS indices indicate both the most limiting nutrient, and the order in which other nutrients measured are either limiting or sufficient. DRIS methodology has been successfully applied to hybrid poplar plantations by Leech and Kim (1981), based on norms developed from greenhouse experiments for the hybrids used. As pointed out by Weetman and Wells (1990), the major drawback in using DRIS for applied forestry is the lack of

appropriate norms on which to base the diagnosis, and uncertainty concerning the appropriateness of applying norms derived from greenhouse tests on seedlings to forest stands.

The success of the diagnosis of stand nutrient status can be ascertained by adding the nutrients thought to be limiting and measuring the response of treated trees or stands to controls. Direct measurements of absolute growth response (height, diameter, basal area, or volume) of forest trees to fertilizer treatments can lead to incorrect conclusions about the effectiveness of the treatment if pretreatment size or rate of growth of test trees is not accounted for in the assessments of growth response (Auchmoody, 1985; Ballard and Majid, 1985; Gagnon, 1975; Lipas, 1979; Miller and Tarrant, 1983; Salonius *et al.*, 1982; Whyte and Mead, 1976; Woolons and Whyte, 1988). Salonius *et al.* (1982), and Ballard and Majid (1985) developed arithmetic indices to account for the pre-treatment growth rate of treated trees. Woolons and Whyte (1988) have analyzed this approach and concluded that, in the case of Salonius *et al.* (1982), valuable information was lost and improper conclusions drawn from the relatively low sensitivity of the approach, compared to covariance analysis using pre-treatment rate of growth as a covariate. The approach taken in this study is to assess the correlations of a variety of pre-treatment size and growth rate variables on response variables, and, where the relationships are significant, to use the most significant measure as a covariate to adjust all response estimates (Woolons and Whyte, 1988).

An assessment of differences in foliar nutrient levels between treated and control trees is often used to help interpret observed responses to fertilizer additions. A frequent anomaly encountered is that foliar concentrations of applied nutrients are often seen to decrease in trees showing a growth response, and this has been attributed to a 'dilution' effect, where increased foliar mass decreases the concentration, but not the absolute amount of the nutrient added (Ballard and Carter, 1986; Leaf, 1973; Morrison, 1974; van den Driessche, 1974; Weetman an Wells, 1990). Heinsdorf (1968) developed a 3-axis graphical procedure, where response of foliar mass, and foliar nutrient concentration and content are used to interpret conditions of luxury consumption, toxicity, and other effects. The method is based on correlations between

foliage response and bolewood production, and has been applied with success in conifer fertilization (Carter and Brockley, 1990; Timmer and Morrow, 1984; Timmer and Ray, 1988; Timmer and Stone, 1978). Timmer (1985) has applied the graphical procedure to young hybrid poplar in Ontario, based on observed correlations between foliar response and wood production as reported by Larson and Isebrands (1972). The application of the graphical method to *Populus* spp. is problematic, because leaf growth is indeterminate, and thus may respond to increases in nutrient status by producing more, rather than larger leaves. For this reason, Timmer (1985) used measures of total leaf mass of 1 year old saplings as the foliar mass response variable. It is not known whether there is a close relationship between wood production and foliage response to fertilizer treatment in juvenile black cottonwoods. The possibility of utilizing the graphical procedure to assess changes in foliar and tree response in juvenile stands of black cottonwood will be assessed in this study.

The specific objectives of the study were:

1) to use the DRIS method (Beaufils, 1973; Leech and Kim, 1981; Schutz and de Villiers, 1986) to diagnose potential nutrient deficiencies in rapidly-growing and poorly-growing natural stands of black cottonwood;

2) to apply fertilizers based on these diagnoses, and measure response in height and basal area increment over a 3 year period;

3) to measure foliar concentrations annually, and re-apply fertilizers based on changes in nutrient ratios as assessed by the DRIS method;

4) to assess and compare the magnitude of growth response;

5) to test the assumptions of the graphical procedure (Timmer, 1985) by assessing relationships between wood production and measures of foliar response; and,

6) utilizing the most rapidly-growing trees, to establish optimal foliar values for black cottonwood that can act as a 'field standard' (Leech and Kim, 1981), and can be used as

preliminary DRIS norms for evaluating nutrient status of black cottonwood stands in coastal British Columbia.

6.2 METHODS

6.2.1 Site Selection and Description

Three young (8 to 19 years) black cottonwood stands, that were neither over- nor understocked (Table 6.1), were selected for fertilization. The three stands included two sites with high site index (Soowahlie, Squamish 23) and one with a low site index (Strawberry 1). Soil characteristics and other relevant information is summarized in Tables 2.1-2.3, and in Tables 6.1-6.3. All sites were on alluvial floodplains, and had Regosols with relatively coarser textures occurring with increasing depth. Soil texture was either sandy loam over loamy sand, or silt loam over sandy loam. Humus form was Mull at all three sites, and the Ah horizon was deeper, and had more granular structure at the Squamish and Soowahlie sites, compared to the Strawberry site (Table 2.2). Soil chemical sampling was carried out as described in Chapter 4 (Table 6.3).

Foliage samples were collected in the last two weeks of August in 1985, 1986, 1987, and 1988 from the upper canopy of experimental trees following sampling protocol outlined in Chapter 3. In 1985, 1986, and 1988, individual, 30 g foliage samples were collected from all experimental trees. In 1987 a composited foliar sample was collected for each treatment group. Foliage concentrations of N, P, K, Ca, Mg, S, SO_4-S, Cu, Zn, Fe, active Fe, Mn and B were determined using the procedures described in Chapter 3.

Table 6.1: Method of establishment, stand age in 1986, stocking, mean DBH, mean height, and site index of 3 fertilized stands. Stand age and site index were calculated using height-age curves from destructive sampling in 1988. Stocking was based on prism data from each experimental block on each site. Mean DBH and height were based on pre-treatment measurements of all experimental trees.

Site	Stand Establishment	1986 Stand Age (years)	Stocking (stems/ha)	Mean DBH (cm)	Mean Height (m)	Site Index (m/15 yrs)
Strawberry	natural - sprouts	19	650	11.7	12.1	11.8
Soowahlie	planted - rooted whips	8	545	14.0	13.5	23.0
Squamish 23	natural - sprouts	14	750	21.8	22.2	24.4

Table 6.2: Selected site and soil properties.

Site	Watershed	Landform	Site association	Soil subgroup	Soil texture
Strawberry	Fraser River	alluvial - low bench	Ac-Willow	Orthic Regosol	SL/LS
Soowahlie	Chilliwack River	alluvial - high bench	Ss-Salmonberry	Humic Regosol	SL/LS
Squamish 23	Squamish River	alluvial - high bench	Ss-Salmonberry	Humic Regosol	SiL/SL

Table 6.3: Soil pH and soil nutrient contents (using a 1 m sampling depth)

Site	Soil pH	Min-N (kg/ha)	$S\text{-}SO_4$ (kg/ha)	Avail-P (kg/ha)	Ex-Ca (kg/ha)	Ex-Mg (kg/ha)	Ex-K (kg/ha)
Strawberry	6.9	118	61	16	14,112	3,575	635
Soowahlie	6.0	136	48	62	14,148	1,455	905
Squamish 23	5.6	205	53	90	4,308	432	888

6.2.2 Fertilizer Experiments

Fertilizer treatments applied in March of 1986 were determined from site-specific DRIS analyses of foliar samples collected in 1985 (Table 6.4). In the absence of data for *Populus trichocarpa*, DRIS norms used to develop the DRIS indices in Table 6.5 were based on those

Table 6.4: Mean foliar nutrient concentrations (% of dry mass) based on 15 samples taken in August 1985 from the upper third of the canopy at three experimental sites.

Site	N	P	K	Mg	Ca
Strawberry	1.95	0.18	1.14	0.33	1.15
Soowahlie	2.42	0.24	2.04	0.23	0.88
Squamish 23	2.38	0.21	1.76	0.25	0.84

Table 6.5: DRIS indices use to develop 1986 fertilizer prescriptions at the Soowahlie, Strawberry Island and Squamish fertilization experiments.

Site	N	P	K	Mg	Ca
Strawberry	-16.1	-55.8	-37.1	26.4	81.6
Soowahlie	-6.2	-47.8	13.7	4.5	35.8
Squamish 23	0.3	-57.2	-0.2	4.8	53.0

presented by Leech and Kim (1981) for N, P, K, Ca, and Mg in *Populus* clone D-38. The norms proposed by Leech and Kim (1981) were very similar to those published for *Populus deltoides* grown under controlled conditions (Bonner and Broadfoot, 1967), and supported their application to other *Populus* species. DRIS diagnoses suggested that phosphorus was the most limiting nutrient in all three stands, and that nitrogen and potassium were the next most limiting, depending on the site. The Strawberry site differed from the other two in that N, P, and K were all determined to be about equally deficient. 1986 fertilizer prescriptions were developed so that N, P, and K were added in the same ratios as their DRIS indices. Fertilizers applied for the 3 year duration of the experiment are shown in Table 6.6.

Table 6.6: Summary of fertilizer treatments at the Soowahlie, Strawberry 1, and Squamish 23 sites.

Site	Treatment	1986 Treatment	1987 Treatment
Soowahlie	control	no treatment	no treatment
	1	177 kg/ha P	no treatment
	2	22 kg/ha N	200 kg/ha N
	3	177 kg/ha P + 22 kg/ha N	200 kg/ha N
	4	brushing	brushing
	5	brushing + 177 kg/ha P	no treatment
	6	brushing + 22 kg/ha N	200 kg/ha N
	7	brushing + 177 kg/ha P + 22 kg/ha N	200 kg/ha N
Strawberry 1	control	no treatment	no treatment
	1	150 kg/ha NPK* (22N+77P+52K kg/ha)	no treatment
	2	150 kg/ha NPK (22N+77P+52K kg/ha)	200 kg/ha N
	3	150 kg/ha NPK (22N+77P+52K kg/ha)	400 kg/ha N
	4	300 kg/ha NPK (44N+154P+104K kg/ha)	no treatment
	5	300 kg/ha NPK (44N+154P+104K kg/ha)	200 kg/ha N
	6	300 kg/ha NPK (44N+154P+104K kg/ha)	400 kg/ha N
	7	450 kg/ha NPK (67N+231P+156K kg/ha)	no treatment
	8	450 kg/ha NPK (67N+231P+156K kg/ha)	200 kg/ha N
	9	450 kg/ha NPK (67N+231P+156K kg/ha)	400 kg/ha N
	10	600 kg/ha NPK (89N+308P+207K kg/ha)	no treatment
	11	600 kg/ha NPK (89N+308P+207K kg/ha)	200 kg/ha N
	12	600 kg/ha NPK (89N+308P+207K kg/ha)	400 kg/ha N
Squamish 23	control	no treatment	no treatment
	1	75 kg/ha P	750 kg/ha 'complete fertilizer'[1]
	2	150 kg/ha P	750 kg/ha 'complete fertilizer'[1] + 200 kg/ha N
	3	225 kg/ha P	750 kg/ha 'complete fertilizer'[1] + 400 kg/ha N
	4	300 kg/ha P	750 kg/ha 'complete fertilizer'[1] + 600 kg/ha N

[1] 'complete fertilizer' composition - 0% N, 19.6% P (triple superphosphate), 10.5% K (KCl, K-MgSO4), 0.60% Fe, 0.20% Zn, 0.26% Mn, 0.10% Cu, 0.10% B, 0.006% Mo.

Stands selected for fertilization were divided into equal area sections, and a random process was used to select dominant or codominant experimental trees within the blocks. At Strawberry and Squamish 23 there were 15 blocks and 5 trees within each. At the Soowahlie site there were 10 blocks with 8 trees in each. Fertilizer treatments were surface-applied evenly in March of 1986 and 1987 over 5 m radius circular plots surrounding each experimental tree.

The fertilizer trial at the Soowahlie site employed a randomized complete block design with a 2x2x2 factorial arrangement of 8 treatments randomly applied within 10 blocks. This

design was used to examine interactions and main effects of phosphorus and nitrogen fertilization, and to test the effects of removing competing vegetation on black cottonwood growth and response to fertilizers. These plots were brushed with a mechanical brush saw monthly, during the growing season, for the three years of the experiment. Based on analysis of 1986 foliar data, an additional 200 kg/ha of N was added in March 1987 to those trees that received N in 1986 (Table 6.6). The block effect was not significant during any year of analysis.

At the Strawberry 1 site a randomized complete block design was employed in 1986, where five treatments were applied randomly within 15 equal-area blocks. Fertilizer treatments were equi-distant and quantitative so the method of orthogonal polynomials could be utilized to analyze growth response (Hicks, 1982). All 1986 responses were tested using this model, and the block effect was not significant. The Strawberry site was flooded in May of 1986, after the fertilizer was applied, and, because there was no uptake of N at that site, it was decided to test the effect of flooding on fertilization with N by applying fertilizer before and after the flood in 1987. However, no flooding occurred in 1987, so only some of the blocks had N applied, and this changed the design of the experiment. Application of 0, 200, and 400 kg/ha of nitrogen across blocks (excluding controls) changed the experimental design from a one-way ANOVA with orthogonal polynomials, to one where 12 treatment groups of 5 trees each were compared with 5 randomly selected control trees using orthogonal contrasts (Table 6.6).

At the Squamish 23 site, a randomized complete block design was used, with 5 treatments applied randomly over 15 blocks. In 1986, increasing amounts of P were applied in 75 kg/ha increments from 75 to 300 kg/ha. In 1987 a 'complete fertilizer' was applied (see footnote to Table 6.6 for composition) in combination with increasing amounts of nitrogen to determine whether or not greater growth performance could be achieved by supplying all necessary macro- and micronutrients. As at the other sites, t The block effect was not significant during any year of analysis.he block effect was not significant during any year of analysis.

Covariance analysis was used to estimate the effects of variance in initial tree size on the amount of response measured (Lipas, 1979; Miller and Tarrant, 1983; Woollons and Whyte, 1988). At each site, regressions of measures of pretreatment rate of growth (basal area increment) or size (basal area, height) on response variables (1986, 1987, and 1988 basal area increment, 3 year height increment) showed that the 1983-1985 basal area increment was the most highly correlated with basal area treatment response for the 1987 and 1988 measurements. The basal area of the trees (1985 basal area) at the beginning of the experiment was the most significant covariate for 1986 basal area increment. Generally, neither height nor basal area covariates was significantly correlated with height response, so in most cases height increment responses were not corrected for pre-treatment size. For all models, covariates were tested for homogeneity of slopes to ensure that the influence of the covariate was consistent across treatment groups. Covariates were then introduced into the ANOVA model for the variables assessed, and adjusted means and variations for each of the treatment cells were calculated.

The approach taken to assess linear model violations followed the procedure outlined in Chatterjee and Price (1977). For all models estimated, the assumption of homogeneity of variance was tested by examining plots of studentized residuals and estimated values. Where patterns of increasing variance were observed, transformations were used to re-estimate the models. This was only necessary in a few cases and the results of the ANOVAs were not significant for those models. Normality of residuals was assessed by probability plotting of the measured values against those expected from a normal population, and noting any deviations from a linear relationship. Deviations from that expected from a normal distribution were not seen for any of the models estimated. Outliers were deleted from the model if they were more than 2.5 studentized residuals from the mean.

6.2.3 Growth Response Measurements

The DBH and total height of all experimental trees was determined in March 1986, before the application of fertilizers (Table 6.1). DBH and height were remeasured each year to

assess year-to-year growth response and, with foliar analysis to prescribe additional fertilizer additions if it was considered necessary.

In October of 1988 all experimental trees were destructively sampled to measure basal areal growth at breast height and 7 m, to provide access to the 1988 terminal leaders of experimental trees, and for another study. All measurements at 7 m were highly correlated with breast height measures, so only the results for breast height measures are reported. 1988 leader length, fresh mass and diameter, number of leader leaves, and total fresh mass of leader leaves were measured for all experimental trees felled. Foliage from a sample of at least 30 leaders at each site was dried to constant mass and used to develop wet weight-dry weight regressions for each of the sites. Using the foliar nutrient concentration data, the regression equations were used to estimate the total content of foliar nutrients in the 1988 leaders of all sample trees.

Three-year height increments were determined for all trees by subtracting 1988 tree heights (determined from felled trees) from pretreatment heights (estimated in March 1986 using a clinometer and tape). Disks were removed from sampled trees at 1.2 and 7 m, kiln-dried, and sanded in preparation for measuring ring width. To account for variation in ring width, measurements of ring increment were made along a radius that was the mean of the longest and shortest radii. Basal area at breast height was calculated for the six years prior to the end of the experiment in 1988, and thus including the three years of the experiment (1986, 1987, 1988) and the three year period before the experiment (1983, 1984, 1985). The increment of basal area for each year was then calculated by subtraction from the previous year and the calculated 'annual basal area increment' was used as a growth response variable.

6.3 RESULTS

6.3.1 Growth Responses and Foliar Nutrient Concentrations

6.3.1.1 First Year Growth Response

Measurements of 1986 basal area increment showed either little change or a significant reduction for fertilized trees compared to controls at the three fertilized sites (Tables 6.7, 6.8, and 6.9). The basal area increment data shown in Tables 6.7 to 6.9 are from the destructive sampling that was carried out in 1988, after disks were removed and measured. Based on DBH measurements made on trees after the 1986 growing season, a mean diameter growth increment was calculated for all treatment groups, and these measurements were used to estimate growth response to 1986 treatments, and to prescribe new treatments for 1987. 1986 mean diameter growth increments were highly correlated with 1986 basal area increments shown in Tables 6.7 to 6.9.

Table 6.7: 1986 basal area increment and important foliar concentrations at the Soowahlie site.

Treatment	1986 BAI (cm2)	P (%)	S-SO_4 (ppm)	B (ppm)	S (%)	N (%)
No P	39.89	.224	446	32.6	.240	2.45
177 kg/ha P	39.08	.259	588	36.5	.256	2.47
Probability	.596	.002	.010	.057	.059	.767

At the Soowahlie site the effects of 22 kg/ha N or monthly brushing were not significant for any of the foliar nutrient concentrations or for 1986 basal area increment. For this reason only the effect of adding 177 kg/ha P is shown in Table 6.7. Although basal area increment did not change, the foliar concentrations of P and SO_4 were significantly higher in the P-fertilized

plots. Concentrations of S (p=.059) and B (p=.057) were also higher in the P-fertilized plots, while foliar N concentrations did not change. Since P was apparently taken up by the fertilized trees, and this uptake did not affect growth response, it appeared that either P was not limiting, trees did not have time to respond to the treatment, or that the P added was not completely available to the trees due to very slow movement of P in the soil. Based on the lack of observable growth response to P, only N was added in 1987 at the Soowahlie site. Given the native level of 136 kg/ha of mineralizable N in the soil, the addition of 22 kg/ha in the treatment was probably not enough to affect uptake, so an extra 200 kg/ha was added to all plots that received N in 1986.

Table 6.8: 1986 basal area increment (BAI) and important changes in foliar concentrations at the Strawberry Island site.

Treatment	1986 BAI (cm2)	N (%)	P (%)	K (%)	Mg (%)	Zn (ppm)
Control	15.84 a	2.13 a	.202 a	1.245 a	.304 a	96.1 a
NPK150	12.79 a	2.07 a	.212 a	1.331 a	.288 a,b	85.1 a,b
NPK300	13.99 a	2.13 a	.220 a	1.324 a	.303 a	83.8 a,b
NPK450	12.68 a	2.21 a	.217 a	1.358 a	.282 a,b	80.9 a,b
NPK600	16.64 a	2.19 a	.221 a	1.423 a	.267 b	77.6 b
Probability	.090	.182	.090	.081	.016	.036

Although not significant (p=0.05), 1986 basal area increments were lower than control trees for all treatment groups except NPK600 at the Strawberry site (Table 6.8). Foliar P (p=.090) and K (p=.081) concentrations increased as fertilizer levels increased, while foliar N concentrations showed a slight increase in the two highest treatments. Concentrations of foliar Mg and Zn decreased significantly as levels of fertilization increased. Since increases in P and K concentrations were not correlated with basal increment response, it was decided to add

different levels of N before and after flooding (as discussed in Section 6.2.1) across blocks in 1987.

Table 6.9: 1986 basal area increment (BAI) and important foliar concentration changes at the Squamish 23 fertilizer site.

Treatment	1986 BAI (cm2)	SO_4 (ppm)	Cu (ppm)	S (%)	P (%)	N (%)
Control	47.04 a	290 a	9.5 a	.205 a	.182 a	2.46 a
P 75	40.62 a,b	505 b	11.4 b	.231 b	.199 a	2.56 a
P 150	32.50 b	360 a,b	9.9 a	.217 a,b	.194 a	2.44 a
P 225	35.6 a,b	406 a,b	9.4 a	.213 a,b	.200 a	2.38 a
P 300	36.20 a,b	498 b	9.4 a	.224 b	.201 a	2.41 a
Probability	.026	.001	.001	.005	.075	.339

Compared to controls, 1986 basal area increment was lower in all fertilized plots, and significantly lower in the P150 treatment, at the Squamish 23 site (Table 6.9). Foliar SO_4 and S concentrations increased significantly with increasing amount of P fertilization. Cu foliar concentrations were significantly higher for the P75 treatment. Foliar P increased slightly, while foliar N did not show any change. Thus, in response to very high additions of P fertilizer, there is some evidence for P uptake, but there is a negative response in black cottonwood basal area increment. The results suggested that either P was not limiting growth, or that the uptake produced a negative growth response. Increasing concentrations of foliar SO_4 suggested that P fertilization may have aggravated N supply (Turner *et al.*, 1977), although foliar N concentrations do not support this interpretation (Table 6.9). To determine the effect of providing all trees with a balanced supply of all the macro- and micronutrients, a 'complete fertilizer' (see Table 6.4 for composition) was applied in conjunction with increasing amounts of N in 1987.

6.3.1.2 Three Year Growth Response

Over three years, all sites showed a similar growth response trend - compared to controls, treatment group basal area response was low or negative in 1986, even or slightly positive in 1987, and significantly positive in 1988 (Figures 6.1, 6.2, and 6.3). Height growth response of treated trees over three years was generally non-significant. Treatment group means shown in Figures 6.1, 6.2, and 6.3 have been adjusted through covariate analysis where applicable.

At the Soowahlie site, both 1988 basal area increment and 1988 height growth were significantly higher than controls for the P and N treatments (Table 6.10a). Table 6.10 compares the direct effects of the three treatments, based on orthogonal contrasts. Comparisons where interaction terms were significant are noted. 1987 basal area increments were significantly higher for the N treatment only, although trees receiving P fertilizer had a larger basal area increment than those that did not. No significant change occurred in three year height response for all treatments or in any variable with the brushing treatment. Foliar concentrations of P, N, S, Ca, and Zn (not shown), and foliar contents of P, were also significantly increased in the P-treated trees. Only the foliar concentration of N increased for the N treatment, and Cu concentration was significantly reduced. For the brushing treatment, all foliar concentrations were lower in brushed plots compared to unbrushed plots, the difference being significant for P, N, S, and SO_4. All significant interactions involved N or P fertilization with a brushing treatment - in all cases foliar concentrations and growth response measures in fertilized plots were lower in combination with brushing treatments.

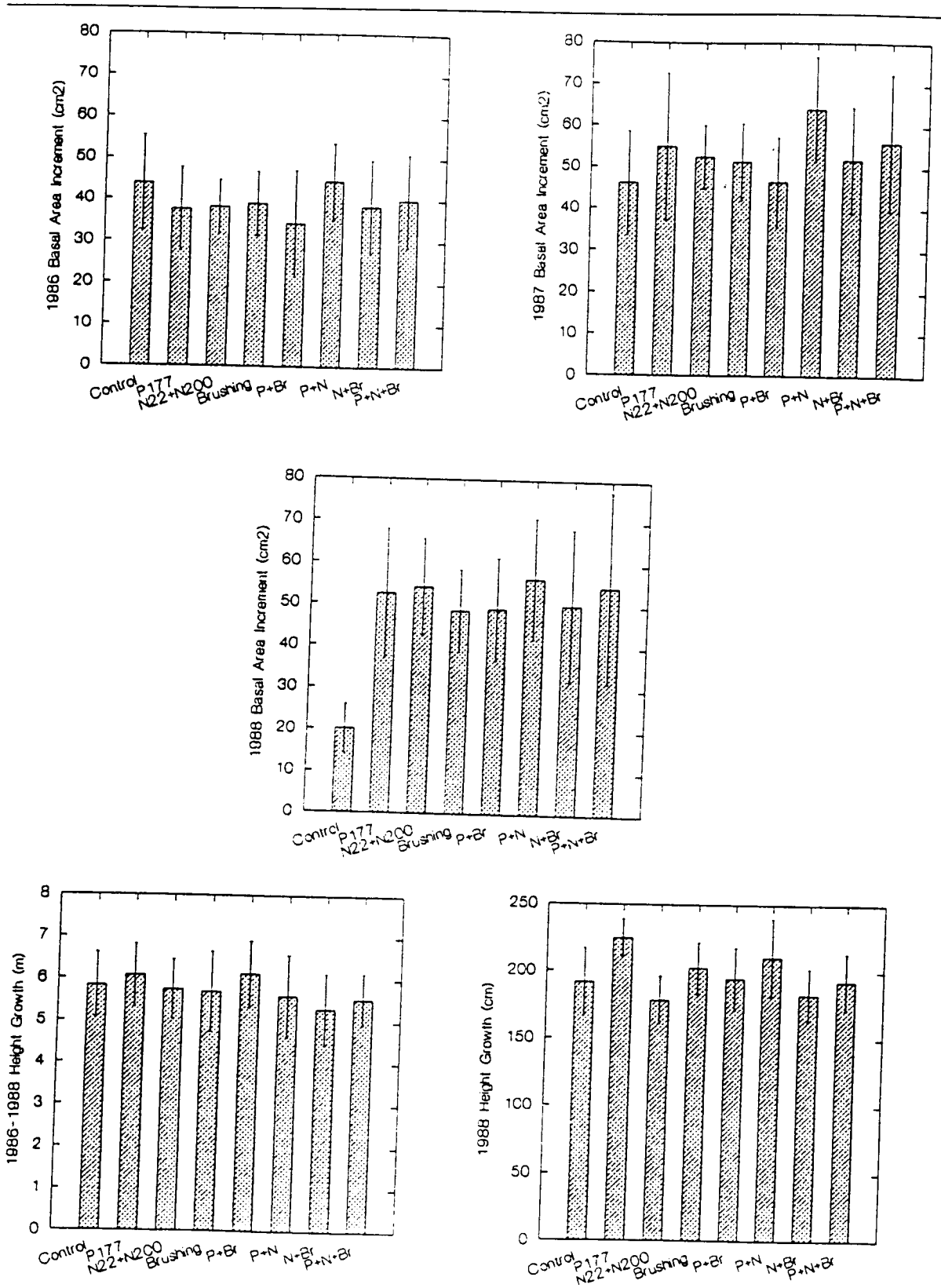


Figure 6.1: 1986-1988 basal area increments, and 1986-1988 and 1988 height growth by treatment at the Soowahlie site. Lines represent 95% confidence limits around group means.

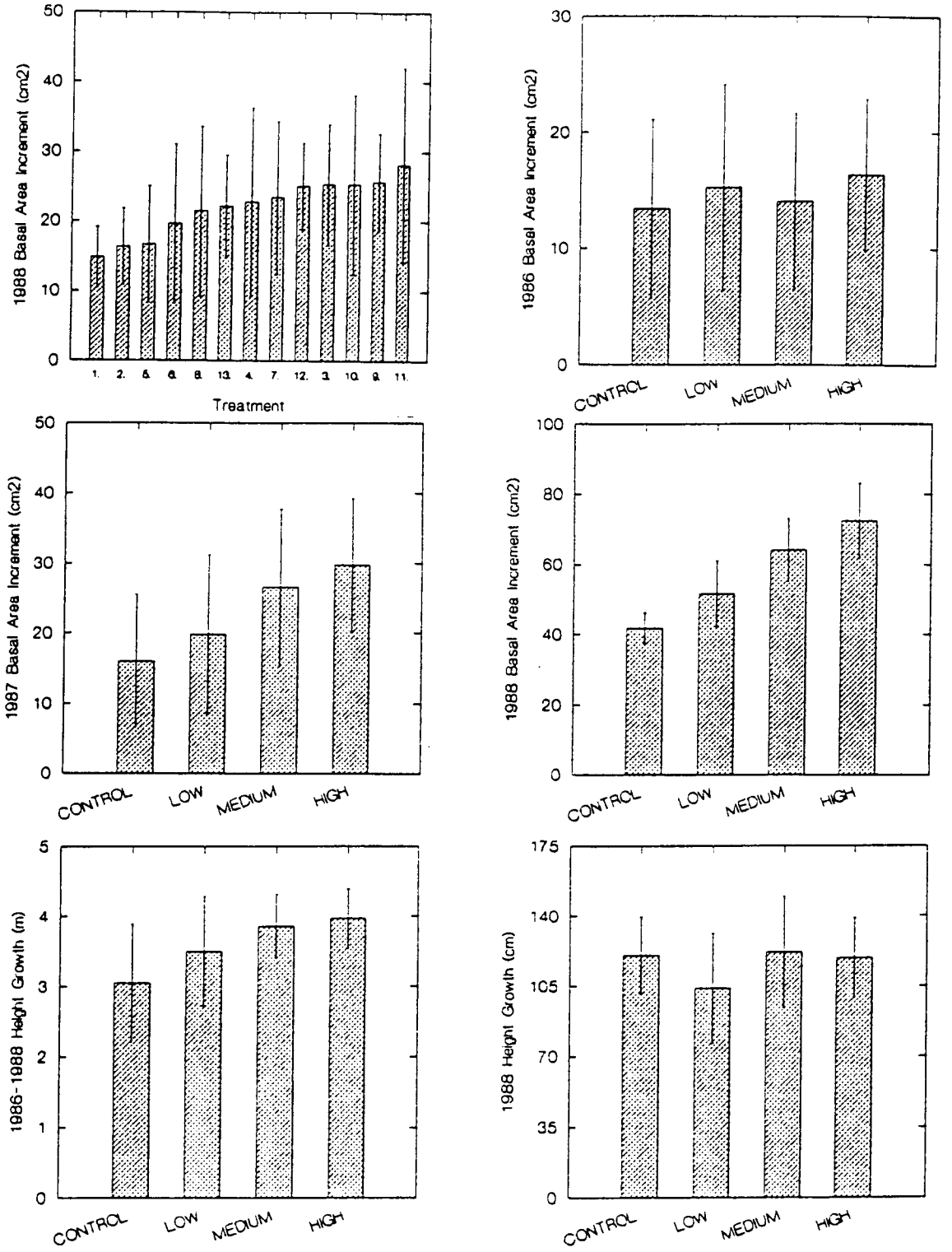


Figure 6.2: 1986-1988 basal area increments, and 1986-1988 and 1988 height growth by treatment at the Strawberry site. Treatment groups are based on 1988 basal area response (Low = Treatments 2,5,6,8; Medium = Treatments 13,4,7,12; High = Treatments 3,10,9,11).

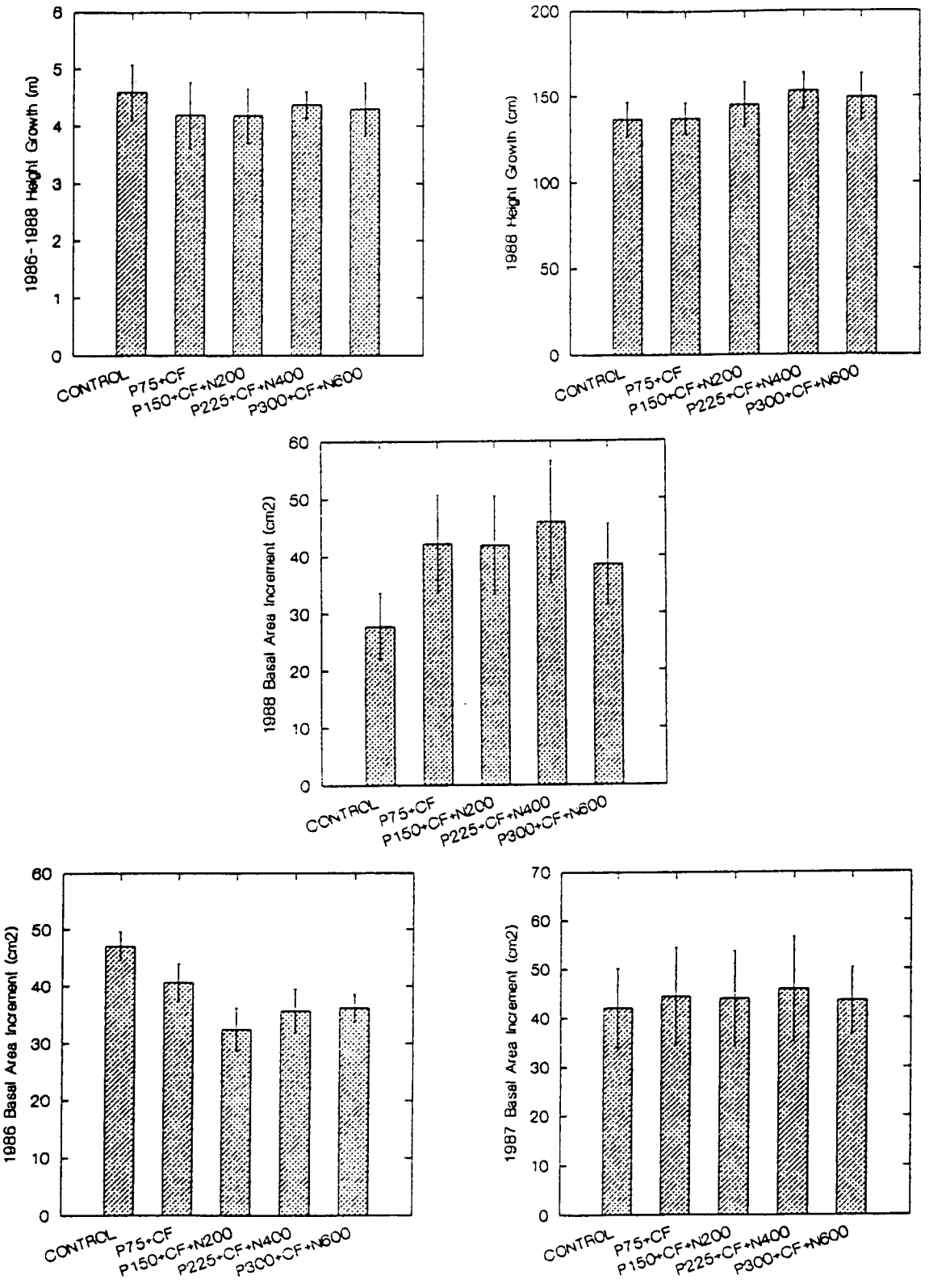


Figure 6.3: 1986-1988 basal area increments, and 1986-1988 and 1988 height growth by treatment at the Squamish 23 site.

Although the ANOVA was not significant, a gradient of increasing 1988 basal area growth response to NPK fertilization was observed at the Strawberry Site (Figure 6.2). Based on these results the 12 treatments were divided into 4 groups - a control group, and 3 response groups - low (treatments 2,5,6,8), medium treatments (4,7,12,13) and high (treatments 3,9,10,11), depending on their position along the gradient displayed in Figure 6.2. Three of the four treatments in the low productivity group were only fertilized in 1986, and generally had lower levels of nitrogen fertilizer additions (see Table 6.4 for treatments). The medium and high productivity groups included the NPK600 group from the 1986 treatment, and trees that had received varying degrees of additional nitrogen fertilization in 1987. Orthogonal contrasts were used to compare the significance of differences in growth response and foliar nutrients between productivity groups and controls (Table 6.10b). The medium and high productivity groups had significantly higher basal area increments in 1987 and 1988 and showed larger 3 year height growth than controls. Significant increases in foliar N and SO_4 concentrations occurred in the medium group, foliar K was higher in the high productivity group, and foliar Zn concentration and foliar SO_4 contents were higher in both the medium and high productivity groups. Foliar P concentration increased with productivity groups but differences from controls were not significant.

Compared to control trees, all treatments showed a significant increase in 1989 basal area at the Squamish 23 site (Table 6.10c, Figure 6.3). Response in 1988 basal area increment increased up to treatment 4 (P 225 + complete fertilizer + 400 kg/ha N) after which response declined for treatment 5 (P 300 + complete fertilizer + 600 kg/ha N). There were no significant differences over controls for 1987 basal area increment, or for 1986-1988 height increments. Although not significant, 1988 height growth showed a similar pattern to 1988 basal area increment response. Increases in 1988 basal area increment were not correlated with significant increase in N or P foliar concentrations, although concentrations of both of these nutrients increased with increasing levels of

Table 6.10 a: Summary of changes in 1987 and 1988 basal area increment, 1988 and 1986-1988 height growth increment, 1988 foliar concentrations, and in foliar contents of the 1988 terminal leader at the Soowahlie site.

Treatment[1]	1988 Basal Area Increment (cm^2)	1987 Basal Area Increment (cm^2)	1988 Height Growth (cm)	1986-1988 Height Growth (cm)	Foliar Concentrations P (%)	N (%)	S (%)	Ca (ppm)	SO_4 (ppm)	Cu (ppm)	Foliar Contents P (mg)
No P	43.26	50.53	1.32	5.64	0.33	2.42	0.271	0.690	788	12.1	0.23
P 177 kg/ha	53.17**	55.39	1.46*	5.83	0.39***	2.59**	0.301**	0.767*	855i	11.2	0.29**
No N	42.57	49.71	1.28	5.93	0.36	2.44	0.285	0.744	834	12.5	0.26
N 222 kg/ha	53.86**	56.20*	1.50*	5.55	0.36	2.58*	0.286	0.712	810	10.7*	0.26
No brushing	45.83	54.46	1.38	5.82	0.38	2.58	0.305	0.733	917	12.0	0.26
Brushed monthly	50.60	51.44	1.39	5.66	0.34*	2.44*	0.267***	0.723	727**	11.4	0.26
Interactions	N*Br P*Br N*P*Br					P*Br			P*Br		

[1] significance is denoted as *, **, and *** to indicate significance between 2 treatments at $p < 0.05$, $p < 0.01$, and $p < 0.001$, respectively

Table 6.10 b: Summary of changes in 1987 and 1988 basal area increment, 1988 and 1986-1988 height growth increment, 1988 foliar concentrations, and in foliar contents of the 1988 terminal leader at the Strawberry site.

Treatment[1]	1988 Basal Area Increment (cm2)	1987 Basal Area Increment (cm2)	1988 Height Growth (cm)	1986-1988 Height Growth (cm)	Foliar Concentrations P (%)	N (%)	K (%)	Zn (ppm)	SO_4 (ppm)	Foliar Contents SO_4 (mg)
Control	14.82	16.02	1.20	3.05	0.194	1.53	1.58	68	512	25.98
Low Productivity	18.51	19.81	1.04	3.50	0.210	1.61	1.72	66	419	17.28
Medium Productivity	23.34**	26.56*	1.22	3.86**	0.212	1.82**	1.65	48**	327*	15.45*
HighProductivity	26.11***	29.71**	1.19	3.97**	0.215	1.68	1.80**	51*	364	15.28*

[1] significance is denoted as *, **, and *** to indicate significance between treatment and control at $p < 0.05$, $p < 0.01$, and $p < .001$, respectively

Table 6.10 c: Summary of changes in 1987 and 1988 basal area increment, 1988 and 1986-1988 height growth increment, 1988 foliar concentrations, and in foliar contents of the 1988 terminal leader at the Squamish site.

Treatment[1]	1988 Basal Area Increment (cm2)[3]	1987 Basal Area Increment (cm2)	1988 Height Growth (cm)	1986-1988 Height Growth (cm)	Foliar Concentrations P (%)	N (%)	Mn (ppm)	B (ppm)	Foliar Contents K (mg)	Mn (mg)	B (mg)	SO_4 (mg)
Control	27.86a	45.27a	1.37a	4.19a	0.284a	2.39a	18.1a	18.9a	1122a	0.885a	0.944a	28.80a
P75+TF	42.14b	44.42a	1.37a	4.19a	0.308a	2.48a	23.1a	36.8b	958a	0.924a	1.381ab	27.34a
P150+TF+N200	41.87b	43.87a	1.45a	4.18a	0.315a	2.49a	27.1b	43.7b	1090ab	1.117a	1.983ab	36.40a
P225+TF+N400	45.83b	45.93a	1.53a	4.37a	0.294a	2.45a	24.0ab	44.3b	1417b	1.221ab	2.135c	37.57ab
P300+TF+N600	40.77b	43.57a	1.50a	4.29a	0.322a	2.50a	35.6c	42.2b	1372b	1.634b	2.189c	44.32b
Significance[2]	***	0.98	0.12	0.66	0.65	0.84	***	***	**	***	***	*

[1] codes for the treatments are as in Table 6.6

[2] significance is denoted as *, **, and *** to indicate significance at $p < 0.05$, $p < 0.01$, and $p < 0.001$ respectively

[3] figures followed by the same letter are not significantly different at p=0.05 using Tukey's test

fertilization. Significant increases occurred in foliar B and Mn concentrations and contents and for foliar K and SO_4 contents (Table 6.10c).

6.3.2 Changes in DRIS Ratios

DRIS indexes in Table 6.11 are based on the same Leech and Kim (1981) greenhouse standards used to make the original nutrient diagnoses, and were used to demonstrate the response of foliar nutrients to fertilizer additions for the most responsive treatments at each site. Changes in basal area increment in Table 6.11 are expressed relative to the control basal area increment. Addition of 225 kg/ha of P at the Squamish 23 site in 1986 did not change the P index, and had only a slight effect on N and K indexes. In 1987, a complete fertilizer (that included more P and K) and 400 kg/ha of N was added, and this had an immediate effect on the N index, with little change in the others. There was little response in basal area to these changes in 1986 and 1987. Although no fertilizer was added in 1988, DRIS indexes for all 3 nutrients show large changes with N becoming negative, P changing from -105 to -43 and K changing from -13 to +72. Basal area increment in this treatment was 1.5 times that of the control in 1988.

Addition of 600 kg/ha NPK in 1986 at the Strawberry site increased DRIS indexes for all 3 nutrients, although basal area increment was slightly lower than controls (Table 6.12). In response to the addition of 400 kg/ha N in 1987, the N index changed from -35 to +8, while indexes for P and K decreased, and basal area showed a 2-fold increase over controls. In 1988, with no fertilizer additions, the N index decreased, DRIS indexes for P and K increased, and basal area increment was about double that for controls.

Addition of P and N fertilizer at the Soowahlie site in 1986 raised both the N and P indexes, but decreased the K index, while basal area increment was about the same

Table 6.11: Changes in N, P, and K DRIS ratios, and basal area increment relative to the control, for the most growth-responsive treatment groups at the Squamish, Soowahlie and Strawberry sites.

Site	Year	N	P	K	BAI	Treatment
Squamish 23	1985	-10	-103	4	na	pre-treatment
	1986	-2	-103	-5	0.75	225 kg/ha P
	1987	26	-105	-13	1.01	'CF' + 400 kg/ha N
	1988	-12	-43	72	1.51	no treatment
Strawberry	1985	-67	-142	-106	na	pre-treatment
	1986	-35	-88	-38	0.95	600 kg/ha NPK
	1987	8	-124	-88	2.17	400 kg/ha N
	1988	-60	-70	31	2.05	no treatment
Soowahlie	1985	-13	-79	25	na	pre-treatment
	1986	-9	-52	-5	1.01	177 kg/ha P+22 kg/ha N
	1987	38	-83	-51	1.39	400 kg/ha N
	1988	-10	-10	9	2.81	no treatment

as controls (Table 6.11). Addition of 400 kg/ha N in 1987 increased the N index, decreased the P and K index, and may have caused a slight increase in basal area increment over controls. With no further additions of fertilizer in 1988, the N index decreased, K and P indexes increased, and basal area increment was almost 3 times that of the control group.

A consistent trend that is evident at all 3 sites is the immediate response of N indexes to the addition of N fertilizer, and the relatively slow or small response of P indexes to additions of similar levels of P fertilizer. The change from a positive N index in 1987 following addition of 400 kg/ha of N fertilizer, to a negative N index at all 3 sites in 1988 when no fertilizers were added, suggests that the effect of the N fertilization, as expressed by the N index, was short-lived. Over the 3 year period of the experiment, P indexes demonstrated an overall increase and suggest a gradual decrease in P deficiency. This trend paralleled the trend in basal area response. The lower P index in 1988 may have been partially brought about by the increase in P concentration for all trees in 1988 (see Section 3.3.4). However, P concentrations in treated trees were significantly higher than in controls, which suggests higher uptake of applied P in treated trees.

The low solubility and slow movement of P fertilizer in the soil system may explain the relatively slow foliar response to P additions at the 3 sites. Figure 6.4 compares changes in the mean concentrations of Mehlich-available P with depth in 15 control plots, and 15 plots that received 300 kg/ha P in 1986, and additional P in the 'complete fertilizer' applied in 1987. Samples were collected in September, 1988. The steep P concentration gradient that occurred over a short soil depth increment, 2.5 years after the P was applied, illustrates the very slow movement and strong fixation of P in the soil at the Squamish site.

6.3.3 Growth Response of the 1988 Terminal Leaders

Measurements of the mean number of leaves, mean leaf fresh mass, and mean total leaf fresh mass in the 1988 leaders of experimental trees demonstrated few significant changes between controls and treatments, and did not follow patterns in basal

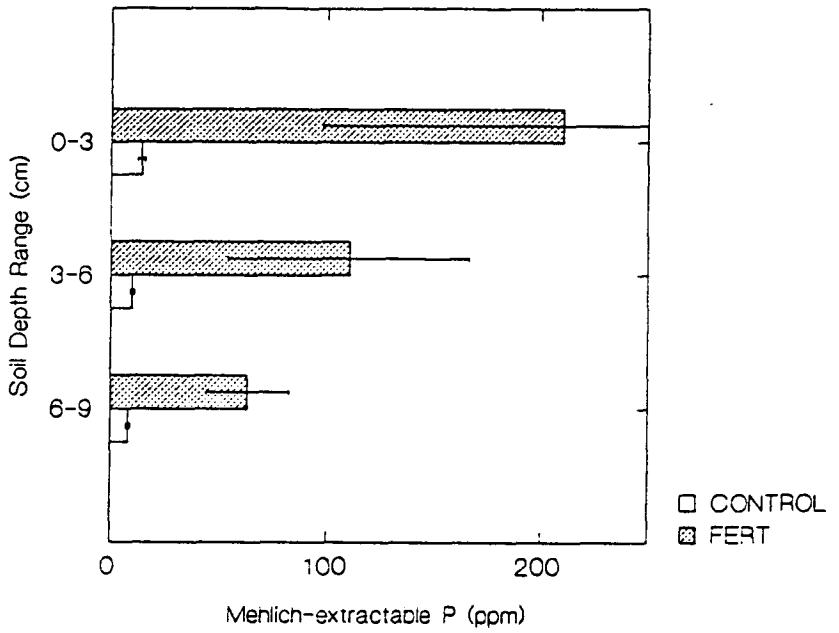


Figure 6.4: Comparison of mean P concentrations (n=15) in the upper 10 cm of the soil profile in fertilized and unfertilized plots at the Squamish 23 site. Lines indicate 95% confidence intervals for P means.

area increment for the same treatment groups (Figure 6.5). At the Squamish site the mean number of leaves was relatively constant, while mean and total leaf fresh mass decreased below controls at low levels of fertilization, and then increased to those of control trees at higher fertilization levels. The Soowahlie and Strawberry sites had a similar pattern, with mean leaf number slightly decreased, mean leaf fresh mass varied among treatments, and total leaf fresh mass decreased compared to controls (Figure 6.5).

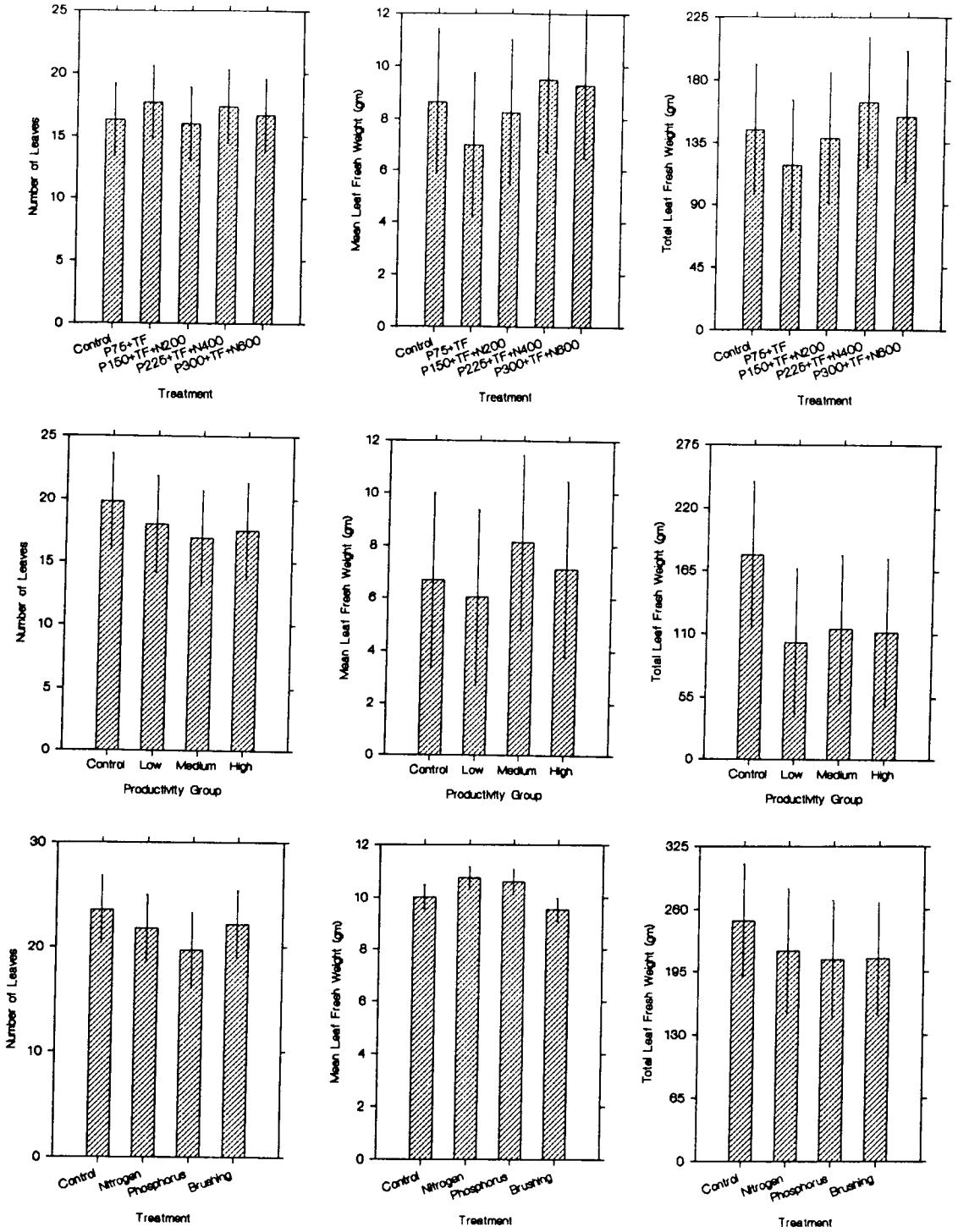


Figure 6.5: Comparisons of mean number of leaves, mean leaf fresh mass, and mean total leaf fresh mass of the 1988 terminal leaders at the Squamish 23 (top), Strawberry (middle), and Soowahlie (bottom) sites.

6.3.4 Determination of Optimal Foliar Levels

1988 basal area response at the Squamish site (Figure 6.3, Table 6.10c), increased from 27 cm^2 to a high of 45 cm^2 in the P225+CF+N400 treatment, after which basal area response decreased at the higher rate of nutrient addition. This response pattern could be interpreted as representing a 'deficiency to sufficiency' response curve (Everard, 1973; Leyton, 1958), where growth response increased until nutrient limitations were overcome. Such a response might be expected if all of the nutrient requirements of the trees were being met. It should be noted for this data that treatment responses were not significantly different from each other and suggested that addition of 75 kg/ha P and the complete fertilizer resulted in a similar level of response as much higher levels of P and N additions. Table 6.12 lists means and variance statistics for 1988 foliar concentrations of macro- and micronutrients of the 25 most rapidly-growing trees under the complete fertilizer treatments at the Squamish site. If it is assumed that, by 1988, fertilized black cottonwoods at the Squamish site were supplied with a complete and balanced nutrient supply, then their foliar nutrient concentration ratios can be utilized to develop foliar norms for DRIS analysis.

6.4 DISCUSSION

Although pronounced responses in basal area and height growth were observed at all 3 sites, the relationships between these responses, the fertilizers added, changes in foliar nutrient concentrations, and the responses of foliar mass and nutrient contents of the 1988 terminal leader, were less clear. Analysis of year to year foliar response and changes in nutrient balance using DRIS norms showed that N concentrations responded directly to additions of N fertilizer, K response was also fairly rapid, but that P response was either minimal or very slow. The slow response of the trees to additions of surface-applied P was probably a function of the slow

movement and P-fixing potential of the soils. This has been discussed and reviewed by many workers (Ballard 1980; Bengston, 1968; Brendemuenl, 1968; Cole *et al.*, 1974; Russell, 1974). Analysis of soil P concentrations over very small depth increments in treatment plots that received large amounts of surface-applied P as super triple phosphate almost 3 years earlier showed that the added P was only very slowly incorporated into subsoils.

Table 6.12: Means, standard deviations, and coefficients of variation (CV) for foliar nutrient concentrations in 25 black cottonwood trees with the highest 1988 basal area increment at the Squamish 23 site.

	MACRONUTRIENTS					
	N (%)	P (%)	K (%)	Ca (%)	Mg (%)	S (%)
Mean	2.50	0.33	2.70	0.56	0.23	0.32
Standard deviation	0.30	0.08	0.55	0.16	0.05	0.05
CV	0.12	0.24	0.20	0.29	0.22	0.16

	MICRONUTRIENTS						
	Cu (ppm)	Zn (ppm)	Fe (ppm)	Mn (ppm)	B (ppm)	SO_4 (ppm)	active Fe (ppm)
Mean	17	85	79	26	44	850	67
Standard deviation	2	22	14	9	11	257	11
CV	0.12	0.26	0.18	0.35	0.25	0.30	0.16

The factorial arrangement of treatments in the experiment at the Soowahlie site permitted an evaluation of the effect of adding P fertilizer alone on growth response and foliar concentration. Both the P and N treatments resulted in a significant increase in 1988 basal area response and height growth and in foliar concentration of the nutrient applied. However, the increase in P concentration with application of P fertilizer was paralleled by significant increases

in the foliar concentrations of N, S, Ca, and in P content. By comparison, the addition of N resulted in a significant increase in N only. These results can be interpreted as indicating a P deficiency that has been alleviated, because, when the concentration of foliar P was increased, the foliar concentrations of other available nutrients were also increased to maintain a state of nutrient balance.

The consistently lower growth and foliar nutrient response to the brushing treatment at the Soowahlie site was unexpected, and largely unexplained by the information collected. It was expected that, by removing competition from understory vegetation, surface applied fertilizers would be more available for uptake by the test trees, and this would result in an increased growth response that would provide some estimate of the importance of competition on uptake of applied nutrients. One explanation may be that repeated traffic at the base of sample trees compacted the upper soil horizons and altered soil structure enough to reduce nutrient uptake.

Larson and Isebrands (1972) showed good correlations between total shoot leaf mass and wood production in young hybrid poplars, and Timmer (1985) used the graphical method to interpret the effects of pH on nutrient availability in a hybrid poplar nursery. The results of the present study indicate that the responses of the foliage mass of the terminal leader were poorly correlated with wood production, as expressed in basal area increment or height growth. These findings suggest that the response of juvenile trees to nutrient additions is much more complex than in first or second year hybrid poplar saplings, and that the utilization of the graphical procedure to interpret growth response to fertilization is of limited value for black cottonwood trees of this age.

Ballard (1978) showed that an application of 224 kg/ha P to the first rotation of *P. radiata* was still measureable 20 years later in the second rotation. Ballard (1980) cited a number of studies carried out on P-deficient conifer plantations where responses to P fertilization lasted for 15-20 years. Ballard (1980) attributed the long response to P fertilization to the fact that nutrients were generally applied in excess of requirements, and to the ability of trees to recycle nutrients. Given the significant increases in basal area increment in response to

as low as 75 kg/ha of P with a complete fertilizer, and the potential for the effect to be long-lived, the operational fertilization of juvenile black cottonwood stand may be economically justified.

6.5 CONCLUSIONS

1. In three juvenile black cottonwood stands, the application of fertilizer based on diagnosis of foliar nutrient concentration using DRIS norms established for greenhouse-grown hybrid poplars, resulted in little growth response in the first year, and considerable growth response in the third year following fertilization.

2. Compared to controls in the highest 3 year treatment response group, basal area increment increased by 65%, and height growth increment by 15% at the Squamish 23 site; basal area increment increased by 65% and height growth increment by 30% at the Strawberry site; and basal area increment increased by 27% without a significant height growth response at the Soowahlie site.

3. Although it is not clear from the observations of growth and foliar response, there is some evidence to suggest that the relatively slow response to P fertilization at the Squamish 23 and Soowahlie sites was due to high rates of fixation and very slow movement of soil surface-applied P.

4. Given that relatively low dosages (ca. 100 kg/ha) of P were required to achieve a significant growth response, and acknowledging that in many forest fertilization programs response to P fertilization occurs for a considerable period of time, the results suggest that the fertilization of fast-growing, juvenile black cottonwood stands in coastal British Columbia may be economically justified.

5. Significant correlations between measures of foliar response and wood production were not seen in the study, and this finding limits the usefulness of the Heinsdorf (1968) graphical procedure for interpretation of the experimental results.

6. DRIS norms for the 25 fastest-growing black cottonwoods at the Squamish 23 site are presented, and are based on the idea that the trees used for the norms were supplied with all required macro- and micronutrients.

CHAPTER 7

SUMMARY AND DISCUSSION

Observations from this study support the previously published conclusion (Smith, 1957; DeBell, 1990, Roe, 1958) that deep, loamy soils, with high nutrient status, circum-neutral pH, and which are abundantly supplied with well-oxygenated soil moisture over the entire growing season, are optimal for black cottonwood growth. These soil requirements are very similar to those reported for eastern cottonwood (*P. deltoides*) in the southern United States (Baker and Broadfoot, 1979; Demeritt, 1990). The ANOVA comparing black cottonwood growth within site units was highly significant ($p < .001$), and explained 87% of the variance in site index within the 29 study sites. This general result suggested that, relative to the ecological requirements of black cottonwood, the site classification provided an ecologically-meaningful differentiation of the edatopic gradients sampled. For operational purposes, this result predicts that black cottonwood site index can be estimated with considerable accuracy by identifying the site unit on which a stand is located. Growth was best on the high bench of alluvial floodplains (Ss-Salmonberry s.a.), and on moist upland sites with seepage (Cw-Foamflower s.a.). Growth was poorest on the low bench of alluvial floodplains (Ac-Willow), and on gleyed, marine site units (Cw-Salmonberry, Cw-Black twinberry).

A general objective of the study was to examine the nature of nutrient limitation in unmanaged black cottonwood stands in south coastal British Columbia. Nutrient availability and uptake is interwoven very closely with the availability and characteristics of the soil moisture, and it is often very difficult to isolate either factor (Cole *et al.*, 1990). In coastal British Columbia, black cottonwood appears to be more or less restricted to those sites without seasonal drought, and all study sites except one were assessed as having no water deficit during the growing season. Differences in soil moisture regime among the site units was due mostly to

the behaviour of soil moisture, i.e., to the nature of flooding, or degree of aeration or gleying in the soil. Site association explained a slightly higher percentage of the variation in black cottonwood site index when only rich sites were included (R^2=.88), and a lower percentage for only very rich sites (R^2=.74). Because soil nutrient regime was constant for these two models, the main effect was that of soil moisture regime on black cottonwood site index.

Although soil moisture regime classes were more highly correlated with black cottonwood site index, many of the mechanisms through which soil moisture regime effects black cottonwood site index are related to soil nutrient regime. For example, one of the major effects of flooding on alluvial floodplains is to decrease soil oxygen levels, and thus impede nutrient uptake by trees (Kozlowski, 1982; Greenwood, 1969; Epstein, 1972). For most tree species, inundation of soil for a few weeks or more during the growing season reduces tree growth (Kozlowski, 1982). Regehr *et al.* (1975) showed an immediate reduction in photosynthesis following rooting-zone flooding of *P. deltoides*, and, after 28 days, photosynthesis was reduced by 50%. The rate at which soil oxygen is depleted will depend on the activity of microorganisms, soil characteristics, and the nature of flooding, and in many soils micro-organisms consume much of the soil oxygen within a few hours of inundation (Ponnamperuma, 1972). Prolonged flooding and anaerobic conditions will also result in a broad range of changes in the soil chemical status of many soil nutrients, and in the activities of the decomposer community. For example, even at relatively low redox levels, nitrification is reduced (Kramer, 1979), and much of the soil nitrate can be denitrifed and leached from the soil (Scott-Russell, 1977; Kozlowski, 1982). Peterson and Rolfe (1982) showed an increase in pH and in Ca concentrations, and a decrease in P availability following seasonal inundation in a broad-leaved floodplain ecosystem in Illinois. Thus, although soil moisture regime was best correlated with black cottonwood site index in the study, it is suggested here that soil moisture regime influences black cottonwood growth primarily through its influence on the availability and uptake of soil nutrients.

Measurements of soil nutrient contents attempt to provide estimates of the amount of the nutrients in readily-available form present in the soil at the time of sampling. In spite of the considerable variability measured in this study, the overall results of this study support the applicability of the soil analytical tests used to determine the availability of soil nutrients (Waring and Bremner, 1964; Curran, 1984; Klinka *et al.*, 1980). Foliar P was especially well correlated with the availability of soil P as determined by Mehlich (1978). The estimation of soil mineralizable N using the anaerobic procedure developed by Waring and Bremner (1964) resulted in good correlations with black cottonwood growth, but it is worth noting that this method measures only the ammonium component of available N (Binkley and Hart, 1989). Black cottonwood ecosystems are characterized by Mull humus where mineralization is very rapid. In Mull humus nitrates often provide an important component of soil N availability (Bobcock and Gilbert, 1957; Aber and Melillo, 1980; Melillo and Aber, 1982; Flanagan and van Cleve, 1983). Estimates of soil nitrate may have provided a more relevant estimate of soil available N for black cottonwood in the soils studied.

The interpretation of foliar nutrient concentrations using DRIS (Beaufils, 1973) methodology provided a useful tool for evaluating and comparing stand nutrient status, using norms derived from published greenhouse standards for hybrid poplar (Leech and Kim, 1981), and from the fertilizer study. These analyses were possible in spite of the considerable temporal and spatial variability in foliar nutrient concentrations shown for black cottonwood.

Using foliar concentrations from the most rapidly-growing trees in the fertilizer experiment as norms, P and K were determined to be limiting to black cottonwood growth in the fastest-growing, unmanaged stands. One reason for this limitation in fast-growing trees may be the manner in which the nutrients are available in the soil solution, and the way they are taken up by the tree. P, for example, is present in very low concentrations in the soil solution and is in rapid equilibrium with P absorbed on soil surfaces (Russell, 1974). Whereas nitrates, sulphates and calcium ions move to the root by mass flow, the majority of K and P ions travel by diffusion along concentration gradients (Barber, 1977). It is possible that, because P and K travel to the

root primarily by diffusion, they may limit growth because they cannot move to the root rapidly enough meet the nutrient requirements of the trees during peak growth periods.

The addition of N, P, and K resulted in pronounced basal area and some height responses in the third year of the fertilizer experiment, but the growth response was not easily correlated with the nutrients added. Much of this uncertainty may be due to the complexity of internal nutrient cycling, and to the way in which black cottonwood responds to higher levels of growth-limiting nutrients. Some evidence was used to suggest that the growth response observed was a result of uptake of P, and that the relatively slow growth reaction was the result of P fixation and slow movement within the soil of surface-applied P fertilizer. The behaviour of nutrients once they entered the black cottonwood trees is a large unknown identified by this study, and a large portion of tree to tree and within tree variability in foliar nutrient concentrations has been attributed to this source. Attiwill (1986) identified physiological studies as an area where considerable research needs to be conducted to understand the growth of forest trees in response to nutrient availability, and the results of this study confirm his statement. The translocation of nutrients within cottonwood, storage and overwintering, and the physiological role of internally-fixed atmospheric N as demonstrated by van der Kamp (1979) are all examples of areas where detailed information is required to more scientifically interpret the ecological factors that determine black cottonwood productivity.

CHAPTER 8

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