

THE RELATIONSHIP BETWEEN FOLIAR AND SOIL CHEMISTRY,  
GROWTH PARAMETERS, AND VARIABLE HEIGHT GROWTH  
IN ADVANCE REGENERATION OF AMABILIS FIR

by

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## ABSTRACT

Many stands of advance amabilis fir regeneration near Courtenay, B.C. exhibit declining height growth after an initially good release response following logging of the overstory. The objectives of this thesis were to investigate the relationship of nutrition, particularly nitrogen, to this height growth pattern on one site.

Foliage from trees representing the range of height growth on the site was collected twice monthly from May to September for chemical analysis. In September, samples from the major rooting zone (H horizon) of well and poorly grown tree microsites were also collected for chemical analysis. Measurements of non-nutritional factors (age and height at release, aboveground competition, diameter growth) were taken to assess the contribution of these variables to height growth. Microsite differences in site moisture were not measured due to lack of time and equipment. However, the foliar chemistry of trees growing on well-drained (mesic) and rapidly-drained (xeric) sites was compared to estimate the effect of microsite differences.

Height growth was significantly related to foliar chemistry, particularly nitrogen in multiple regression equations. This relationship was better in most cases with summer rather than fall foliar chemistry measurements. There were significant differences in nitrogen, carbon:nitrogen ratios, magnesium and calcium between the humus of well and poorly grown tree microsites. A proposed scenario for the decline in height growth following initially good release growth was proposed.

None of the non-nutritional factors measured related significantly to height growth after release. Differences in crown size at release and microsite water availability are the most likely factors accounting for differences in the rate of height growth decline other than nutrition.

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## INTRODUCTION

In 1976, Crown Zellerbach of Canada Ltd. foresters became concerned about poor height growth in approximately 2,500 ha of young amabilis fir (Abies amabilis (Dougl.) Forbes) stands located in Tree Farm License No. 2 near Courtenay, B.C. Ten to twenty years ago these areas had been clearcut logged but not slashburned in order to preserve the existing advance regeneration of amabilis fir. Use of advance regeneration can shorten rotation time and also reduce the cost of site preparation and planting providing that release<sup>1</sup> height growth is satisfactory.

Initially, release height growth of the Courtenay amabilis fir was promising, ranging from 20 to 40 cm annually. However, this early release growth was not always sustained. By 1976, height increments of many trees were steadily declining (stagnating) (Figure 1) or erratic with one or more periods of slow growth separated by periods of satisfactory growth (Figure 2).

The unsatisfactory height growth was found to some extent on all sites regardless of slope, aspect or elevation (Wetten 1977), but there was no consistent pattern of height growth within stands on similar sites. The year of initiation, the duration, and the degree of poor growth varied from tree to tree on many sites, eliminating the possibility of annual macroclimatic fluctuations as a sole causal agent. Some trees resumed normal height growth after 2 or 3 years of poor growth; others continued to stagnate for more than 10 years.

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<sup>1</sup>Growth once overstory is removed and advance regeneration is no longer suppressed.

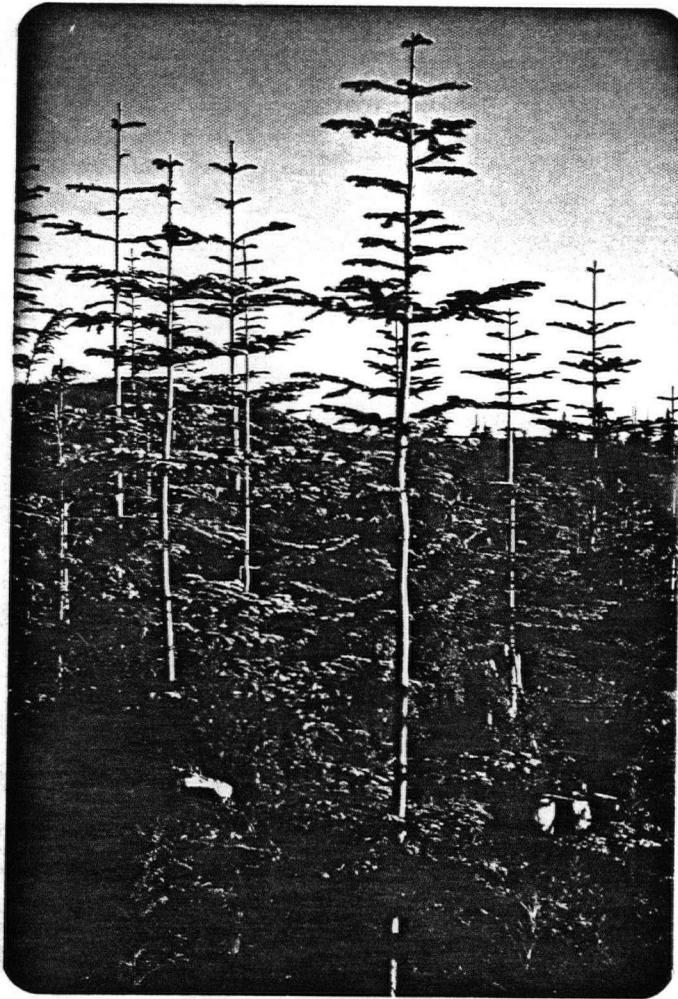


Figure 1. Steadily declining (stagnating) height growth in unmanaged stands of advance amabilis fir regeneration.



Figure 2. Erratic height growth in advance amabilis fir regeneration growing at 750 m a.s.l. Pointer is below 1974 height increment which was shorter than normal for most Courtenay amabilis fir.

Crown Zellerbach foresters are juvenile spacing many of these stands. Because they are unable to predict if height growth of currently vigorous amabilis fir will be satisfactory in the future, they tend to give preference in spacing to smaller hemlock or Douglas-fir regeneration, thereby losing up to 10 to 20 years of the volume accumulated in vigorous amabilis fir trees. The foresters are also concerned about the future height growth of natural and planted amabilis fir regeneration, should they decide to reforest high elevation sites with this species.

Since 1972, entomologists, pathologists, soil scientists, ecologists, and foresters from government agencies, universities, and private companies have examined the problem but have not been able to determine the cause of stagnating or erratic growth. There was no evidence of insect or disease damage on trees with stagnating height growth<sup>2</sup>. Many factors, including genetic make-up, root pathogens, competition, age at release, redistribution of growth from height to diameter increment in response to wind stress, microsite differences in nutrient or water availability and variations in mycorrhizal associations and an inappropriate climate for amabilis fir<sup>3</sup> have been suggested as possible explanations for the dramatic differences in height growth exhibited by adjacent trees within a stand of advance amabilis fir regeneration.

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<sup>2</sup>Pers. comm. from Dr. A. Funk, Canadian Forest Service, Victoria, B.C., November, 1977.

<sup>3</sup>See Appendix A for a brief description of Klinka's off-site hypothesis.

Following a field trip to the problem area near Courtenay, Klinka<sup>4</sup> (1977a) concluded the problem should be studied in detail. This thesis reports on part of a subsequent study. Other parts of the study examined:

- (a) the height of growth patterns in amabilis fir regeneration over a range of elevations and moisture regimes, and
- (b) the correlation between release age, release height, degree of aboveground competition, and years of needle retention and height growth over a range of sites.

This descriptive approach was felt to be necessary in order to obtain an overall view of the factors which might influence height growth over the range of sites on the Tree Farm.

Several observations in the problem area suggested that a severe nitrogen deficiency might be a major factor causing reduced height growth after promising early height growth in some advance amabilis fir regeneration:

- (a) Trees exhibiting stagnating height growth also exhibited the visual symptoms of nitrogen deficiency described for amabilis fir seedlings by Davidson (1957): stunted needles, reduced leader growth, slender twigs and chlorotic foliage. One- and 2-year-old needles of the poorly grown trees were yellow green (5GY 6/8 on the Munsell colour scale). The chlorosis was slightly accentuated at the needle tips. The foliage of well-

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<sup>4</sup>Research Pedologist, B.C. Ministry of Forests.

grown trees was 5 GY 4/3 on the Munsell colour scale.

According to Davidson, this is the typical colour of healthy *amabilis* fir foliage.

- (b) A mid elevation stand of *amabilis* fir in Tree Farm License No. 2 was thinned in 1974. A control area was not thinned in the spring of 1976, a small area in the thinned stand was experimentally fertilized by hand with urea at the rate of 224 kg nitrogen per ha. During the 1976 growing season, needle size of the fertilized trees almost doubled and the foliage colour darkened to a deep blue-green. In 1977, both height and diameter growth of the fertilized trees responded well to the fertilizer treatment.
- (c) Klinka (1977a) observed that trees with good height growth and colour were usually rooted at least partly in mineral soil or humus, whereas chlorotic, slow-growing *amabilis* fir were often rooted mainly in decaying wood. He hypothesized that micro-site differences in the nutrient supply of the rooting medium might be responsible for the variability in height growth within a site.

For my thesis research, I decided to study the relationship between nutrition and variable height growth in an advance *amabilis* fir stand located on a moderately well-drained (mesic) site.

The objectives of this thesis were:

- (a) to determine if a significant relationship existed between variable height growth on the study site and fall foliar

chemistry, particularly N or N:P ratio. N:P ratios may be a more sensitive indicator of nitrogen deficiencies than foliar N alone (Heilman and Gessel 1963).

- (b) to determine if nutrients in current, 1- or 2-year-old foliage collected during the growing season were better related to height growth than fall foliage values. This information would add to our knowledge of amabilis fir chemistry.
- (c) to determine if there were significant differences in the nutrient status of humus collected from microsites of well and poorly grown trees.
- (d) to determine if other, non-nutritional, factors contributed significantly to variable height growth within a stand.

## LITERATURE SURVEY

The literature survey is divided into three sections. The first provides a brief summary of the climatic and edaphic requirements of amabilis fir. The second outlines the factors thought to limit amabilis fir growth at low elevations. The third section is a review of the techniques for studying nutrient status and deficiencies of trees.

### 1. Site Requirements of Amabilis Fir

#### 1.1 Climatic Requirements

Amabilis fir grows best on sites with abundant soil moisture and low evaporative stress. In B.C., Krajina (1969) reported that these requirements are met if annual rainfall exceeds 2550 mm. This amount could be reduced to as little as 1900 mm if a substantial portion of the precipitation falls as snow. Packee (1976) suggested that the moisture requirements of this species are met on sites with a negligible late summer moisture deficit, rarely exceeding 75 mm if the soil moisture capacity of the site was at least 100 mm.

Cold air drainage and the depth and duration of snow packs are important factors influencing moisture conditions. Amabilis fir sites often have snowpacks lasting into May or June (Packee, 1976).

Low summer temperatures also favor amabilis fir growth (Krajina 1969). Fowells (1965) reported that amabilis fir sites are characterized by moderate temperatures with only moderate daily and seasonal variations. A mean July temperature of 16° or 17°C is considered to be the upper threshold for amabilis fir sites by Packee (1976).

## 1.2 Edaphic Requirements

B.C. ecologists differ in their opinion about the importance of soil fertility for the growth of amabilis fir. Krajina (1969) stated that an abundant supply of calcium and magnesium, and some nitrogen in the form of nitrate were necessary for best amabilis fir growth. He observed that the optimum growth of amabilis fir in the biogeoclimatic zones where it grows, occurs on sites with good to very good base status. Packee (1976) and Schmidt (1957) concluded from their observations that amabilis fir was tolerant of a wide range of soil types and that its growth was rarely affected by low nutrient availability. Since it is often found on acidic soils with negligible nitrification potential, Packee (1976) concluded that low levels of nitrate should not limit its growth.

Two Washington studies documented the effects of soil fertility on amabilis fir growth. Williams (1968) measured an average annual height increment of 11.5 cm for juvenile amabilis fir established on soils developed from an old mud flow, compared to 37.8 cm for those growing on richer basic soils derived from lava beds. Since the slope, aspect, elevation, stocking and growing season were similar on both sites, he ascribed the difference in height growth to soil fertility. Gessel and Orians (1967) observed poor growth of amabilis fir regeneration on mid elevation sites with adequate precipitation and snowcover to satisfy this species moisture requirements. They found that the poor growth resulted from low soil fertility, in particular a poor supply of

nitrogen. Growth response to nitrogen fertilization was good on these sites.

Adequate soil moisture is often considered the edaphic factor most critical to good amabilis fir growth (Packee 1976). Amabilis fir grows best on well drained soils, with abundant but not excessive moisture during the growing season (Fowells 1965; Kotar 1972; Packee 1976). Optimum growth occurs on hygric or seepage sites (Krajina 1969).

## 2. Factors Limiting Amabilis Fir at Low Elevations

The factors controlling the survival and growth of amabilis fir at low elevations are not well known, and although low moisture levels are probably a major limiting factor, there is little experimental evidence to verify that low precipitation and high evaporative demand limits its growth to higher elevations. However, in laboratory experiments, Kotar (1972) found that amabilis fir seedlings were less tolerant of low moisture levels than western hemlock seedlings. He also observed that seedling mortality during prolonged summer drought was the most important single factor limiting amabilis fir distribution at low elevation. But despite this evidence in support of the idea of an important influence of moisture, amabilis fir distribution has not been successfully correlated with total annual precipitation (Schmidt 1957; Kotar 1972; Packee 1976). Three factors may contribute to this lack of correlation:

- (a) it is difficult to quantify the relative contribution of snow, rain, fog drip, and seepage water in satisfying the moisture requirements of amabilis fir;

- (b) annual precipitation may be a less important parameter than precipitation during periods of active growth. The duration of dry-soil periods may be poorly correlated with total precipitation.
- (c) temperature and moisture interactions are difficult to evaluate. Cool temperatures, cold air drainage and deep snow-packs may compensate for low annual precipitation.

Fowells (1965), Fonda and Bliss (1971) and Packee (1976) concluded that high temperatures limited amabilis fir distribution at low elevations more than low precipitation. Amabilis fir may not be physiologically tolerant of high evapotranspiration stress associated with high temperatures (Kotar 1972). Packee (1976) suggested that sites with a mean July temperature greater than 17°C would be too warm for amabilis fir. However, because of temperature and moisture interactions, amabilis fir distribution may not correlate any better with one temperature parameter than with total annual precipitation.

Competition and fire history may also restrict amabilis fir to high elevations. Kotar (1972) felt that the absence of amabilis fir on low elevation sites with adequate moisture may be due to the slow juvenile growth of amabilis fir compared to other plant species better adapted to low elevation conditions. Schmidt (1957) suggested that warm dry summers limited amabilis fir, not for physiological reasons, but rather through the high frequency of forest fires. Because of its large seeds and slow migration potential, amabilis fir is slow to re-invade large burned areas. Packee (1976) also mentioned that the frequency of fires on the east side of Vancouver Island may have greatly reduced fir distribution.

### 3. Diagnosing Nutrient Deficiencies

Four techniques (visual symptoms, soil or foliar chemical analyses, and field fertilizer trials) have been used to diagnose nutrient deficiencies. Visual symptoms are useful as a preliminary guide in cases of severe deficiencies, but in most cases they are not specific enough to diagnose individual nutrient deficiencies (Morrison 1974a). Field fertilizer trials are the only sure way of identifying a single or multiple nutrient deficiency and quantifying tree growth response to varying levels of the deficient nutrient(s). However, field trials can be time consuming, expensive, and subject to operational difficulties (Morrison 1974a). I will discuss the remaining two techniques in more detail.

#### 3.1 Soil Analysis

Soil analysis is used to assess nutrient status mainly in nurseries, young plantations, and sites devoid of trees. Significant relationships between soil and tree growth or foliar nutrient levels have been reported (Titus and Boynton 1952; Leyton and Leaf 1957; Tamm 1964; Lowry 1970; Adams 1974; Malm et al. 1974; Isik 1978). However, these relationships usually have a large random error component because of soil sampling problems, inadequate extraction and analysis techniques, and the confounding effects of chelation, mycorrhizae, and soil moisture on nutrient availability (Leyton 1958; Morrison 1974a; Baule and Fricker 1970; Zottl 1975). The use of soil analysis is further limited by the lack of published guidelines to evaluate the adequacy of

soil nutrient levels (Zottl 1975), by the differing abilities of individual tree species to extract soil nutrients, and partly by the interaction between elements in the soil.

Despite these limitations, soil analysis in conjunction with foliar analysis and visual symptoms is a useful diagnostic procedure (Bould 1968)

### 3.2 Foliar Analysis

#### 3.2.1 Introduction

Tissue nutrient concentrations are related to the availability and uptake of plant nutrients. Foliar analysis, which has become synonymous with plant tissue analysis in forestry, is the most common method of assessing tree nutrition. Foliage is usually sampled because it contains the highest concentration of plant nutrients and is the site of photosynthesis. In a study of grand fir, for example, Loewenstein and Pitkin (1972) determined that 50% of the aboveground tree nitrogen was contained in foliage produced in the latest growing season. Foliar nutrient levels correlate well with tree growth when a single nutrient is severely deficient (Leyton and Armson 1955; Madgwick 1964a; Morrison 1974a; van den Driessche 1974).

Numerous greenhouse and laboratory studies have described the relationship between tree seedling growth, nutrient concentration and nutrient supply. These studies have been used to estimate the optimum nutrient concentrations for growth. Figure 3 illustrates the general

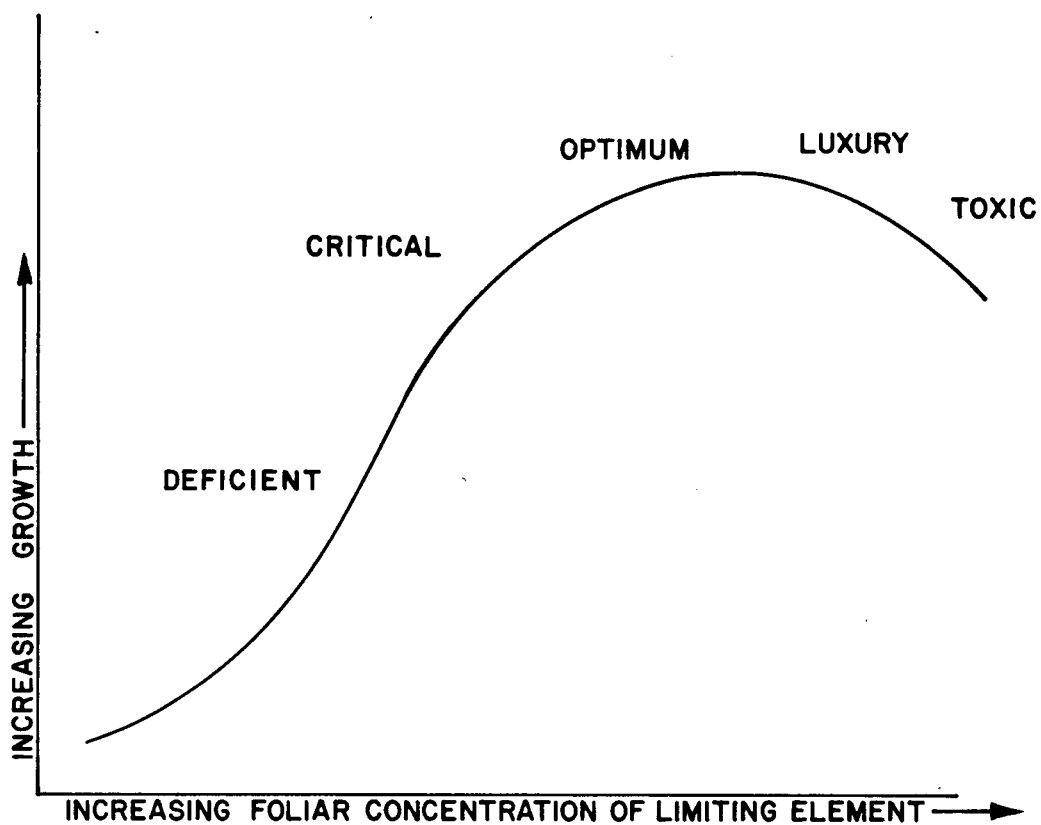


Figure 3. Generalized relationship between foliar concentrations of a limiting nutrient and tree growth (from Morrison 1974a).

growth response curve that results when nutrient concentrations are increased from sub-to-supra-optimal levels.

For a consistent and successful application of foliar analysis, knowledge of this relationship and the factors which affect it is essential. The variation caused by some factors can be minimized by carefully planned standardized sampling. Others cannot and they impose significant problems for data interpretation.

The following literature survey is a less-than-comprehensive review of foliar analysis sampling and interpretation. Goodall and Gregory (1947), Morrison (1974a), van den Driessche (1974a), Turner et al. (1978) have published good reviews of foliar analysis.

### 3.2.2 Standardized foliar sampling

Errors introduced into foliar analysis by non-standardized sampling are much greater than those introduced during chemical analysis (van den Driessche 1974). Variations in nutrient concentrations caused by differences in the time of foliage sampling, the age of the foliage or the position of the foliage in the crown must be minimized in order to reduce the sampling error component in foliar nutrition studies.

#### (i) Time variables

Seasonal changes in nutrient concentrations are a major and controversial source of variation in foliar analyses. Most macronutrients tend to have a seasonal maximum in foliar concentration and content during the late summer or early fall, followed by a gradual decline to a

spring minimum (Lowry 1968; Morrison 1974a). K concentrations, however, are usually highest in late spring or early summer (Morrison 1974a).

"Optimum sampling time is a compromise between selecting the period of maximum sensitivity to treatment or site difference, the time of year with minimum between tree variability and the need for a stable period in which to complete a sampling program" (Mead and Pritchett 1974).

Most foliar sampling is completed in late fall and early winter when nutrient levels are most stable (White 1954; Tamm 1955; Leyton 1958; Gessel 1962; Lowry 1968; Mead and Pritchett 1974). Waring and Youngberg (1972) and Smith et al. (1970) warned that this practise sacrificed "valuable biological information" and recommended foliar sampling during periods of rapid growth and high demand on nutrient reserves. Smith et al. (1970) found that foliar concentrations in nutrient-sufficient and nutrient-deficient loblolly pine (Pinus taeda L.) approached uniform levels during the dormant season, obscuring differences in nutrient status.

Spring and early summer sampling may be preferable but is much more time-consuming if stands of different elevations, aspects or geographical regions are to be compared. Since nutrient concentrations fluctuate with the phenological stage of the tree, spring sampling must be standardized by collecting foliage a certain number of days after bud burst (Waring and Youngberg 1972), or after a certain set number of accumulated degree days above a threshold temperature (Shaw and Little 1977).

Annual climatic fluctuations, particularly in precipitation, cause a small but significant variation in nutrient concentrations (Plice

1955, 1964; Lowry 1969). In a 9-year study of nutrient concentrations in 12 Monterey pine trees (Pinus radiata L.), Humphreys et al. (1972) found that N, S and Cl levels were significantly correlated with the number of days per year with rain, K, Ca and Mn with total rainfall, and Fe, Na and Al with the amount of precipitation per rainy day. The average amount of rainfall prior to the sampling date also influence N, P and K concentrations (Miller 1966). Amabilis fir foliage formed in years with a long growing season has higher nutrient concentrations than that formed in years with a short growing season (Turner et al. 1978).

Diurnal variation in nutrient concentrations exist but no systematic pattern for this variation has been described. Fonda (1979) suggested that late afternoon may be the best time to sample nitrogen as nitrogen content is least variable then. Since some of the diurnal variation reported is related to transpirational patterns (Klashes 1972), it may be best to sample foliage during periods of low or stable transpiration rates.

#### (ii) Age variables

Systematic variation in nutrient levels associated with needle age is an important source of variation. Morrison (1974a) summarized the general trends for tree species:

- (a) concentrations of mobile elements such as N, P and K are highest in current or one-year-old foliage;
- (b) concentrations of immobile elements, for example Ca, Mn, Fe, tend to increase in older foliage;
- (c) Mg concentrations show no systematic pattern.

These general trends were found to be true for *amabilis* fir by Schwab (1979) who studied nutrient concentration changes from 1-year to 17-year-old foliage in mature dominant and co-dominant trees. Nitrogen concentration decreased sharply from current to 1-year-old foliage and then declined steadily with age. K and P concentrations declined sharply for two years and then decreased gradually.

Most studies recommend sampling current foliage in the fall (Leyton and Armson 1955; Leyton 1958; Lowry and Avard 1969; Zottl 1975) because concentrations of mobile ions are greatest in current foliage and seem to correlate best with total height growth (Leyton and Armson 1955), with site quality and site index (Lowry and Avard 1969), and with available soil nutrients (Lavender and Carmichael, 1966). However, older foliage sometimes correlates better with other tree growth parameters. Nitrogen levels in 1-year-old needles may correlate best with current height increment (Leyton and Armson 1955) and site index (Wehrmann 1959). Goodall (cited in Goodall and Gregory 1947) found that K levels in older foliage were a better indicator of K nutrition in K deficient trees than those in younger needles. Deficiencies of immobile nutrients such as Ca may also be best detected in older foliage because their concentrations are highest in older tissues (Goodall and Gregory 1947; Wells and Metz 1963; van den Driessche 1974; Raupach et al. 1972).

Tree age is a little studied source of variation in nutrient concentrations. In a study of 15-to-114-year-old Norway spruce (Picea abies (L.) Karst.), Hohne (1964) discovered that N, K and Ca concentrations varied with tree age. N concentrations peaked at 30 years; K at 20 to 50 years; and Ca between 50 and 90 years. In a similar study

with Scots pine (Pinus sylvestris L.), Hohne (1967) reported that concentrations remained constant with tree age. Morrison (1974b) noted that the only foliar nutrient concentration difference between the juvenile balsam fir he studied and the concentrations reported for mature trees by Brazeau and Bernier (1973) was a slight tendency for mature trees to have higher Ca and Mg levels in the upper crown. No one has studied nutrient variations with tree age in amabilis fir. Even if such a study existed, the results might not be widely applicable. Variations with age are not systematic even within a tree. In a study of Pinus radiata (D. Don), Humphreys et al. (1972) detected no nutrient changes with age, Raupuch et al. (1972) found a slight increase in N with age and Askew (1973) reported a decrease in Ca, P, Na, and Cl and an increase in N, Mg, and F with age.

(iii) Effect of crown position

In most trees, N, P and K concentrations decrease from the upper to lower crown position; Ca levels increase, and Mg levels fluctuate (Morrison 1974a). The general pattern varies with stand age, vigor, and density.

Crown position effects are most important in medium dense stands of mature or vigorous trees (Wells and Metz 1963; Morrison 1974a). Cameron (1979) compared N and P concentrations at different crown levels of poor and well-grown advance amabilis fir regeneration in a spaced stand. He found that crown position significantly affected nutrient concentrations only in vigorous trees (Table 1).

TABLE 1: Mean nitrogen concentrations (% oven-dry weight) of amabilis fir foliage from three crown levels. Confidence limits are at 95% level (from Cameron 1979)

		Age of foliage	
Crown position		Current	1-year-old
Well grown trees	upper	1.04 $\pm$ .07	1.05 $\pm$ .08
	middle	0.84 $\pm$ .11	0.93 $\pm$ .08
	lower	0.85 $\pm$ .08	0.93 $\pm$ .06
Poorly grown trees	upper	0.78 $\pm$ .09	0.76 $\pm$ .07
	middle	0.73 $\pm$ .08	0.73 $\pm$ .05
	lower	0.72 $\pm$ .07	0.70 $\pm$ .06

The amount of light reaching the lower crown is influenced by stand density. Because dry matter production is lower in shaded than in fully illuminated branches, the former may have higher nutrient concentrations than illuminated branches (Gagnon 1964). If shading is random or the same for all crown levels, nutrient concentrations are likely to be similar throughout the crown. In a study of nutrient concentrations of mature, evenly shaded, amabilis fir, Schwab (1979) reported that only phosphorus levels in 2-year-old needles varied between crown levels. Since upper crown foliage is least likely to be influenced by the degree of shading in stands with variable stocking, Wells and Metz (1963) recommended it may be the most reliable sample position.

Nitrogen concentrations in upper crown foliage tend to correlate best with tree growth (Leyton 1958). Cameron's 1979 data (Table 1) suggests this is the case with amabilis fir. Differences in foliar nitrogen concentrations between well and poorly grown trees were greatest in the upper crown foliage although statistically significant differences between the two growth classes occurred also in the lower crown foliage.

However, for some nutrients, tree species, or stand densities, nutrient concentrations in the mid or lower crown position may be equally, or more, sensitive to the nutrient status and growth potential of the tree. In a comparison of well grown and poorly grown Pinus resinosa Ait., Madgwick (1964b) discovered that lower crown K and P concentrations correlated best with the nutrient status of the trees. Gagnon (1964) found that nutrient concentrations in the lower crown foliage of black spruce Picea mariana (Mill.) B.S.P. correlated with

site quality and site index as well as did upper crown samples, with the advantage of being easier to collect.

Non-standardized sampling positions within a branch can add small, but unnecessary variations to foliar analyses (Dice 1970). In studies of intrabranh variation in Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco), Brackett (1964) and Dice (1970) reported that nutrient concentrations were highest in outer branch segments and increased with distance from the secondary and higher order branch tips. McClarnon (1979) found branch order and its distance from the central stem had no significant effect on N and P concentrations in even-aged foliage of amabilis fir. Within-branch variation was much less than between-branch variation. Nitrogen contents, (mg/100 oven-dry needles) of lower branch order needles were significantly greater, however, than those of high order branch needles of the same age. He concluded that if nutrient content determination were a part of foliar analysis, stratifying by branch order would eliminate a small but unnecessary source of variation.

Differences in assimilation rates between north-facing and south-facing foliage may have some effect on nutrient concentrations. Peterson (1961) and Tamm (1951) studying Kauri (Agathis australis) and birch (Betula sp.) species respectively, reported higher N and P concentration in north-facing branches compared to south-facing branches. However, the effect of aspect on nutrient concentrations is probably minor (Tamm 1955). White (1954) and Humphrey and Kelly (1962) concluded that aspect did not significantly influence foliar concentrations in three pine species.

Even though aspect is probably a minor source of variation; Leyton and Armson (1955), Wells (1956) and Hoyle and Mader (1964) standardized their foliar sampling to one aspect. Such systematic sampling might reduce variation on open stands, but may not be the best strategy in denser stands, where uneven shading or competition from adjacent trees is likely a greater source of variation than crown aspect.

(iv) Effect of crown class

Hohne (1964), Lowry and Avarad (1968), and Carter and White (1971) reported negligible differences in mean nutrient concentrations associated with crown class. Lower nitrogen concentrations (Lavender 1970), and slightly lower P, K, Ca and Mg concentrations (Wright and Will 1958) have been recorded in suppressed trees. Except for greater N and lower Ca concentration in 1-year-old needles of subdominant trees, Schwab (1979) found that nutrient levels in mature codominant and dominant *amabilis* fir were similar. Inconsistent trends with crown class probably reflect the changing balance between competition for light, moisture and nutrients.

Between-tree variation in foliar nutrients is greater in suppressed trees compared to other crown classes (Lavender 1970; Schwab 1979). This means that a larger number of sample trees from the codominant or suppressed classes is required to meet a desired degree of precision. Lavender (1970) reported that 14 dominant, 24 codominant or 40 suppressed trees were required to estimate foliar N within 5% of the mean.

(v) Provenance effects

Provenances of tree seedlings grown in uniform environments differ in foliar nutrient concentrations (Mergen and Worrall 1965; Walker and Hatcher 1965; Steinbeck 1965, 1966; van den Driessche 1973). Part of this variation can be attributed to the varying growth rate of different provenances under uniform environmental conditions, and part to the differing abilities of provenances to absorb nutrients. Van den Driessche (1973) found that mathematical nutrient-growth relationships differed between two provenances of Douglas-fir. In most field studies, genetic variability must be included with the random error component unless the seed source of the sample trees is known.

(vi) Effect of disease

The effect of various diseases on foliar nutrient levels has not been thoroughly investigated. Tamm (1968) reported no effect of Fomes on nutrient concentration in spruce. However, Ferrel and Hubert (1957) found P and Ca foliar concentrations in western white pine (Pinus monticola Dougl.) were affected by pole-blight. Singh and Bhure (1974) detected an increase in most foliar micronutrients and a decrease in most macronutrients in several tree species infected with Armillaria mellea (Vahl ex Fr.) Krummer root rot. To avoid unnecessary disease-induced variation, foliage sampling should be restricted to healthy trees.

(vii) Effect of reproductive state

Cone-bearing tree branches have lower foliar nutrient levels than other branches (Brackett 1964; Turner et al., 1978). Therefore, unless

cone-bearing branches are the normal case (e.g. in seed orchards) they should not be sampled. Since the seasonal distribution and levels of nutrient can vary between the sexes in dioecious trees, male and female trees should be sampled separately (Fletcher and Ochry-Meirch 1955).

(viii) Effect of silviculture treatment and location

Silvicultural treatments (thinning, burning, or fertilizing) and location variables (aspect, elevation, proximity to ocean or factories) are also likely to influence foliar nutrient concentrations. Schwab (1979) noted that N, P, K and Mg foliar concentrations increased with elevation in amabilis fir.

3.2.3 Methods of data presentation

Foliar nutrients are reported as a percentage of oven-dry needle weight (concentration data), as mass per 100 oven-dry needles (content data), or as a ratio between 2 nutrients. Foliar nutrient concentrations are the most common method of presentation, and therefore it is useful to present such data for comparison purposes. However, nutrient concentration data expresses a ratio between two variables (nutrient uptake and dry matter accumulation) which are not always governed by the same physiological or environmental factors. For example, growth or dry matter accumulation may fluctuate with changes in light intensity or temperature, resulting in a change in nutrient concentrations even though nutrient uptake and content remain constant.

If dry matter fluctuations obscure the relationship between nutrient concentration and supply, nutrient content data may be a better

reflection of nutrient availability and tree nutrient status. Tree growth is often better correlated with nutrient content data than with concentration data (Mader 1964; Mader and Howarth 1968).

Since maximum plant growth depends not only on an adequate supply of individual nutrients, but also on a correct balance between nutrient ions (Shear et al., 1968), nutrient status is often expressed as ratios between various nutrients. Optimum nutrient ratios are thought to exist for tree species independent of different environmental conditions (Leyton 1958). Based on a study of birch, pine and spruce seedlings Ingestad (1967) proposed optimum proportions of foliar nutrient:  $N = 100$ ,  $P = 13$ ,  $K = 65$ ,  $Ca = 6$ ,  $Mg = 85$ , (mass basis). Lavrichenko (cited in Morrison 1974a) devised another means of expressing optimum ratios of N, P and K. The concentration of each of these elements was expressed as a percentage of the total concentration of all three elements. Optimum N, P, K proportions for pine using Lavrinchenko's scheme are 67:7:26.

#### 3.2.4 Interpreting foliar nutrient data

Morrison (1974a) discussed the three stages in the development of foliar analysis interpretation. Initially, investigators compare foliar nutrient levels in poorly grown and well grown trees, healthy and unhealthy trees to see if differences in growth are associated with differences in nutrient concentrations. Simple correlations are used to relate foliar nutrients to tree growth or soil nutrients. However, intercorrelations between nutrients and environmental factors make it difficult to assess the independent contribution of a nutrient to tree growth or the total effect of several nutrients.

The second stage in interpretation, according to Morrison, is the development of simple and multiple linear regression models. This technique, popularized by Leyton and Armson (1955), is designed to isolate the independent contributions of nutrients to growth, to indicate the most significant growth-nutrient relationships, and to explain more of the variability in these relationships by combining the effect of several factors (Hoyle and Mader 1964). Although multiple regression models can be a useful diagnostic tool, they have not been very successful in predicting tree growth response to fertilizers.

"When growth is limited only by the availability of a particular nutrient, all other factors being optimal, the relationship between supply, growth and the concentrations of that nutrient in the foliage are more or less uniquely determined, i.e. a particular level of supply corresponds to a particular level of growth and concentration. However, this situation is not realistic for field conditions where growth to a lesser or greater extent is influenced by a number of factors" (Leyton 1958). Some of these factors can be eliminated by standardized sampling. Others, such as ion interaction, nutrient redistribution, and soil moisture or temperature cannot be readily controlled or quantified and consequently they complicate data interpretation.

The uptake and distribution of individual plant nutrients is not independent of the concentrations of other nutrients (Lundegardh 1951).  $\text{NH}_4^+$  and  $\text{K}^+$ ,  $\text{Ca}^{2+}$  and  $\text{K}^+$ ,  $\text{SO}_4^{2-}$  and  $\text{PO}_4^{3-}$  are reported to be antagonistic ion pairs (Baule and Fricker 1970). High concentrations of one of these ions adversely affects the uptake of the other. Growth dilution is

another form of ion interaction. If tree growth is promoted by an increased supply of one nutrient, the concentration of other nutrients may decrease due to increased dry matter production, even though the availability and uptake of these other nutrients remains constant. Phosphorus concentrations often decrease after nitrogen fertilization because of growth dilution (Leyton 1957; Heilman and Gessel 1963; Lee 1971; Donald and Glen 1974).

Timmer and Stone (1978) employed a graphical technique to study changes in foliar nutrients after fertilization. Changes in needle weight, concentration, and content of a foliar nutrient are plotted on one graph. This technique, first used by Kraus (cited in Timmer and Stone 1978), allows clearer interpretations of growth dilution effects.

Internal nutrient reserves are a source of nutrients which has not been thoroughly investigated for many tree species. They may supply a significant proportion of the annual requirements for new growth, especially in high elevation species with long needle retention. Turner and Singer (1976) calculated that 54% of the annual requirements of N, 58% of P, 40% of K, 11% of Ca and Mg in old growth *amabilis* fir was supplied by internal reserves of nutrients stored in older foliage. Current nutrient status is influenced by past conditions, the internal nutrient reserves, and by current nutrient availability.

Moisture and temperature are important variables which influence both nutrient availability and tree growth. Burr (1961) reported that soil temperature, air temperature and light intensity affected N concentrations in sugar cane. Lowest N and P concentrations were associated with high light intensity, warm air temperatures and low soil

temperatures, conditions which promoted shoot growth. Although there is no simple rule governing the effect of soil moisture on foliar nutrient concentrations (van den Driessche 1974), drought stress tends to increase foliar nitrogen levels in forest trees (Walker 1962; Pharis et al. 1964; Hoyle 1969; Schomaker 1969; Broadfoot and Farmer 1969), and has a similar effect on P and K levels (Walker 1963; Schomaker 1969). However, Brix (1972) and Leaf et al. (1970) found no significant differences in foliar nitrogen concentrations between irrigated and non-irrigated trees. Black (1968) suggested that drought would tend to increase nitrogen concentrations if dry matter production was reduced more than nutrient uptake, and vice versa. Both nutrient concentration and nutrient content data should be collected to fully interpret the affect of soil moisture (Black 1968). If both moisture and nutrients are limiting growth, the interpretation of foliar data becomes very difficult.

"Extreme deficiencies can be detected on most sites by foliar nutrient levels but interpretation of the significance of variation in foliar nutrient levels where stands are not suffering from extreme deficiencies has remained largely a mystery because of the interactions among nutrients and environmental factors" (Hoyle and Mader 1964).

Incorporation of site parameters such as soil moisture in multiple regression relationships (Morrison 1974a) or the use of curvilinear regressions or multivariate statistics (van den Driessche 1974a) may improve the diagnostic and predictive value of foliar analysis in the future.

## LOCATION AND DESCRIPTION OF RESEARCH SITE

### 1. Location

The study site is situated on a flat to gently sloping, northeast facing area at an elevation of 550 m on Branch 101 k logging road, in the Tsolum Block of the Tree Farm License No. 2, approximately 16 km northwest of Courtenay, Vancouver Island, British Columbia (Figure 4).

### 2. History

A mature forest of Douglas-fir (200 years+), western hemlock and amabilis fir that previously occupied the site was clearcut logged in 1969. The following year the site was slashburned and planted with Douglas-fir. However, the fire was very patchy and amabilis fir advance regeneration ( $\leq 1.5$  m tall) and the associated understory plants survived in numerous areas that were not burnt. These trees had been growing extremely slowly prior to clearcutting, but height growth released in 1971 and by 1973 averaged 30 cm. This good early height growth has not been sustained. Since 1974, some trees have exhibited steadily declining height increments and by 1978 current height growth ranged from 1 to 80 cm. Average annual height growth for the poorly grown trees (Figure 5) peaked in 1975 at 26 cm, and then declined to 8 cm in 1978. In contrast, height growth of well grown trees increased to 52 cm in 1977 and then dropped slightly to 48 cm in 1978.

This study site was selected because:

- (a) there was a good range of height growth;

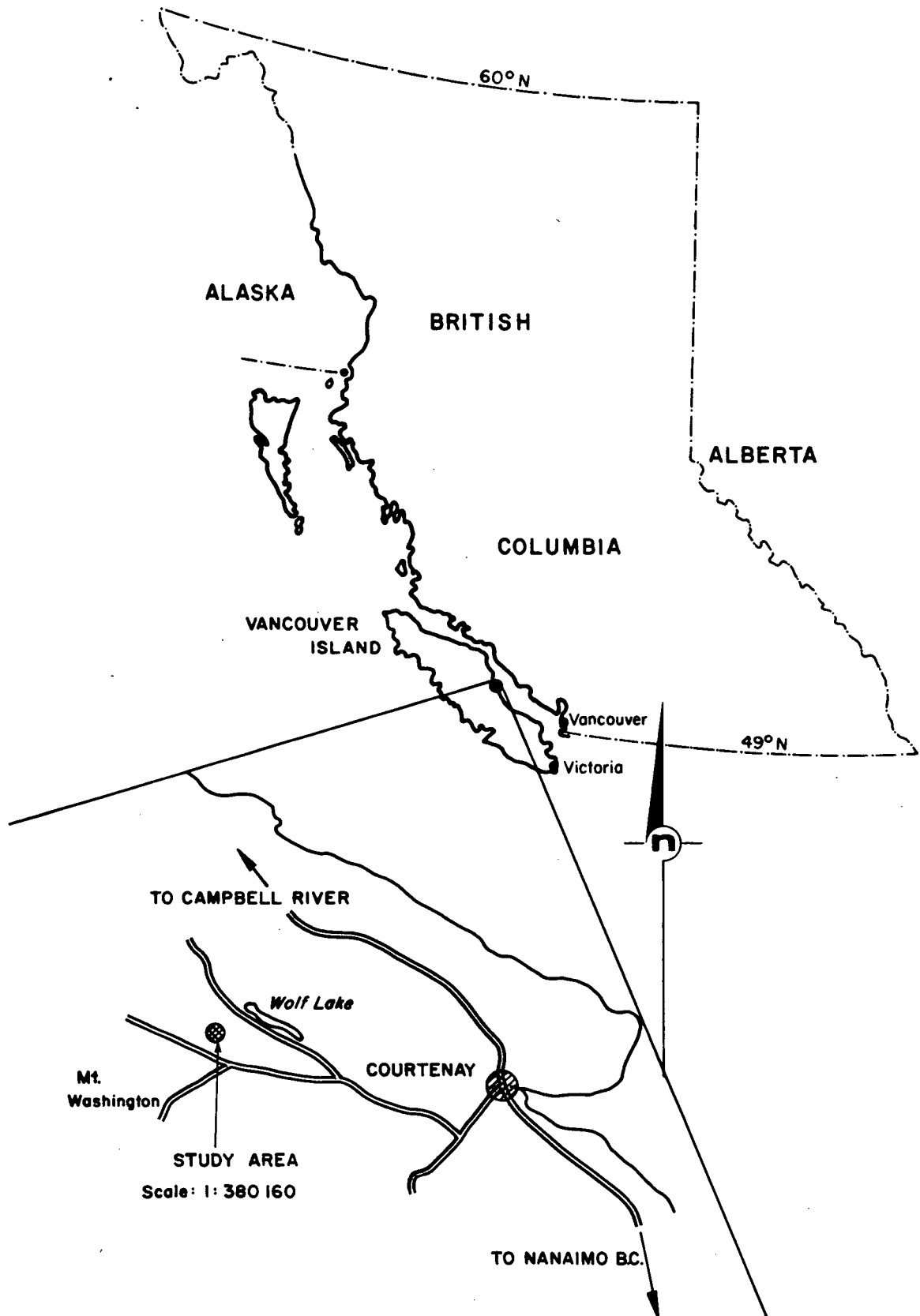


Figure 4. Location of study site on Vancouver Island, British Columbia.

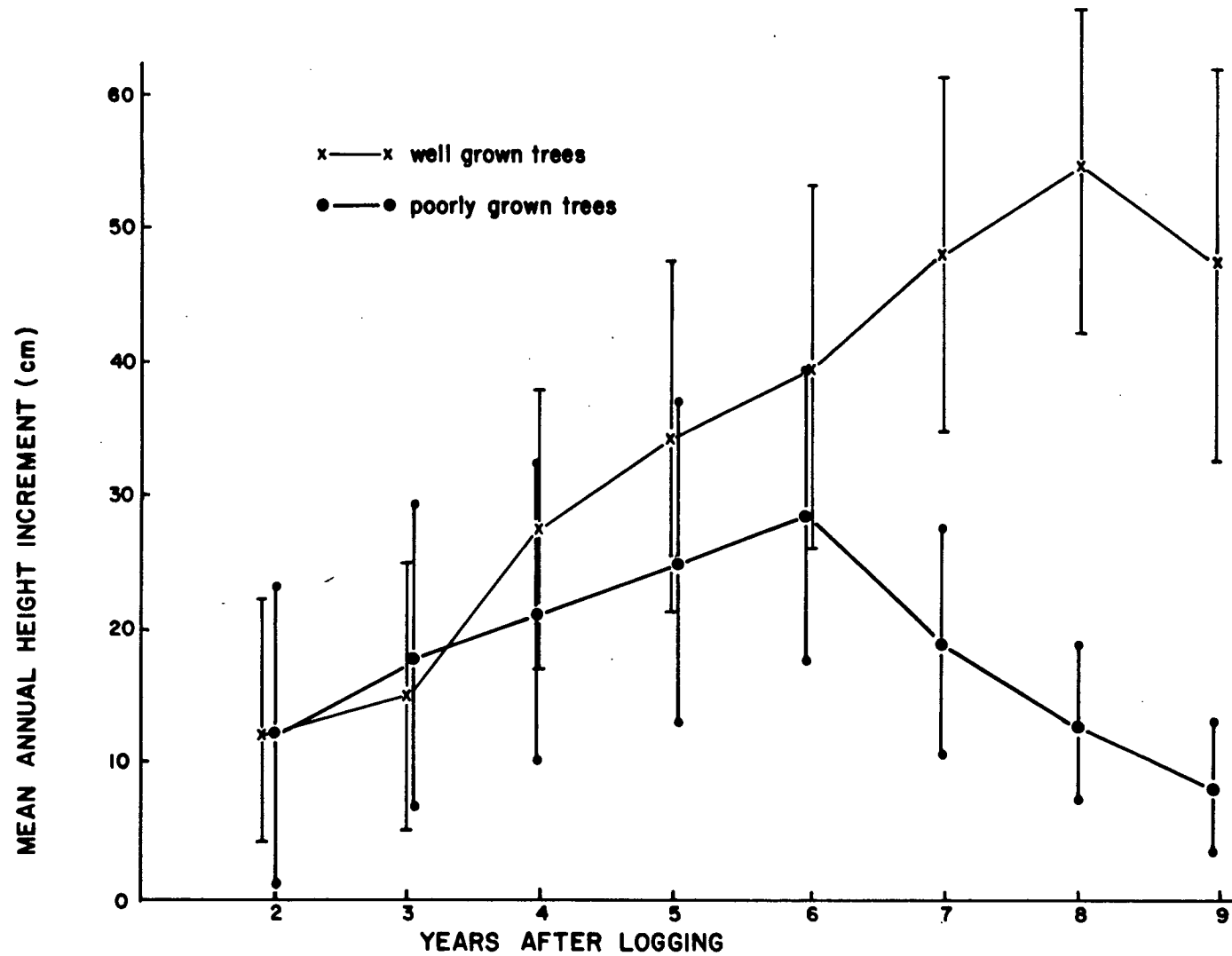


Figure 5. Mean annual height growth of well and poorly grown amabilis fir regeneration at the research site (95% confidence limits are shown).

- (b) root rot or feeder root diseases were not detected by Dr. G. Wallis (Pacific Research Centre, Victoria, B.C.) or Dr. B. van der Kamp (Faculty of Forestry, University of British Columbia, Vancouver, B.C.). Therefore, these factors could be eliminated as causal agents;
- (c) past and current leader damage by snow, wind or animals was negligible;
- (d) mycorrhizae were abundant on the roots of both poorly and well grown trees;
- (e) elevation, soils, vegetation and initial release growth patterns were similar to those in a nearby nitrogen fertilizer trial site, permitting comparisons to be made between these two sites.

### 3. Climate

Because of the rain shadow cast by the Vancouver Island Mountains, the east coast of Vancouver Island has a drier, more continental climate than that of the west coast of Vancouver Island. Only 10 per cent of the total annual precipitation falls in the 3 summer months. A dry period is normal in late July or early August (Keser and St. Pierre 1973). Prevailing winds are from the southeast in winter and northwest in summer.

No climatic data were available for the study site. However, the Climatic Division of the Resource Analysis Branch, B.C. Ministry of the Environment, was able to supply climatic estimates for the study area. These were based on records from the Comox weather station located at

sea level 20 km east of the study site, after corrections for differences in elevation, longitude, latitude, and slope. A January mean of  $-0.9^{\circ}\text{C}$ , a July mean of  $14.4^{\circ}\text{C}$ , and a total annual precipitation of 142 cm were predicted for the site.

From 1970 to 1977, daily temperature and weekly rainfall data were collected from May to August at a weather station a few km from the research site by Zwickel (1977) as part of a grouse habitat study. His temperature data agreed closely with the predicted data, but his average rainfall data for May to August was 29.2 cm compared to the 18.1 cm predicted. Monthly precipitation averages recorded by Zwickel for May to August were respectively 10.1, 7.8, 6.0 and 6.3 cm. Predicted averages for the same months were respectively 4.3, 3.3, 4.9 and 5.6 cm. This suggested that predicted climatic data may underestimate precipitation especially during May and June.

No information was available on snow depth or duration. However, local foresters have observed snow in the vicinity of the study site in late April.

#### 4. Geology

The study site is located on a till parent material with a loose (ablation) layer deposited over a compacted (basal) till which is largely impermeable to water and roots. The till deposit is underlain by basalt bedrock of the Karmutsen formation.

#### 5. Soils

Soils in the study area were classified as Humo-Ferric Podzols (Canadian System of Soil Classification 1978) with a mor humus but minimal Ae development. A soil pedon is described in Table 2.

TABLE 2. Profile description of the study site soil

Horizon	Depth (cm)	Description
L	18-16	Undecomposed conifer needles, angiosperm leaves, and twigs; abundant fine roots; very strongly acid.
F	16-13	Partially decomposed needles, leaves, twigs; abundant yellow and white mycelium; abundant fine roots; strongly acid.
H	13-0	Reddish-black (10 R 2.5/1 m), dark reddish brown (5 YR 2.9 12 d); varying amounts of decaying wood; slightly matted; yellow mycelium; abundant fine and medium, plentiful coarse roots; clear smooth boundary; 10-50 cm thick; extremely acid.
Ae	0-2	Dark reddish gray (5 YR 4/2m), light brownish gray (10 YR 6/2 d); sandy loam; blocky; slightly sticky; friable; very few fine roots; 50% gravel; clear smooth boundary; extremely acid.
Bf <sub>1</sub>	2-15	Dark reddish brown (5 YR 3/4 m), yellowish red (5 YR 4/6 m); loam; weak to moderate, medium sub-angular blocky; slightly sticky; friable; few fine, plentiful medium, plentiful coarse roots; 60% gravel; diffuse irregular boundary; extremely acid.
Bf <sub>2</sub>	15-50	Dark red (2.5 YR 3/6 m), reddish brown (2.5 YR 5/4 d); loam; moderate, coarse sub-angular blocky; slightly sticky, friable; very few fine, few medium, very few coarse roots, 60% gravel; clear irregular boundary; very strongly acid.
Ca	50+	Reddish yellow (7.5 YR 6/b d); massive; sticky, very firm.

The soils of the study site were mapped as Woodhus gravelly loamy sands by Ferguson and Pegues (1976). Woodhus soils are described by these authors as moderately stony, moderately well to well drained, and moderately well-suited to intensive forest management of Douglas-fir, western hemlock and amabilis fir. They are found from 500 to 850 m on poorly drained gentle slopes. A thick mor humus tends to accumulate on the surface. Ferguson and Pegues (1976) recommended slashburning these soils to improve plantation survival and growth.

The chemical and physical properties of some soils in the Woodhus soil map unit were described by Laing (1979) with emphasis on the forest floor horizons, which are the major rooting zone for the advance amabilis fir regeneration (Table 3).

#### 6. Biogeoclimatic Classification

Klinka (1977a) classified the problem area as part of the wet subzone of the Coastal Western Hemlock Biogeoclimatic Zone (CWHb). The presence of amabilis fir regeneration is a major vegetative characteristic separating the wet and dry subzones of the Coastal Western Hemlock Biogeoclimatic Zone. Clintonia uniflora, Rubus pedatus and Rhytidiopsis robusta, common CWHb plant species, are present in the herb and moss layer. Vaccinium alaskaense, which is typical of mesic to subhygric sites in the CWHb subzone (Krajina and Kojima, 1976) is the most common shrub species. The occurrence of some natural regeneration of two higher elevation tree species, yellow cedar (Champaecyparis nootkatensis D. Don Spach) and mountain hemlock (Tsuga mertensiana Bong, Carr), suggested that the study site was affected by cold air drainage. Cold

TABLE 3. Mean depth and chemical properties of the LFH horizons of Woodhus soil series  
(adapted from Laing 1979) (n = 6; standard deviation in brackets)

Horizon	Depth (cm)	pH (in H <sub>2</sub> O)	Organic matter %	Total N %	C:N ratio	Total P %
L	2.8 (2.2)	5.1 (0.2)	78.3 (9.6)	1.32 (0.44)	38.6 (17.5)	0.11 (0.03)
F	2.8 (1.5)	4.7 (0.3)	76.3 (4.0)	1.70 (0.20)	26.4 ( 2.5)	0.14 (0.02)
H	16.2 (9.6)	3.7 (0.3)	83.5 (1.6)	0.90 (0.10)	46.8 (11.8)	0.07 (0.01)
Cation Exchange (me/100 g Soil)						
	Total capacity	Ca	Mg	Na	K	
L	98.9 (9.0)	30.0 (13.6)	4.8 (1.4)	0.02 (0.01)	2.12 (0.60)	
F	166.4 (104.2)	28.3 (11.3)	4.7 (1.6)	0.12 (0.04)	2.76 (1.3)	
H	146.1 (98.7)	21.0 (7.2)	4.2 (1.9)	0.22 (0.07)	1.76 (1.70)	

air drainage might be compensating for the lower precipitation on the site but perhaps not enough to support uniformly good growth of *amabilis* fir (see Appendix A).

In 1979, the problem area was reclassified (Klinka et al., 1979) with the lower portion (below 760 m) separated from the upper portion (approx 760 m - 1000 m) as submontane and montane variants, respectively, of the CWHb subzone. The study site lies between the mesic and subhygric classes (4 and 5, respectively) on the edaphic grid for the CWHb subzone (Klinka 1977b).

## METHODS

### 1. Field Sampling

Ten well grown and ten poorly grown trees with steadily declining height growth were chosen to represent the range of tree height growth on the study site. All these trees had released well after logging (Figure 5). Vigorous, well grown trees were characterized by consistently good height growth since release, spire-shaped crowns, normal needle length, and dark green foliage. Poorly grown trees were characterized by steadily declining height growth after the initial period of good release growth, reduced needle length, chlorotic yellow-green foliage, and flat-rounded crowns.

The twenty trees were paired with another twenty trees on the basis of similar size, height growth pattern, foliage colour, and degree of aboveground competition. This second set were used for the growing season foliar sampling. Since the members of each pair were similar in external characteristics, it was hoped that their foliar chemistry would not be significantly different, and that alternate sampling of the trees in each pair would provide information on seasonal variation without removing excessive foliage from individual trees. This sampling scheme resulted in data analysis problems which are described in the next chapter. Foliage from all forty trees was collected on the last sampling date in September.

Random samples of current, 1- and 2-year-old foliage on tertiary and higher order branches from the fourth whorl from the top of the tree

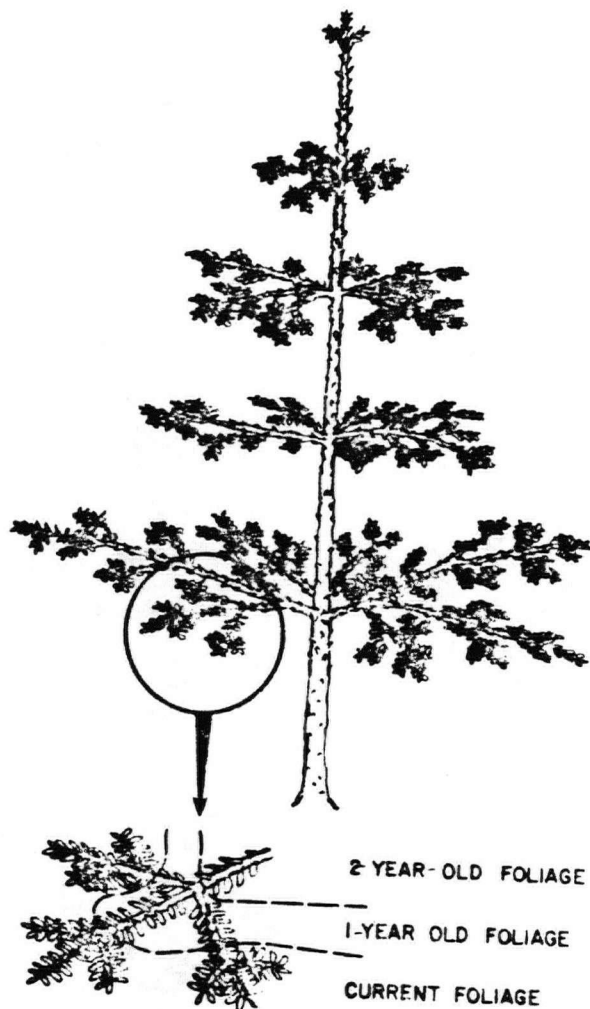


Figure 6. Foliar sampling position on the fourth whorl.

(Figure 6) were collected twice monthly from May to September from one member of each pair. Foliage from all 40 trees was collected on the last sampling date at the end of September. Samples were collected in the afternoon. Weather conditions were briefly recorded at the time of sampling.

The foliage samples were either stored in a refrigerator for 2 weeks at approximately 4°C or transported immediately to the lab for oven drying. The effect of refrigerator storage on foliar N and P concentrations was tested by collecting current and 1-year-old foliage from two tertiary branches on the fourth whorl sampling position of twenty *amabilis* fir outside the study area. One branch from each was oven dried immediately, the other was stored in a refrigerator for two weeks before drying. Refrigeration had no significant effect ( $p < .05$ ) on either foliar N or P. The data for the two treatments were compared by paired t-tests.

At the end of September, 10 of the vigorous and 10 of the poor trees were randomly selected for destructive sampling to obtain the following information:

- (i) height increments to the nearest cm from 1970 to 1978<sup>5</sup>;
- (ii) radial increments to the nearest 0.1 mm at breast height from 1976 to 1978;
- (iii) height and age at release;
- (iv) needle retention in years on the lower crown branches;

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<sup>5</sup>The 1970-1978 height growth is called release height growth in this study. The 1978 increment is current height growth.

- (v) estimate of aboveground competition (obtained by counting the number of tree stems (except for seedlings) within 2 m of the sample tree.
- (vi) three samples of humus (H horizon of forest floor) were collected with a core sampler from beneath each tree and bulked for chemical analysis. One of the three samples was collected adjacent to the sample tree stem, the other two were collected from the north and south edges of the tree canopy.

A study of microsite differences in water availability was not possible because of lack of time and appropriate equipment. However, in order to gain some insight into the effect of moisture regime on foliar nutrient concentrations in the study area, 10 well grown trees were randomly selected for fall foliar analysis at 3 xeric and 3 mesic sites close to and at the same elevation as the study site.

## 2. Laboratory Analysis

Foliage samples were oven-dried for 24 hours at 70°C, and then the needles were stripped from the twigs and weighed. This was done because fresh needles, (especially soft, current growth) collected during the summer were too difficult to remove cleanly from twigs. The needles were not ground prior to chemical analysis. The weight of each needle sample averaged 2.0 g, and losses during grinding might have resulted in insufficient sample for analysis. Saloni et al. (1978) reported that

measured concentrations of N, P, and K did not vary significantly between ground and unground samples.

Total foliar N and P were measured colorimetrically on a Technicon Industrial Analyzer (Anonymous 1974) following a semimicro - Kjeldahl digestion (Bremner 1965). Total foliar Ca, Mg, and K were determined on HCl extracts of dry ashed samples (Allen et al. 1974) using atomic absorption spectrophotometry with a Varian-Techtron AA5 machine<sup>6</sup>. An air-acetylene flame was used for the K and Mg analysis. A nitrous oxide-acetylene flame was used for Ca.

Humus samples were air-dried and ground. Total N and P were analyzed as described for the foliar samples. pH was measured in a 1:5 soil to water suspension. Total carbon was determined by the Walkley-Black method (Allison 1965). Exchangeable cations were extracted with  $\text{NH}_4\text{OAc}$  (adjusted to pH 7.0). The exchangeable cations were analyzed by atomic absorption spectrophotometry.

### 3. Data Analysis

Nutrient concentrations (% oven-dry weight), contents (mg/100 needles) and ratios were calculated for the fall foliar data. N and P concentrations and N:P ratios were calculated for the growing season samples. The relationships between height growth and nutrient data were analyzed by stepwise regression analysis using MIDAS<sup>7</sup> programs.

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<sup>6</sup>Refer to Appendix B for comment on this chemical analysis method.

<sup>7</sup>Michigan Interactive Data Analysis System.

## RESULTS AND DISCUSSION

The results are presented and discussed in six sections. The first section is a comparison between fall foliar nutrient data and values reported in the literature for true firs. The second describes the relationships between these data and height growth. Seasonal trends in foliar N and P are presented in section three and the relationship between height growth and these N, P and N:P data are presented in section four. The relationships between humus nutrient data and amabilis fir release growth are described in section five. Finally, in section six, the effects of non-nutritional factors on variable height growth are discussed.

### 1. Comparison of Fall Foliar Data with Literature Values

#### 1.1 Nitrogen

Nitrogen concentrations in current and 1-year-old fall foliage were .71% and .74% respectively for well grown trees and .55% and .58% respectively for poorly grown trees. These concentrations were lower than most values reported in the literature for true fir species (Table 4). Nitrogen concentrations in poorly grown trees were the lowest reported in any study of true fir foliar nutrition, indicating that these trees were severely deficient in nitrogen. Interestingly, in all the studies except those of Courtenay amabilis fir stands (Cameron 1979; Briggs 1979; and this study), current foliar nitrogen concentrations were higher than those of 1-year-old foliage. In many conifer species,

TABLE 4. Some fall foliar nitrogen concentrations (% oven-dry weight).  
Reported for true fir species

	Current foliage	1-year-old foliage
<u>Amabilis fir (<i>Abies amabilis</i>)</u>		
This Study		
well grown trees	.71	.74
poorly grown trees	.55	.58
Schwab (1979)		
dominant, mature trees	1.20 - 1.30	1.05 - 1.15
Gallagher (1964)		
juvenile trees with poor growth	.92 - 1.22	.81 - .94
Beaton et al. (1965)		
8-year-old trees	.99	.91
Cameron (1979)		
30-year-old, thinned well grown trees	1.05	1.04
30-year-old, thinned poorly grown	.78	.76
Briggs (1979)		
thinned	.89	.93
thinned and fertilized	1.11	1.14
<u>Subalpine fir (<i>Abies lasiocarpa</i>)</u>		
Beaton et al. (1965)		
3-6 year-old trees	1.64, 1.85, 1.05	1.59, .91
<u>Grand fir (<i>Abies grandis</i>)</u>		
Loewenstein and Pitkin (1971)		
fertilized	1.29	
not fertilized	1.18	
<u>Balsam fir (<i>Abies balsamea</i>)</u>		
Morrison (1974b)		
juvenile trees	1.09 - 1.15	1.02 - 1.07
Brazeau and Bernier (1973)		
mature trees	1.34	1.23

fall foliar N concentrations less than 1.0 to 1.1% indicate a nutrient deficiency (Leaf 1973).

The difference in nitrogen nutrition between poorly and well grown trees was accentuated when nitrogen contents (mg nitrogen/100 oven-dry needles) were compared. Nitrogen content for current, 1-year-old and 2-year-old foliage of poorly grown trees averaged respectively 1.39, 2.54 and 2.77 mg nitrogen per 100 needles. Comparable values for well grown trees were 2.60, 5.35, and 5.65 mg nitrogen per 100 needles.

There are only a few other reports of nitrogen content data for true firs. Brazeau and Bernier (1973) found current and 1-year-old needles of balsam fir contained 3.42 and 5.44 mg N/100 oven-dry needles respectively. Briggs (1979) compared nitrogen contents in amabilis fir fertilized with nitrogen at the Crown Zellerbach pilot trial and unfertilized trees. Nitrogen contents were 7.5 and 14.8 mg/100 needles for current and 1-year-old foliage, respectively, of trees fertilized 2 years previously; 4.2 and 6.5 mg/100 needles in current and 1-year-old foliage, respectively, of unfertilized trees. The nitrogen content data for well grown trees in this study are similar to those of Brazeau and Bernier (1973). However, nitrogen content of poorly grown trees is much less than reported in the other studies of true firs.

## 1.2 Phosphorus

Phosphorus concentrations in both well and poorly grown trees were similar to those reported in the literature for true fir species

(Table 5). Mean current foliar P concentrations, .18% for both well and poorly grown trees, are within the range considered adequate for many conifer species (Leaf 1973; Morrison 1974a).

Phosphorus contents were .61 and .94 mg per 100 needles respectively for current and 1-year-old foliage of well grown trees. Comparable values for poorly grown trees were .45 and .69 mg P per 100 needles. These values are similar to those reported by Brazeau and Bernier (1973) for mature balsam fir (.49 and .58 mg P per 100 current and 1-year-old needles, respectively) but lower than the values reported by Briggs (1979), of 1.0 and 1.4 mg P per 100 needles for current and 1-year-old foliage, respectively, of fertilized trees, and .90 and 1.0 mg per 100 needles, respectively, for current and 1-year-old foliage of unfertilized trees.

### 1.3 Ca, Mg and K

Mean cation concentration and content data were calculated for the fall foliage (Table 6). Calcium concentrations in both well and poorly grown trees were above .12%, the level which is considered adequate for many conifer species (Leaf 1973; Morrison 1974a). They were similar to concentrations reported by Beaton et al. (1965) (.30 and .41% respectively for current and 1-year-old foliage of juvenile amabilis fir), but higher than those reported by Schwab (1979) for mature amabilis fir (.20-.25% for current foliage).

Magnesium concentrations for both well and poorly grown trees were below the levels considered adequate for many tree species (Leaf 1973; Morrison 1974a). Leaf (1973) stated that magnesium concentrations were

TABLE 5. Some fall foliar phosphorus concentrations (% oven-dry weight).  
Reported for true fir species

	Current foliage	1-year-old foliage
<u>Amabilis fir (Abies amabilis)</u>		
This Study		
well grown trees	.18	.14
poorly grown trees	.18	.16
Beaton <u>et al.</u> (1965)		
juvenile trees	.16	.12
Schwab (1979)		
mature amabilis trees	.20	.12
Cameron (1979)		
well grown, thinned amabilis fir	.17 - .19	.14 - .17
poorly grown, thinned amabilis fir	.18 - .19	.15 - .18
Briggs (1979)		
fertilized	.16	.31
not fertilized	.14	.11
<u>Subalpine fir (Abies lasiocarpa)</u>		
Beaton <u>et al.</u> (1965)		
juvenile trees	.18 - .26	.15 - .25

TABLE 6. Mean fall foliar Ca, Mg, and K concentrations and contents in well and poorly grown advance amabilis fir regeneration (n = 20; standard deviations in brackets)

	Well grown trees		Poorly grown trees		
<u>Cation Concentrations (% Oven-Dry Weight)</u>					
<u>Current foliage</u>					
Ca	.34	(.06)	.26	(.06)	**
Mg	.066	(.084)	.058	(.063)	**
K	1.06	(.15)	1.08	(.24)	NS
<u>1-year-old foliage</u>					
Ca	.46	(.092)	.42	(.09)	NS
Mg	.051	(.014)	.059	(.088)	*
K	.88	(.15)	.92	(.23)	NS
<u>Cation Contents (mg/100 Needles)</u>					
<u>Current foliage</u>					
Ca	123.58	(67.44)	66.73	(29.45)	**
Mg	23.62	(10.68)	14.60	(3.93)	**
K	372.51	(149.31)	264.84	(63.42)	**
<u>1-year-old foliage</u>					
Ca	318.66	(120.34)	180.96	(41.53)	**
Mg	33.52	(10.63)	25.59	(6.81)	**
K	617.41	(259.64)	390.23	(102.14)	**

\* Significant difference at  $p < .05$  between well and poorly grown tree means.

\*\* Significant difference at  $p < .01$  between well and poorly grown tree means.

usually similar to P concentrations. Young amabilis fir in the Beaton et al. (1965) study had .08 and .07% magnesium respectively in current and 1-year-old foliage. Current magnesium concentrations in mature amabilis fir studied by Schwab (1979) ranged from .096 to .110%.

Mean potassium concentrations were within the range considered high for many conifer species (Leaf 1973; Morrison 1974a) and were higher than the values of .57-.65% reported by Schwab (1979) for current foliage of amabilis fir. However, they were similar to the K concentrations for current and 1-year-old foliage, 1.2 and 1.1%, respectively, reported by Beaton et al. (1965) for juvenile amabilis fir. The higher values of K in juvenile amabilis fir may reflect the rapid cycling of K found by Yarie (1975) in Vaccinium spp., common shrubs on amabilis fir sites.

#### 1.4 Nutrient Ratios

N:P ratios for current and 1-year-old foliage were 3.9 and 5.3, respectively, for well grown trees and 3.1 and 3.6, respectively, for poorly grown trees. N:P ratios for both types of advance regeneration are below the range 6.7 to 12.5 considered optimum for many coniferous species (Ingestad 1967), the N:P ratios calculated from Beaton et al.'s (1965) data for juvenile amabilis fir (6.2 and 7.5 respectively for current and 1-year-old foliage) and those calculated from Schwab's (1979) data for current foliage of mature amabilis fir (4.8 to 7.2).

Ca:Mg, K:Mg, N:K, and K:Ca ratios were calculated from the fall foliage data and compared to ratios from Beaton et al. (1965), Schwab (1979), and Ingestad (1967) (Table 7). The results of this study were closest to ratios reported by Beaton et al. (1965) for juvenile amabilis fir. Ingestad's ratios seemed to have limited value for comparison. Current foliar nutrient ratios calculated from Beaton et al.'s (1965) study of Vancouver Island Douglas-fir were 2.7, 5.2, 1.8, and 1.92, respectively, for the Ca:Mg, K:Mg, N:K, and K:Ca ratios. These ratios are similar to those reported by Schwab (1979) for mature amabilis fir and may be closer to the ratios that are optimum for conifer trees growing in coastal B.C. forests.

The comparison of mean fall foliar nutrient and nutrient ratio data from this study with literature values indicates that a severe nitrogen deficiency and a possible magnesium deficiency are related to the variable height growth of the amabilis fir trees.

## 2. Relationships Between Fall Foliar Chemistry and Height Growth

The relationships between fall foliar chemistry and height growth were analyzed by a MIDAS stepwise multiple regression program using a level of significance of .05. Sixty-four per cent of the variation in release height growth was explained by four variables: the N:P ratio in 2-year-old foliage, Mg% in 1-year-old and current foliage, and P% in current foliage. The standard error for this regression was 52.2 cm. Seventy-five per cent of the variation in current height growth was explained by 4 variables: N:P ratio in 2-year-old foliage, Mg% in

TABLE 7. Comparison of nutrient ratios in fall foliage of well and poorly grown amabilis fir regeneration with other studies

	Well grown trees	Poorly grown trees	Mature amabilis fir <sup>1</sup>	Juvenile amabilis fir <sup>2</sup>	Ingestad ratios <sup>3</sup>
<u>Current foliage</u>					
Ca:Mg	5.2	4.4	2.1	3.8	.70
K:Mg	16.4	18.8	6.4	15.0	7.6
N:K	.69	.55	2.0	.83	1.54
K:Ca	3.2	4.4	3.2	4.0	10.8
<u>1-year-old foliage</u>					
Ca:Mg	9.7	7.3	2.7	5.9	
K:Mg	18.8	16.1	6.5	15.7	
N:K	.87	.68	1.8	.76	
K:Ca	2.0	2.3	1.9	2.7	

<sup>1</sup>Calculated from Schwab's (1979) data.

<sup>2</sup>Calculated from Beaton et al.'s (1965) data.

<sup>3</sup>Calculated from Ingestad (1967) proportions (on mass basis).

1-year-old and current foliage, and Ca% in current foliage. The standard error of this regression was 12.1 cm.

N:P ratios were the most significant independent variables explaining 51 and 46% of the variation in current and release height growth, respectively. Although the relationship between N:P ratios and release height growth appears curvilinear when plotted (Figure 7), the coefficient of determination and standard error did not improve with a polynomial regression of the form  $y = b_0 + b_1x_1 + b_2x_1^2$ . N:P ratios below 7.5 seemed to be sub-optimal for height growth.

Nitrogen concentrations alone explained 44 and 45% of the current and release height growth, respectively. N:P ratios seem to be a slightly more sensitive indicator of nitrogen status than N concentrations alone. Phosphorus concentrations were lower in well grown trees but phosphorus contents (mg P per 100 needles) rose with increasing nitrogen concentrations (Figure 8). Therefore, the N:P interaction seems to be accounted for by growth dilution of P content (as nitrogen concentrations increase) in well grown trees and by P accumulation relative to growth (as nitrogen concentrations become deficient) in poorly grown trees. Barker et al. (1965) reported that an increase in the nitrogen status of seedlings accelerated seedling respiration and consequently the use of ATP, creating a demand for phosphorus.

Nitrogen concentrations in 2-year-old fall foliage were more positively related to release height growth than current or 1-year-old foliar N. Current height growth was most significantly related to nitrogen concentrations in current foliage. In contrast, Leyton (1958) found that current height growth in nitrogen-deficient trees was best

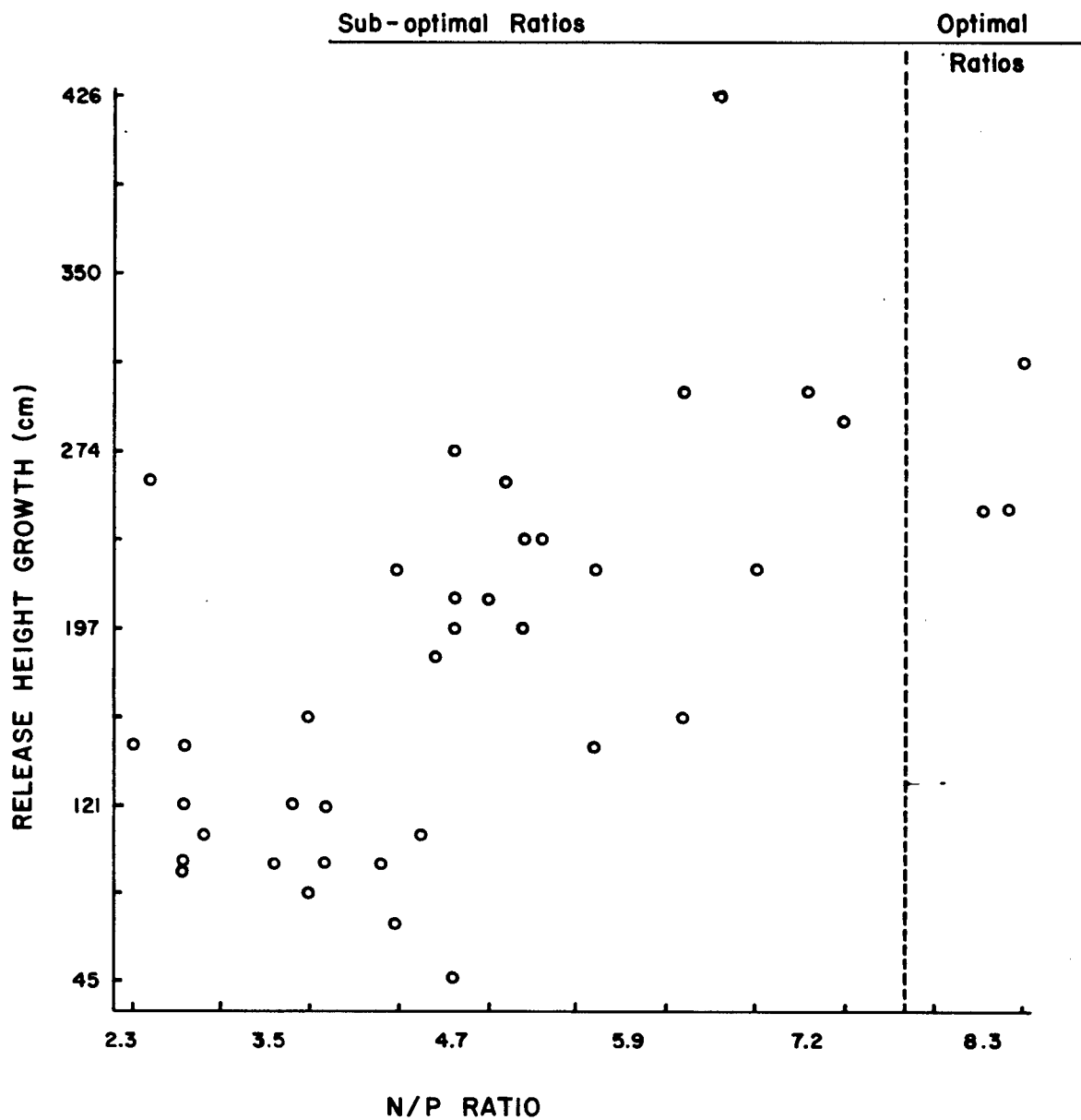


Figure 7. Relationship between N:P ratios in one-year-old amabilis fir foliage and release height growth.



related to the nitrogen status of needles formed the previous year. Total height in his studies was best correlated with nitrogen levels in current foliage.

In tree species with high needle retention, N% in older foliage may better reflect the total tree N reserve and therefore correlate better with tree growth than current or 1-year-old foliage. Additional foliar-tree growth studies are needed to determine the best sampling age for determining the nitrogen status of *amabilis* fir.

Magnesium concentrations were the second most significant variable in the regression equations. Current and 1-year-old foliar Mg explained an additional 21% and 15% of the variation in current and release height growth, respectively. The regression coefficient for 1-year-old foliar Mg was negative, whereas, the coefficient for current Mg was positive in the multiple regressions. This difference in sign was not an artifact of the analysis. In simple regressions, current foliar Mg% was positively, and 1-year-old foliar Mg% was negatively related to height growth. Since Mg contents (mg per 100 needles) were higher in both foliage age classes of well grown trees compared to poorly grown trees, the negative relationship between foliar Mg in 1-year-old needles and height growth may due to accumulation in 1-year-old foliage of slower growing trees. Mg concentrations do not vary systematically with needle age (Schwab 1979) or with increasing nitrogen supply (Ingestad 1979). Until more is known about tree physiology and ion interactions, interpretation of foliar Mg data will remain difficult.

In experimental field trials testing the effect of nitrogen and potassium fertilizers on advance *amabilis* fir growth, Gallagher (1964)

noted that height growth decreased and needle chlorosis increased when the trees were fertilized only with potassium. High K concentrations alone did not seem to be injurious to tree growth since potassium concentrations were .87%, 1.07% and .88% respectively for control, nitrogen-fertilized trees, and potassium-fertilized trees. Trees fertilized with both nitrogen and potassium responded as well to fertilizations as nitrogen-fertilized trees. Gallagher (1964) hypothesized that potassium may interfere with calcium uptake (which he did not measure) in nitrogen-deficient trees fertilized with potassium. It is possible it also interfered with Mg uptake.

In this study, Mg content (mg/100 needles) was positively related to N concentrations but negatively related to K concentrations (Figure 9), suggesting a negative effect of K concentrations on Mg uptake. In a greenhouse study, Drake and Scarseth (1939) found that high levels of K caused chlorosis on a variety of agricultural crops. At the same time, Mg uptake, and to a lesser extent Ca uptake, was reduced.

Current calcium levels were positively correlated with current height growth even though mean values for both well and poorly grown trees were within the adequate range reported for many conifers. Foliar calcium levels optimum for height growth in juvenile amabilis fir may be higher than those of other conifer species or those of mature amabilis fir. The positive correlation between foliar calcium and height growth might also be due to interactions between calcium levels in the rooting zone and nitrogen mineralization or micronutrient availability.

In field and experimental trials with red fir seedlings, Powers (1980a) reported that poor growth and chlorosis of fir seedlings on many



sites were associated with high concentrations of foliar manganese (>300 ppm) and low concentrations of calcium (<.3%). Powers suggested that the concentrations of manganese in litter from mature stands, as reported by Vallee (1967), might adversely affect fir seedlings. Mature red fir foliage contained higher levels of Mn (averaging 1174 ppm Mn), which suggested to Powers that Mn tolerance increased as the tree aged. In a field trial which tested a variety of fertilizers, Powers<sup>8</sup> found that all treatments which added nitrogen increased red fir seedling height growth significantly. The only other nutrient which seemed to positively increase growth was calcium. Adding lime or promoting seedling growth with nitrogen seemed to ameliorate manganese toxicity.

Although it was possible to relate needle weights and height growth in a statistically significant manner to nitrogen concentrations, a causal relationship between height growth and nitrogen or other nutrients cannot be assumed, regardless of the degree of mathematical correlation. Growth is a function of many factors, not all of which were measured in this study. One of these unknown factors might cause growth and nitrogen concentrations to increase or decrease simultaneously, resulting in a statistically significant, positive but indirect mathematical relationship. Only a fertilizer trial will provide conclusive proof that nitrogen is limiting growth. The time needed to establish and evaluate a field trial was beyond the scope of this thesis.

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<sup>8</sup>Unpublished data on file at Pacific Southwest Forest and Range Experiment Station, Redding, California.

However, two fertilizer trials had earlier been established in stands of amabilis fir exhibiting declining height growth. In both trials, nitrogen fertilizer improved height growth.

The first of these fertilizer trials was established by Gallagher (1964) on Blue Mountain (Washington State, U.S.A.) in amabilis fir regeneration which was exhibiting poor growth. Annual precipitation (2500 mm) was adequate for good amabilis fir growth. Gallagher applied nitrogen and potassium fertilizers, alone and combined. Height growth was significantly increased by all fertilizers containing nitrogen. Nitrogen levels in current foliage of control trees were between .92 and 1.22%; much higher than those reported in this study. The maximum foliar nitrogen level recorded in the nitrogen-fertilized trees was 1.34%. A linear regression analysis ( $n = 8$ ) by Gallagher (1964) described a positive relationship between foliar nitrogen concentrations in current and 1-year-old foliage and current height growth ( $r = .80$  and  $.79$ , respectively). He concluded that foliar nitrogen concentrations were a good indicator of tree growth potential.

The second fertilizer trial was a pilot trial established by Crown Zellerbach at a location close to my study areas on a site which was similar in elevation, aspect, slope, and stand history except that the old growth had been clearcut approximately 10 years earlier. The trees in the fertilizer trial had released well for 3 to 7 years and then height growth had steadily declined for 10 years or more. This stand was spaced in 1974. A small control area was left untreated. In 1976, part of the spaced area was hand fertilized with urea at the rate of 224

kg N/ha. One plot was established in each of the treatment (spaced, spaced + fertilized) and control areas of the stand.

Height growth increased dramatically when the trees were fertilized with nitrogen (Figure 10). The height data for this trial were analyzed by covariance with the combined 1976-1977 height growth used as the response variable. Since 1975 height increment was significantly correlated ( $r = .47$ ;  $p < .01$ ) with the 1976-1977 height growth, 1975 height growth was used as the covariate. The adjusted means (49.7, 39.3, and 63.9 cm, respectively) for the control, spaced 1974, and spaced 1974 + fertilized 1976 plots were compared by t-tests. There was no significant difference between means of control and spaced-only plots. Mean 1976-1977 height of the fertilized trees was significantly greater ( $p < .01$ ) than that of either the control or spaced trees. Mean height in the spaced and fertilized plot was 63% greater than the mean height of the spaced trees and 29% greater than that of control trees (Figure 10).

These data, which were collected on a similar site to the present study site, suggest that nitrogen deficiency is likely a major factor in the stagnation of the poorly grown trees after an initial good release period.

Cameron (1979) analyzed N and P concentrations in the spaced area of this pilot trial and Briggs (1979) compared foliar N and P concentrations and contents in the fertilized trees with trees that were only spaced (Table 4). Since foliar nitrogen concentrations reported by them were similar or higher than those reported in this study for the poorly grown trees, one would expect the study site trees to respond well to fertilization.

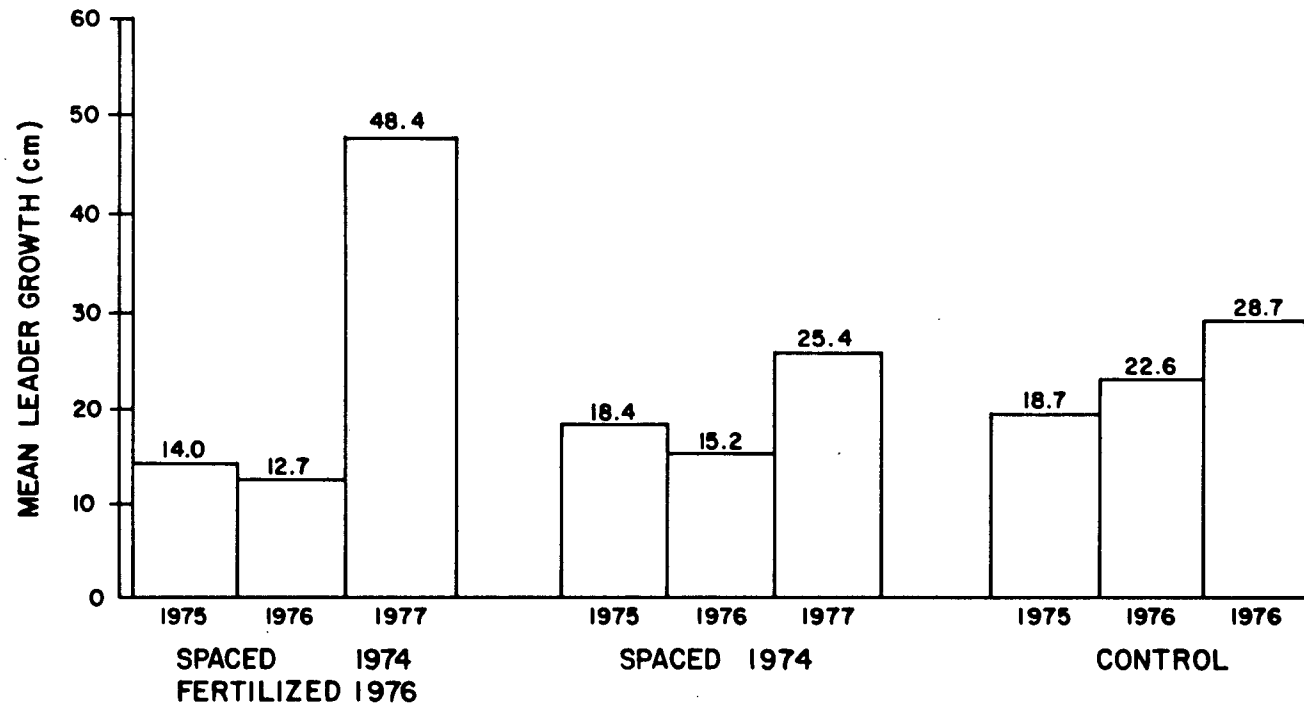


Figure 10. Results of Crown Zellerbach's pilot fertilizer trial (from Crown Zellerbach 1978).

Fall foliar nutrient concentrations explained at most 75% of the variation in height growth at my research site. This relationship might have been improved by different sampling procedures:

1. Leyton (1958) reported that the best mathematical relationships between height growth and foliar nitrogen concentrations were obtained by sampling foliage from the leader or top branch whorl.
2. New shoot production in amabilis fir is dependent to some extent on internal reserves of nutrients. Turner et al. (1976) estimated that 54% of the nitrogen required for new growth in mature amabilis fir was translocated from older tissue. The remainder was supplied by current root uptake. Although foliar nitrogen levels in top whorl foliage is a good indicator of the nutrient status of a tree, it may not be linearly related to the total nitrogen reserves in a tree with many years of needle retention. Miller et al. (1976) reported a second order polynomial relationship between top whorl nitrogen concentrations and the total N reserves of Corsican pine. Therefore, N% in upper crown foliage may not adequately reflect the size of the internal nitrogen reserve which in addition to root uptake determines the potential for new shoot production.

Height growth may be more closely related to foliar nitrogen content than nitrogen concentrations since the former parameter would likely reflect the size of internal nitrogen reserves more accurately. However, the use of nutrient content data as an independent variable in correlation or regression

analyses with a growth parameter as the dependent variable is questionable although statistically valid because the content data includes a measure of growth (the weight of 100 needles) and is therefore not strictly independent of other growth parameters (Tamm 1964). In this study, height and needle weights are highly, positively correlated, preventing the use of nitrogen content data in correlation analyses.

3. Foliar nitrogen levels measured during the growing season may be more positively related to height growth than dormant season levels. This possibility is examined in the next chapter.

### 3. Seasonal Trends in Foliar N and P

Analysis of these data are complicated by a significant interaction between the sampling date and foliar N and P concentrations for individual trees. For example, the foliar N values in 1-year-old needles of 10 poorly grown trees are graphed in Figure 11. Not all trees show the same trend in foliar N during the growing season.

Foliar N and P concentrations of paired trees were not significantly different at the fall sampling date (paired t-tests,  $p < .05$ ). However, this may not have been the case at all sampling dates during the growing season because of tree-to-tree variation in patterns of foliar N and P changes from May to September. Therefore, two sets of N and P values are plotted in Figures 12 and 13. The first set ( $\blacktriangle$  or  $\bullet$ ) represents data from first sampling date in each month; the second set ( $\triangle$  or  $\circ$ ) represents data from the second sampling date in each month.

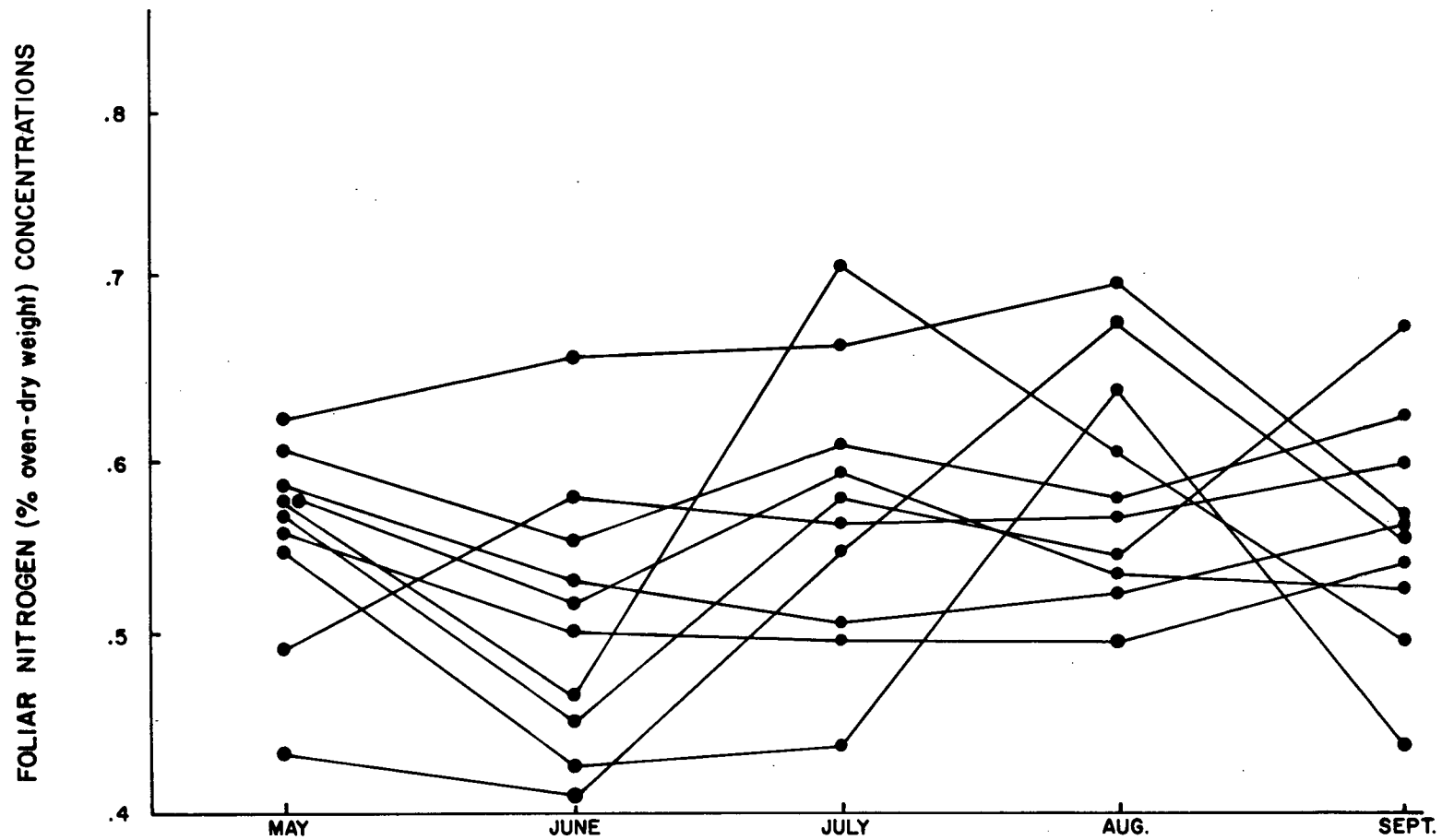


Figure 11. Tree-to-tree variation in May to September nitrogen concentrations of 1-year-old foliage from 10 poorly grown trees sampled early each month.

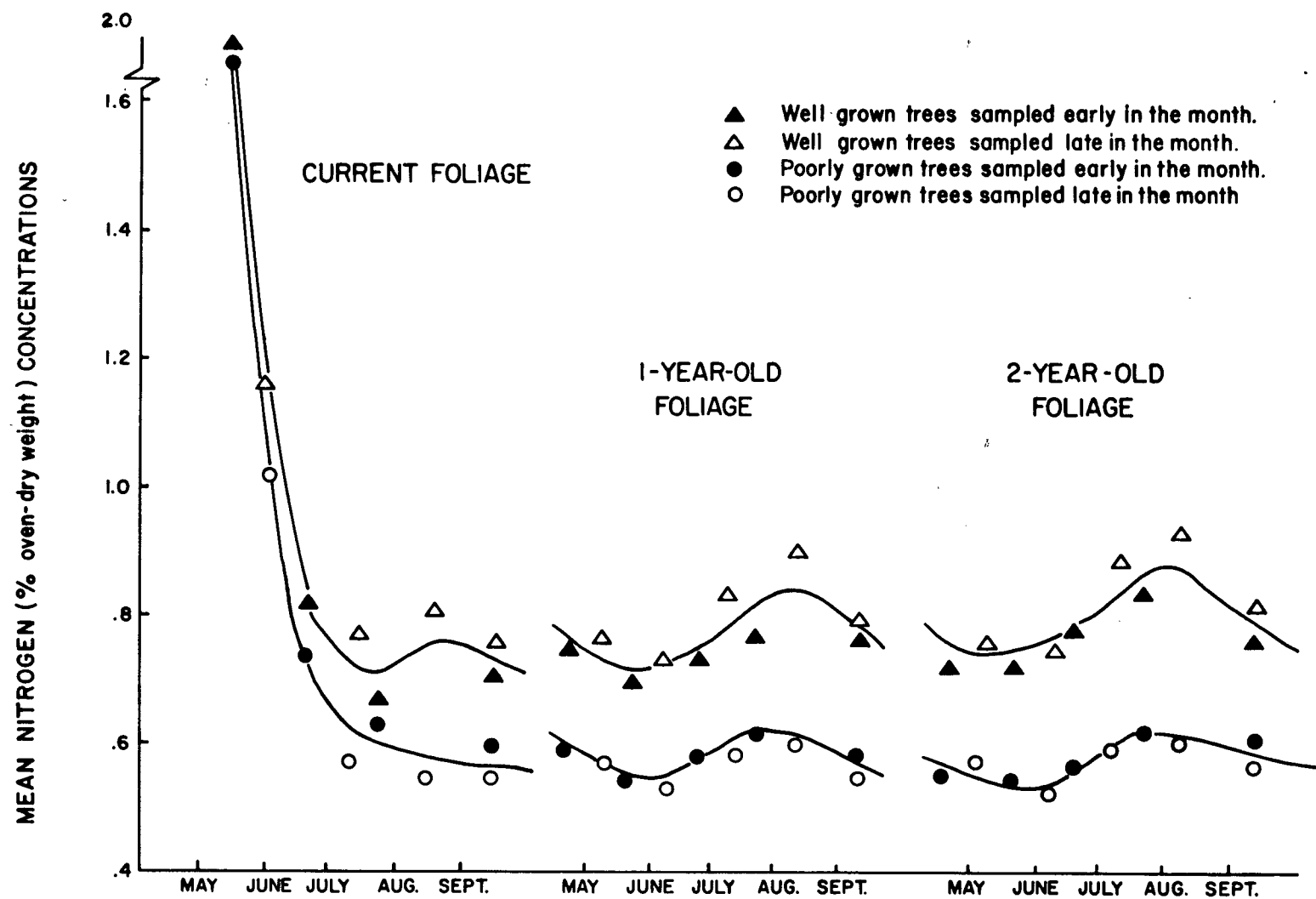


Figure 12. Mean N% in current, 1-year-old, and 2-year-old foliage from May to September.

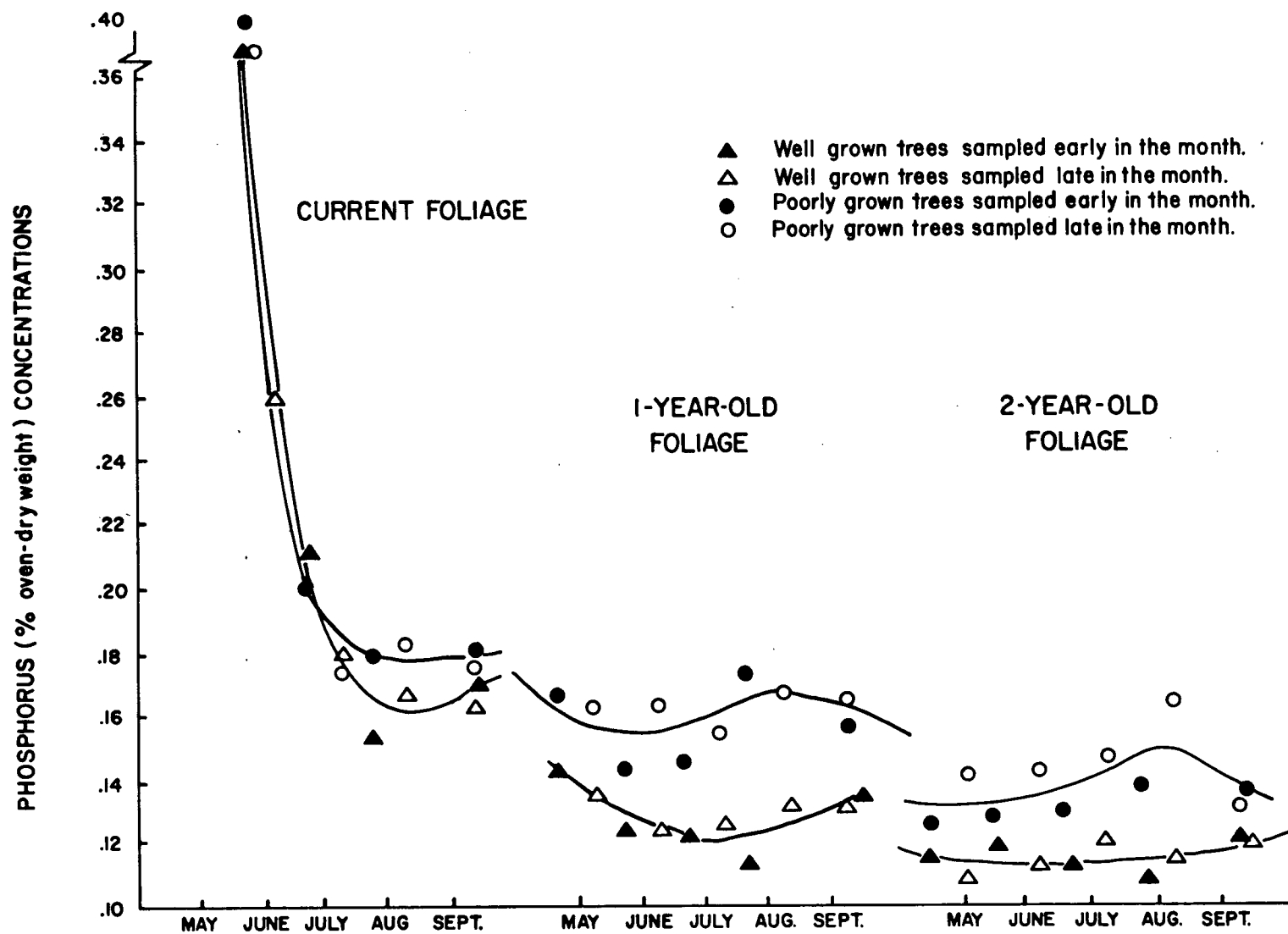


Figure 13. Mean P% in current, 1-year-old, and 2-year-old foliage from May to September.

A line was interpolated through all the data points. Changes in foliar concentrations during the growing season were tested for significance by paired t-tests only for the same trees sampled in different months.

Mean nitrogen concentration in current foliage dropped rapidly from about 2.0% to between .6% and .8% from June to August as the new foliage expanded. There was little seasonal variation in nitrogen concentrations of 1 and 2-year-old foliage. Mean N concentrations in 1 and 2-year-old foliage from poorly grown trees ranged from .52% to .62%. Mean N concentrations ranged from .68 to .90% in 1-year-old foliage and from .71% to .92% in 2-year-old foliage of well grown trees.

Seasonal variations in the nitrogen concentrations of 1 and 2-year-old needles were similar. Nitrogen concentrations dropped during May and June; rose during July and August; and then decreased again in late August to September (Figure 8). The initial decrease coincided with the most active period of new foliage production and shoot growth; the mid-summer peak with hot, dry weather; and the late summer decline with moister, cooler weather. The late summer decline may reflect movement of nitrogen into newly formed buds.

The decrease in foliar N during May and June was statistically significant ( $p < .05$ ) for both age classes of foliage from poorly grown trees and for 1-year-old foliage from well grown trees. The increase in late July and August was statistically significant for all groups. The coefficient of variation for foliar N concentrations at any one sampling data ranged from 7 to 17% for poorly grown trees and from 14 to 21% for well grown trees.

A more dramatic decline in nitrogen levels in 1-year-old foliage had been expected during May and June due to translocation of nutrients from old needles to new foliage biomass. Krueger (1967), Waring and Youngberg (1972) reported sharp decreases in nitrogen concentrations of 1-year-old needles during this active period of growth.

There are two possible reasons for the relatively stable foliar nitrogen concentrations in 1-year-old foliage during the period of active shoot growth. First, the levels of nitrogen were so low that much of the nitrogen was probably immobile (structurally bound) and not available for transport to new tissues. Gessel (1962) felt that when foliar nitrogen levels dropped to .6% in Douglas fir most of the nitrogen would be structurally bound. The lowest levels recorded by Schwab (1979) for 15 to 17-year-old amabilis fir needles ranged from .6 to .7%.

Secondly, the Douglas-fir seedlings in Krueger's study and the low elevation Douglas-fir in Waring and Youngberg's study probably had fewer years of needle retention than amabilis fir. Perhaps, in tree species with higher needle retention, translocation is less dramatic in 1-year-old needles because nutrients are being withdrawn from a greater number of needle ages. In Eastern Canada, Gordon (1975) reported low seasonal variation in nitrogen concentrations of 1-year-old foliage collected from three species of spruce, all of which had needle retention of 6 to 7 years, with some retaining needles up to 14 years. He found that there was a gradual removal of nutrients from all needle age classes.

In poorly grown trees, nitrogen concentrations were lowest at two critical periods during the growing season; at bud break and during bud

initiation in late summer. When modelling growth response to nitrogen fertilizer, Fagerstrom and Lohm (1973) found it useful to separate foliar nitrogen into two pools; one consisting of mobile or potentially mobile nitrogen and the other structurally bound nitrogen. They proposed that the level of mobile nitrogen at the time of bud formation sets an upper limit to the production of new foliage the following year in nitrogen-deficient determinate tree species. Whether this maximum potential growth was realized depended upon the levels of mobile nitrogen available at the time of budburst and needle elongation.

The lowest nitrogen concentration measured in this study was .42%. At this concentration, most of the nitrogen is probably structurally bound. The mean nitrogen concentration in poorly grown, 1-year-old foliage at the time of bud break was only .57% compared to .75% in well grown trees. If .42% is subtracted from both means, and the remainder considered an estimate of the pool of mobile nitrogen, this pool in well grown trees based on concentration alone was 2.2 times larger than that of poor trees. A similar calculation for the late July to early August period also showed a 2.4 fold greater mobile N pool in well grown trees.

Phosphorus concentrations during the growing season exhibited different trends in 1-year-old foliage of poor and well grown trees (Figure 13). The greatest difference occurred in the August samples. Phosphorus concentrations rose significantly in foliage from poor trees but remained constant in that of well grown trees. This might be explained by continuing P uptake during the summer which was diluted by continuous needle growth in well grown trees but not in poorly grown trees. Height growth terminated earlier in poorly grown trees than well

grown trees. Seasonal changes in 2-year-old foliage were less than in 1-year-old foliage. Current P concentrations dropped rapidly during the growing season and followed a similar pattern in both well and poorly grown trees.

4. The Relationship Between Height Growth and Foliar N, P, N:P  
Measured during May to September

These relationships were analyzed by stepwise multiple linear regression. Because of the design of the sampling, two sets of analyses were conducted: one with the 20 trees sampled in the first half of each month and the second with the 20 trees sampled in the last half of each month (Table 8).

The first variables selected in both analyses were N:P ratios. In 3 out of 4 cases, the August N:P ratio (in 1- or 2-year-old foliage) was chosen. This N:P ratio explained 15 to 20% more of the variation in height growth than fall N:P ratios.

Because the data were split for analyses it was not possible to pinpoint the best sampling date. However, July and August values were chosen over May, June and September values by the stepwise regression program.

In 3 out of 4 cases, the inclusion of more than one N:P ratio increased the  $R^2$  value (percentage of height growth explained).

These data suggest that foliar sampling during the growing season may improve the relationship between foliar nutrients and growth. Seasonal variation in 1 and 2-year-old foliage was low especially in

Table 8. Stepwise regression with growing season N, P and N:P data measured on current, 1- and 2-year-old foliage

Dependent variable	Step	R <sup>2</sup> *	SE**	Regressor variables***
<u>Twenty Trees Sampled in First Half of Each Month</u>				
<u>Current height</u>	1	.65	14.2	N:P August (1-year-old foliage)
	2	.65	12.4	N:P July (current foliage)
	3	.72	11.4	N:P August (current foliage)
	4	.83	9.4	N July (2-year-old foliage)
	5	.87	8.4	N:P August (2-year-old foliage)
	6	.91	7.1	N August (2-year-old foliage)
<u>Release height</u>	1	.62	42.8	N:P August (2-year-old foliage)
	2	.74	38.7	N:P August (current foliage)
	3	.83	30.2	N:P July (current foliage)
	4	.91	23.7	N:P June (1-year-old foliage)
<u>Twenty Trees Sampled in Second Half of Each Month</u>				
<u>Current height</u>	1	.71	16.2	N:P June (1-year-old foliage)
	2	.84	11.3	N:P August (2-year-old foliage)
	3	.89	9.7	N July (current foliage)
<u>Release height</u>	1	.62	62.2	N:P August (2-year-old foliage)

\* Coefficient of determination.

\*\* Standard error.

\*\*\*All significant at  $p < .05$ .

poorly grown trees. Therefore, it may be possible to sample these 2 age classes of foliage over a period of at least 2 weeks without introducing significant seasonal variation. Current foliage values do change rapidly and significant variation could be introduced by sampling over a period of a week from May to the end of July.

The data are limited to one year and to one site. Seasonal variation may be greater in other years or sites. Therefore, more studies are needed before recommending a change in the standard practice.

## 5. The Relationship Between Humus Nutrient Status and Amabilis Fir Growth

### 5.1 Nitrogen and C:N Data

Chemical analysis of humus from beneath well and poorly grown trees supported the hypothesis that nitrogen deficiency was an important determinant of declining tree height growth. At the research site, 80 to 100% of the amabilis fir fine feeder roots appeared to be located mainly in a thick, felty mat of humus with varying proportions of decaying wood. Mean total nitrogen concentrations in the humus of well grown and poorly grown tree microsites were .94 and .83% respectively. C:N ratios were 53.7 and 65.6 for well and poorly grown tree microsites respectively (Table 9). Total humus nitrogen % was significantly higher ( $p < .05$ ) and the C:N ratio was significantly lower ( $p < .05$ ) for well grown tree microsites. pH and % total P were similar beneath both classes of trees.

Table 9. Comparison of mean pH, macronutrients and C:N ratios in humus collected from well and poorly grown tree microsites.  
(n = 10; standard deviations in brackets)

	pH	C:N	Total N (% oven-dry weight)	Total P (% oven-dry weight)	Exchangeable cations (me/100 g)		
					Ca	Mg	K
Well grown	3.97	53.7	.94	.101	33.4	2.85	2.73
tree microsites	(.20)	(9.24)	(.13)	(.013)	(17.6)	(1.07)	(1.37)
Poorly grown	3.95	65.6	.83	.101	25.7	2.21	3.03
tree microsites	(.14)	(11.2)	(.14)	(.016)	(10.9)	(.68)	(1.52)
	NS	**	**	NS	*	*	NS

\*. Significant difference in means at  $p = .10$

\*\* Significant difference in means at  $p = .05$

Mean % total humus nitrogen under both well and poorly grown trees was lower than the range, 1.02 to 1.77%, reported by Klinka and Lowe (1976) for humus on mesic sites in the CWHb subzone; and at the low end of the ranges reported by Quesnel and Lavkulich (1980) for humus collected from xeric (very rapidly drained), mesic (moderately well drained) and hygric (poorly drained) sites in the CWHb subzone of northern Vancouver Island. In their study, total N varied from .643 to 1.014% ( $\bar{x}$  = .83) on xeric sites, .817 to 1.288% ( $\bar{x}$  = 1.02) on mesic sites, and 1.067 to 1.848% ( $\bar{x}$  = 1.42) on hygric sites.

Mean C:N ratios were higher than those reported by both studies. Klinka and Lowe (1976) found humus C:N ratios ranged from 30.1 to 52.9. Mean humus C:N ratios were 58.3, 47.5, and 29.5 respectively for xeric, mesic, and hygric sites in Quesnel and Lavkulich's study.

High C:N ratios are associated with low nitrogen mineralization rates. A ratio of 25 is considered optimum for decomposition (Bollen 1969). Even though the total N capital of thick humus layers with high C:N ratios is large, nitrogen availability is likely to be low leading to competition between decomposers and trees for the available N. Immobilization of essential nutrients by decomposers may exceed mineralization rates in mor humus. In a study of nitrogen availability in a mature *amabilis* fir stand, Grier<sup>9</sup> found that significant decreases in total mineralizable nitrogen occurred in trenched plots immediately after litterfall. This decrease was attributed to the high

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<sup>9</sup>Pers. comm. from Dr. C. Grier, University of Washington, January, 1981.

C:N ratio of amabilis needle litter and uptake of mineralizable N by decomposers.

No significant linear relationships (at  $p < .05$ ) between humus N% or C:N ratio and current foliar nitrogen per cent were apparent in a correlation analysis of the data. However, the simple correlation coefficient between C:N ratio and foliar N was higher ( $r = .40$ ) than that between humus N and foliar N ( $r = .28$ ). Evers (1967) found that carbon/nutrient ratios, in particular C:N and C:P, in the top 4 cm of soil (in his study, mainly F and H horizons) were better related to tree growth than any other chemical analyses.

If a better measure of nitrogen availability had been obtained either by sampling more soil horizons or by using an anaerobic incubation for mineralizable nitrogen (Powers 1980b), the relationship between humus and foliar N might have been significant.

## 5.2 Ca, Mg, and K Data

The foliar concentration study suggested that magnesium (Mg) and calcium (Ca) nutrition may be below optimum for height growth. Exchangeable Ca and Mg levels in humus under well grown trees were significantly greater ( $p < .10$ ) than those in humus under poorly grown trees.

Exchangeable K and Ca levels for all microsites were within the upper range of values reported by Williams and Dyrness (1967) for forest floors (LFH) in the Mt. Baker and Mt. Rainier Ecological Provinces in Washington and by Quesnel and Lavkulich (1980) for humus (H) collected

from rapidly drained, well drained, and poorly drained soils in the west subzone of the Coastal Western Hemlock Biogeoclimatic Zone.

Exchangeable Mg data were at the low range of values reported in these two studies. Williams and Dyrness (1967) found exchangeable Mg ranged from 3.3 to 7.0 me/100 g ( $\bar{x}$  = 4.8). Exchangeable Mg levels ranged from 4.58 to 13.36 me/100 g ( $\bar{x}$  = 8.33), 8.60 to 22.33 ( $\bar{x}$  = 12.35), and 1.68 to 14.07 ( $\bar{x}$  = 6.79) me/100 g, respectively for (rapidly, well, and poorly drained) sites in Quesnel and Lavkulich's study.

The most important factor influencing nutrient status of the rooting medium on the study site was the quantity of rotting wood incorporated into the humus. However, the type of rotting wood may have also been important. Minore (1972) compared nutrient levels of hemlock duff and rotting wood of three tree species (Table 10) in the field for a seedbed study. Hemlock duff had a much higher nutrient content than any type of rotting wood. Rotting wood of Douglas-fir and western hemlock differed in total cation content. Minore did not state whether these differences were significant. However, his data suggest that some microsite variation in cation status of the rooting medium may be due to the type of rotting wood (Douglas-fir or western hemlock) on a site.

Although foliar Ca and Mg explained a significant portion of variation in height growth, there were no significant relationships between exchangeable Ca or Mg in the humus samples and foliar Ca and Mg or height growth. Exchangeable cations were extracted by  $\text{NH}_4\text{OAc}$  at pH 7.0. A better relationship between foliar cations and humus cations might have resulted from extracting the humus cations with  $\text{NaOAc}$  at

Table 10. Chemical analysis of seedbed materials (from Minore 1972)

Seedbed	P			K		Total <sup>3</sup> Ca	Total <sup>6</sup> Mg
	Total <sup>1</sup> N	Total <sup>2</sup>	Extractable <sup>3</sup>	Total <sup>3</sup>	Exchangeable <sup>3</sup>		
	%	----- ppm -----					
Hemlock duff	1.096	1,230	325	635	614	1,750	2,325
Douglas-fir wood	.104	72	45	210	210	700	275
Sitka spruce wood	.135	129	45	245	215	940	530
Hemlock wood	.98	72	50	140	108	1,220	550

<sup>1</sup>Kjeldahl.

<sup>2</sup>Colorimetric, after perchloric acid oxidation.

<sup>3</sup>Sodium bicarbonate extraction.

<sup>4</sup>Flame emission after perchloric acid oxidation.

<sup>5</sup>Ammonium acetate extraction.

<sup>6</sup>Atomic absorption after perchloric acid oxidation.

pH 4.8. Klinka et al. (1980) reported that the quantities of cations extracted by this latter method correlated better with forest productivity. They also reported that cation quantities extracted from the whole soil profile (mineral soil + LFH) correlated better with tree growth than those from the LFH alone.

Whether the difference in exchangeable Ca or Mg between microsites is biologically as well as statistically significant is difficult to determine because adequate levels of soil nutrients for different tree species have not been established.

### 5.3 Proposed Relationship Between Variable Height Growth and Nutrition

Accumulations of humus can lead to site degradation in cool, temperate forests with mor humus development (Roberge et al., 1968; Miller et al., 1976). As a forest stand matures, an increasing proportion of the site nutrient supply is immobilized in tree tissue and slowly decomposing organic material. Decomposition may be slow due to low temperatures, low nitrogen or phosphorus availability or to the formation of stable polyphenol-protein complexes which resist degradation (Benoit et al., 1968).

Individual nutrients are released from fresh conifer litter at various rates. Water-soluble cations are released rapidly compared to organically bound nutrients. De Catanzaro (1979) found that nutrients were released from conifer litter in the following order:  $\text{Ca} > \text{Mg} > \text{K} > \text{P} > \text{N}$ . Therefore, N and P are the nutrients most likely to become limiting when decomposition is slow. P availability to trees is enhanced by

mycorrhizae but N availability is more closely associated with the decomposition rate.

Advance regeneration becomes established in the accumulation of organic matter developed by the preceding old growth forest. If the site has developed a thick layer of slowly decomposing humus, growth of the advance regeneration may be limited by low levels of mineralizable nitrogen in the rooting zone.

There is evidence that nitrogen availability is temporarily increased when mor humus sites are clearcut and the forest floor disturbed due to both increased surface temperatures and moisture (Likens et al. 1970; Dominsky 1971) and decreased competition between plant roots and decomposers (Gadgil and Gadgil 1975). Lutz and Chandler (1946) stated that clearcutting often improved nutrient conditions in mor humus because decomposition is increased, acidity is reduced and nitrification is promoted. In a study of clearcutting effects on nutrient availability and decomposition rates, Page (1974) discovered that the thickness of the LFH layer on mor humus decreased 1.3 to 3.8 cm after clearcutting on gleysols, brunisols, and podzols in Eastern Canada; pH increased .5 of a unit; and C:N ratios decreased as much as 1.5 units at the 2.5 cm depth on the forest floor. These changes lasted for variable periods and were greater on podzols than brunisols. After clearcutting of old growth amabilis fir-western hemlock forests, there is a 30 to 35% decrease in the forest floor of mesic sites for at least 8 to 10 years<sup>10</sup>.

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<sup>10</sup>Pers. comm. from Wayne Martin, Graduate Student, University of British Columbia, January, 1982.

A temporary increase in decomposition and nitrogen availability is most likely the reason for the initially good response exhibited by all advance regeneration on the research site. The following is a proposed scenario for the release growth of advance regeneration established on a thick forest floor accumulation of varying composition:

- (i) advance regeneration accumulates a pool of mobile nitrogen in all needle ages over and above that required for immediate growth during the temporary period of increased nitrogen availability after clearcutting;
- (ii) the amount of nitrogen accumulated is proportional to the size of the root and crown system of advance regeneration at or shortly after the time of logging;
- (iii) this pool of mobile nitrogen, like a chemical nitrogen fertilizer application, sustains growth on sites where low decomposition prevails;
- (iv) once all this pool of additional nitrogen has been utilized for new growth, height growth begins to decline if the advance regeneration is rooted mainly in slowly decomposing humus;
- (v) advance regeneration established on microsites with greater supplies of available nitrogen continue to grow in height for a longer period of time.

Miller et al. (1976) studied internal nitrogen cycling and growth of Corsican pine on an N deficient site. They expanded Fagerstrom and Lohm's (1977) concept of separate foliar nitrogen pools by separating the mobile pool into two levels: the first, consisting of recent root

or foliar uptake; and the second, of potentially mobile internal reserves accumulated during previous seasons. When tree nutrition becomes sub-optimal, and level 1 nutrients are insufficient to support growth, Miller et al. (1976) found the level 2 nutrients were gradually mobilized, often at the expense of efficient or continued functioning of the older tree tissue. This withdrawal eventually led to a decline in tree growth.

## 6. Examination of Alternate Hypotheses to Explain Variable Height Growth

Foliar nutrient concentrations did not account for all the variability in height growth within a site. Therefore, alternative hypotheses were examined to determine if any explained a significant portion of height growth differences. Mean and standard deviations of parameters studied are summarized in Table 11.

### 6.1 Age and Height at Release

Within the range of ages and heights at release measured there was no significant relationship between height or age at release and release height growth. These results agree with those of Herring and Etheridge (1976). Ferguson and Adams (1979) reported that age of release influenced the degree of release response in grand fir. Younger trees responded more quickly than older trees (greater than 30 years at the time of release) because older trees were more likely to be infected with Echinodontium tinctorium.

TABLE 11. Comparison of growth parameters between well grown and poorly grown *amabilis* fir (n = 20; standard deviations in brackets)

	Well grown trees		Poorly grown trees	
Mean height at the time of logging	.64	(.41) m	.55	(.25) m
Mean total height 9 years after logging	3.43	(.84) m	2.01	(.37) m
Mean current (1978) height increment	47.8	(14.8) cm	8.3	(5.6) cm
Mean 1978 secondary branch increment in third whorl <sup>1</sup>	8.3	(2.0) cm	4.5	(1.1) cm
Mean 1977-78 diameter increment <sup>2</sup>				
earlywood	5.46	(1.53) mm	2.69	(.62) mm
latewood	2.42	(.70) mm	1.17	(.32) mm
Mean age at the time of logging	52.5	(30.6) yrs	45.0	(23.7) yrs
Mean wt. of 100 oven-dry 1-year-old needles sampled in the fall	699.4	(268.3) mg	433.8	(111.9) mg
Mean wt. of 100 oven-dry current needles sampled in the fall	358.1	(167.0) mg	252.4	(64.7) mg
Estimate of 1-year-old foliar biomass from the third whorl sampling position	3035.1	(1621.7) mg	1116.8	(757.3) mg
Mean needle length <sup>3</sup>				
1-year-old	19.8	(5.2) mm	16.5	(2.1) mm
current	16.3	(4.5) mm	12.1	(1.6) mm

<sup>1</sup>The sampling position is shown in Figure 5.

<sup>2</sup>Measured at breast height.

<sup>3</sup>Needles from mid shoot positions were measured in the fall.

Herring and Etheridge (1976) reported a very low incidence of Echinodontium tinctorium in advance amabilis fir stands although the incidence did increase with the proportion of stems older than 60 years at the time of release.

## 6.2 Degree of Aboveground Competition

Release and current height growth were not significantly related to the competition stress index (number of competing stems within 2 m of the sample tree). Stocking densities expressed as trees per ha ranged from 800 to 8,000 trees per ha. In several other studies, competition has not related significantly to height growth.

In a study of subalpine fir stands with stocking densities ranging from 1,700 to 3,000 trees per hectare, Ivanko (1976) found no statistically significant effect of stocking density on height growth. Baskerville (1966) reached the same conclusion in stands of balsam fir stocked with 1,750 to 7,500 trees per hectare. In Gallagher's (1964) study of advance amabilis fir regeneration the density of stock varied from 7,400 to 22,200 trees per ha, but appeared to have little effect on tree height. Hunt<sup>11</sup> attributed some of the erratic height growth at Courtenay to tree competition but emphasized that both open and densely grown trees exhibited poor or erratic height growth.

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<sup>11</sup>Pers. comm. from Dr. A. Hunt, Canadian Forest Service, Victoria, B.C.

Herring and Etheridge (1976) reported that release growth in advance amabilis fir regeneration tended to increase with increasing competition on 3 of the 10 coastal B.C. sites which they studied. Differences in competition stress accounted for at most 14% of the variation in height growth. Diameter growth was more strongly correlated with competition stress. Since competition stress influences growth of amabilis fir on some sites, stocking density should be considered when studying the relationship between growth and nutrient data.

### 6.3 Redistribution of Growth

Schmidt<sup>12</sup> observed that some trees with poor height increment exhibited normal diameter increment in the same year. This observation indicated that redistribution of growth from height to diameter increment might be occurring at certain periods in the development of the advance regeneration and could be responsible for periods of poor height growth. It is known that after logging, root and diameter growth accelerates before height growth in advance regeneration. There is a one to two-year delay in height growth release attributed to root expansion, foliar adaption to full sunlight and stem buttressing.

In this study, height and diameter increment were positively correlated ( $r = .66, .90, \text{ and } .90$ , respectively for 1976, 1977, and 1978). There was no evidence of a redistribution of growth between height and

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<sup>12</sup>Pers. comm. from Mr. R. Schmidt, B.C. Ministry of Forests. Letter following a field trip to Tree Farm License No. 2, November, 1976.

diameter. Schmidt's observation may have been in relation to trees with leaders snapped off by squirrels. Some of these trees were slow to recover normal height growth but diameter growth was not affected by loss of the leader.

Needle weights were also positively correlated with height and diameter growth (Table 12). Mean lengths and weights of well grown trees needles were statistically ( $p < .01$ ) significantly higher than those of poorly grown trees. Lengths of midshoot needles averaged 16.3 and 19.8 mm, respectively, for current and 1-year-old foliage of well grown trees; but only 12.1 and 16.5 mm respectively for poorly grown trees. Mean oven-dry weights for 100 current and 100 1-year-old needles were 358.1 and 699.4 mg respectively for well grown trees, and 252.4 and 433.8 mg respectively for poorly grown trees.

Reduced needle length and weight in poorly grown trees strongly suggested that foliage production was much lower than in well grown trees. In a study of balsam fir, Morris (1955) found that average needle length and the needle biomass of a shoot were correlated ( $r = .9$ ). In a study of advance amabilis fir regeneration, Briggs (1979) also reported a highly significant correlation ( $r = .8$ ) between needle length and needle biomass per shoot. Unfortunately, Morris (1951) reported that average needle length was less strongly correlated ( $r = .71$ ) with total annual foliage biomass because of the variable number of shoots produced in any one year.

An estimate of relative foliar biomass production was obtained by oven-drying and weighing all the foliage from the fourth whorl sampling

Table 12. Simple correlation coefficients (r) between needle weight, height, and basal area increment

	Oven-dry weight <sup>1</sup> of 100 1-year- old needles	Oven-dry weight of 100 current needles	Estimate of foliar biomass in fourth whorl sampling position
1978 height increment	.81 <sup>2</sup>	.71	.89
Release height <sup>3</sup>	.73	.63	.89
1977 basal area increment	.53	NS	.68
1978 basal area increment	.64	.52	.82

<sup>1</sup>Needles weighed in the fall.

<sup>2</sup>All correlation coefficients are significant at  $p = .05$ .

<sup>3</sup>Height growth from time of logging to 1978.

position at the end of September (Table 12). This estimate indicated that foliage production in the upper crown was 3 times greater in well grown trees compared to poorly grown trees. The foliar biomass estimate correlated better with height and diameter increments than the weight of 100 oven-dry needles (Table 12).

The positive correlations between needle weight, foliar biomass estimate, height, and diameter increment suggest that whatever factor is limiting height growth affects all aboveground tree growth. The strong correlations between needle weight and height growth prohibits use of nutrient content data (mg nutrient per oven-dry mass of 100 needles) as an independent variable in regressions with growth parameters as dependent variables.

#### 6.4 Genetics

Two observations suggested that ecotypic differences might possibly exist between good and poor trees. Firstly, Hunt<sup>13</sup> noted that the current fall foliage of poor trees was paler than that of well grown trees, suggesting that the poor trees had flushed later. Secondly, prior to the study, Kimmins<sup>14</sup> had observed needle retention of 12 years in trees at 400 to 600 m, which he felt might be unusually high for this elevation. Amabilis fir needle retention near Vancouver and Squamish, B.C. increases with elevation from as little as 6 to 8 years at low elevations (about 400 m) to as high as 24 to 30 years in some

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<sup>13</sup>Pers. comm. Dr. A. Hunt, Canadian Forestry Service, Victoria, B.C.

<sup>14</sup>Pers. comm. Dr. J.P. Kimmins, Faculty of Forestry, U.B.C.

high elevation sites (about 1800 m). If needle retention is a genetically influenced character (this has not yet been established) Kimmins suggested that high needle retention at lower elevations in the study area could reflect the presence of high elevation ecotypes in the low to mid elevation stands. Differences in chilling requirements, respiration, or assimilation rates between the ecotypes might cause between tree variability in height growth. Differences in genetic make-up may also introduce variability in nutrient-height growth relationship as reported by van der Driessche (1973) for Douglas-fir trees of different seed sources.

The needle retention for both well and poorly grown trees on the research site ranged from 9 to 11 years with no significant difference between tree growth and years of needle retention. Schwab (1979) reported 12 year needle retention for amabilis fir growing between 400 and 700 m in several coastal B.C. locations. Therefore, needle retention of study trees was not unusual.

The phenology of 1978 height growth was recorded to determine if a major portion of the height variation could be explained by differences in the time of height growth initiation and termination (Figure 14). Emergence of needles from the bud scales was used as an indication of flushing. Buds in all crown positions of the well grown trees had flushed by May 25th and height growth was evident by May 31st. In poorly grown trees, flushing was not widespread in all crown positions until June 3rd and height growth was not general until June 7th. However, in comparison to the dramatic differences in the rate of shoot elongation, the eight day difference in height growth initiation between

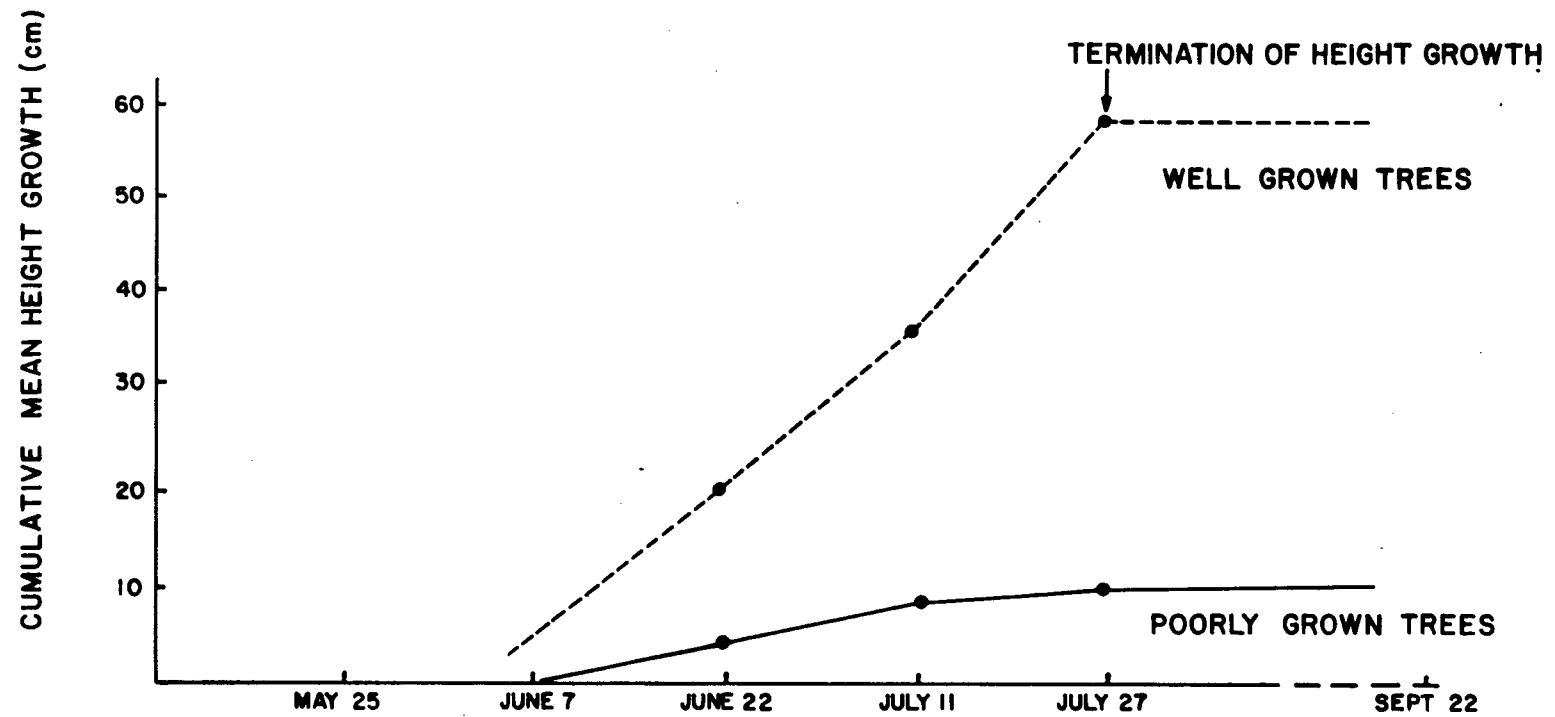


Figure 14. Phenology of current height growth of well and poorly grown trees in 1978.

well and poorly grown trees was a minor contribution to height growth variation. This eight day difference may have been caused by differences in genetic make-up. It seemed more likely, however, that needle and shoot elongation out of the bud scales was weaker in poor trees (giving the appearance of later flushing) due to a nutrient deficiency. Nitrogen fertilized trees in the Crown Zellerbach pilot fertilizer trial flushed and began height growth before unfertilized, thinned trees or control trees. The pale foliage in poorly grown trees observed by Hunt may be inadequate nutrition for normal chlorophyll production or shoot extension. Worrall<sup>15</sup> found no differences in the chilling requirements of *amabilis* fir ecotypes.

Although a mixture of ecotypes might exist in low elevation stands, their existence would be difficult to prove. von Rudloff and Hunt (1977) did not detect any altitudinal differences in foliar chemistry of *amabilis* fir. Parker et al. (1979) found that periderm thickness was the only morphological characteristic which varied with altitude in mature *amabilis* fir. Since needle retention is probably affected by tree age, environment and nutrition, as well as genetics, with our present state of knowledge, it cannot be used as strong evidence for the existence of ecotypes.

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<sup>15</sup>Pers. comm. Dr. Worrall, Faculty of Forestry, U.B.C.

### 6.5 Root Disease

No obvious symptoms of feeder root diseases were evident on trees at the research site<sup>16</sup>. Some amabilis fir in the Courtenay stands were infected with Armillaria mellea. These infections seemed to be secondary infections which were not responsible for the initial slowdown in tree growth. However, there was no conclusive information available to determine if the infections were secondary or primary infections. Funk<sup>17</sup> warned that stagnating amabilis fir would be susceptible to secondary fungal infections. This seemed to be the case in several stagnating stands in the vicinity of the study area.

### 6.6 Micronutrient Toxicity

Concentrations of Fe and Mn in acid soils may reach levels toxic to tree growth. Since other tree species on the study site grew normally, Mn and Fe toxicity was not considered a likely cause of variable height growth in amabilis fir. In future studies of amabilis fir Mn and Fe nutrition would be worthy of investigation in light of Powers' (1980a) findings.

### 6.7 Microsite Differences in Moisture Availability

On sites with suboptimum precipitation for good amabilis fir growth, Klinka (1977a) hypothesized that regeneration may establish more

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<sup>16</sup>Pers. comm. from Dr. G. Wallis, Canadian Forestry Service, Victoria, B.C. after a visit to the research site, May 1978.

<sup>17</sup>Pers. comm. from Dr. A. Hunt, Canadian Forest Service, Victoria, November 1977.

successfully on microsites with a high proportion of decaying wood in the rooting zone rather than on mineral soil or shallow humus microsites. The decaying wood microsites would tend to have sufficient moisture for growth but low nutrient availability. Moisture stress would affect growth and/or nutrient availability on other microsites.

There was insufficient time and equipment to monitor differences in water availability at well grown and poorly grown tree microsites during the growing season. As an alternative, foliar and FH chemistry were measured at three mesic (well drained) and three xeric (rapidly drained) sites similar in elevation and aspect to the study area. The sites had been logged approximately 15 years ago.

Two forest floor samples were collected at each site and separated into the F and H components for chemical analysis. Mean values for the xeric and mesic sites are summarized in Table 13. Significant differences between mesic and xeric site FH chemistry were found for the C:N ratios in both horizons and total N% in F horizons (t-tests;  $p < .10$ ). Mean C:N ratios in xeric F and H horizons, 55.2 and 80.8, respectively, were almost double those of mesic sites. Mean total N% for both F and H horizons were lower on the xeric sites. There were no significant differences in total P or exchangeable cations between mesic and xeric sites.

Current and 1-year-old fall foliage was sampled from 10 *amabilis* fir at each site (Table 14). There were no significant differences between the foliar P, Ca, Mg or K concentrations of xeric and mesic site *amabilis* fir. However, mean N concentrations were significantly higher ( $p < .05$ ) in mesic site trees. Nitrogen concentrations were respectively

Table 13. Mean depth (cm), total N and P (% oven-dry weight), C:N ratio, and exchangeable Ca, Mg, and K (me/100 g) in the FH horizons of 3 xeric and 3 mesic sites (n = 6; standard deviations in brackets)

	xeric sites				Mesic sites			
	F		H		F		H	
Depth	3.8	(3.7)	9.0	(8.6)	2.8	(1.5)	16.2	(9.6)
Total N	1.13	(0.51)	0.72	(0.28)	1.70	(0.20)	0.90	(0.10)
Total P	0.12	(0.06)	0.08	(0.04)	0.14	(0.02)	0.07	(0.01)
C:N	55.2	(38.4)	80.8	(54.3)	26.4	(2.5)	46.8	(11.8)
Ca	26.5	(11.8)	17.3	(7.9)	28.3	(11.3)	21.0	(7.2)
Mg	3.7	(1.2)	3.7	(0.8)	4.7	(1.6)	4.2	(1.9)
K	3.0	(2.2)	1.8	(1.3)	2.7	(1.8)	1.8	(1.70)

Table 14. Mean needle weight (mg per 100 needles) and nutrient concentration (% oven-dry weight) in fall foliage of amabilis fir on 3 xeric and 3 mesic sites (n = 6; standard deviations in brackets)

	Mesic site trees <sup>1</sup>		Xeric site trees <sup>1</sup>	
	Current foliage	1-year-old foliage	Current foliage	1-year-old foliage
N	.98 <sup>2</sup> (.15)	1.14 (.28)	.84 (.10)	.86 (.10)
P	.17 (.02)	.13 (.02)	.18 (.03)	.14 (.02)
Ca	.35 (.07)	.64 (.12)	.31 (.07)	.57 (.08)
Mg	.08 (.01)	.08 (.01)	.08 (.01)	.08 (.02)
K	.67 (.15)	.56 (.09)	.61 (.15)	.54 (.12)
Mean needle weight	802.00 <sup>3</sup>	998.00	761	976

<sup>1</sup>Trees that exhibited best height growth for the sites.

<sup>2</sup>Mean of 30 trees.

<sup>3</sup>No sample variation was calculated.

1.32 and 1.19 times greater in 1-year-old and current foliage of mesic site trees. Mean needle weights of mesic site trees, however, were only 1.03 and 1.05 times greater. These data suggest that nitrogen availability or uptake was reduced proportionately more than dry matter production on the xeric site. The significantly higher C:N ratios in the FH horizons of the 3 xeric sites suggests that low nitrogen availability is a major factor limiting nitrogen uptake. The xeric sites had a higher proportion of decaying wood in the FH horizons.

These results provide some support for Klinka's (1977a) hypothesis. However, much more detailed study is required to fully assess the impact of moisture stress in growth and nitrogen nutrition of *amabilis* fir. Of all the non-nutritional factors examined, microsite differences in water availability seem to have the greatest potential to influence foliar nitrogen-tree growth relationships.

## SUMMARY AND CONCLUSIONS

Foliar N and Mg concentrations in both well and poorly grown amabilis fir regeneration were below levels considered adequate for many conifer species. Nutrient ratios were comparable to those calculated for coastal Douglas-fir and amabilis fir by Beaton et al. 1965 and Schwab 1979 but not to Ingestad's proportions.

Height growth was significantly related to fall foliar chemistry in multiple regression equations. Sixty-four per cent of the variation in release height growth was accounted for by 4 fall foliar values: N:P ratio in 2-year-old foliage, Mg% in current and 1-year-old foliage, and P% in current foliage. Seventy-five per cent of the current height growth was explained by the N:P ratio in 2-year-old foliage, Mg% in 1-year-old foliage, and Ca% in current foliage. Nitrogen concentrations alone explained 44 and 45% of the current and release height growth variability, respectively. N:P ratios seemed to be a more sensitive indicator of nitrogen status than N concentrations alone because of growth dilution of P content in well grown trees and P accumulation relative to growth in poorly grown trees. Nitrogen concentrations in 2-year-old foliage correlated more positively with release height growth than current or 1-year-old foliar N. Current height growth was most significantly related to nitrogen concentrations in current foliage.

Although mean values of foliar calcium for both well and poorly grown trees were within the range considered adequate for many conifers, foliar calcium was positively correlated with current height growth. Calcium availability may influence nitrogen mineralization rates or

micronutrient levels which in turn affect tree growth, or adequate levels of Ca for juvenile amabilis fir may be higher than those of mature amabilis fir. Future studies of foliar nutrition in amabilis fir should include Fe and Mn and future fertilizer trials in amabilis fir stands should include Mg and Ca, in addition to N, if foliar levels of Mg and Ca are low. It was hypothesized that the high concentrations of K in the poorly grown trees may be caused by an antagonistic effect of K on Mg and/or Ca uptake.

The relationship between foliar chemistry and height growth may be improved by sampling during the growing season. Seasonal changes in foliar nutrient concentrations of 1- and 2-year-old foliage were not as great as expected. Regressions with July and August foliar N:P values explained more variation in height growth than fall foliar N:P values. A study of these relationships over several years is needed before the standard practice is changed.

Nitrogen concentrations were significantly lower and C:N ratios higher in humus collected from poorly grown tree microsites. Because of high immobilization potential of these (high C:N ratio) humus layers, experimental fertilizer trials should test relative effectiveness of urea versus a more soluble fertilizer such as ammonium nitrate on these sites. It was hypothesized that microsite differences in nutrient availability lead to significant differences in post-release height growth within a site. Release growth gradually declines on microsites with low nutrient availability. The rate of decline is likely related to the size of internal tree nutrient reserves and the nutrient capital of the rooting zone.

Height and age at release and competition did not explain a significant proportion of height growth variation. Study of the effect of genetic variation and microsite differences in moisture availability were beyond the scope of this thesis. However, a comparison of xeric and mesic site trees lent some support to Klinka's (1977a) hypothesis that amabilis fir regeneration on droughty sites establishes more frequently on microsites with a high proportion of decaying wood which help meet its moisture requirements but not its nutrient requirements.

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## APPENDIX A

Off-site Hypothesis

A joint field trip to the problem amabilis fir stands in Tree Farm License No. 2 was made by Dr. Kimmins<sup>18</sup> and Dr. Klinka<sup>19</sup> in April 1977. After this field trip, Klinka (1977a) hypothesized that amabilis fir was off-site as a commercial tree species in the lower elevations (below 750 m) of the wet subzone of the Coastal Western Hemlock Zone (CWHb).

This off-site hypothesis was generally accepted by many industry, government, and university foresters as the most likely explanation of variation in height growth along elevation or moisture gradients.

The major portion of the problem area lies between 460 and 1000 m in the CWHb subzone (Klinka 1977a). Forest sites in this subzone should receive enough precipitation to support good amabilis fir growth (Krajina 1969). However, when Klinka compared mean precipitation data for the CWHb subzone (Krajina 1969) and predicted climatic data<sup>20</sup> for 760 m a.s.l. in the study area (the mean elevation of the problem amabilis fir stands), he found that the predicted annual precipitation of 1535 mm was much lower than the 1900 mm reported by Krajina (1969) for the drier parts of the CWHb subzone.

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<sup>20</sup>The predicted climatic data was provided by Mr. R. Chilton, B.C. Ministry of Environment, Victoria, B.C.

Cold air drainage or higher than average snowfall might ameliorate the lower slope climate somewhat for amabilis fir by lowering temperatures, increasing humidity, and shortening the growing season, thereby, increasing the effectiveness of the available water supply.

## APPENDIX B

Comment on Ca, Mg, and K Analysis

Because of time limitations, Ca, Mg, and K concentrations were measured only for the last (fall) sampling date. Caro's acid digest as described by Lindner and Harley (1942) has replaced dry-ashing in many labs for routine foliar analysis of N, P, Ca, Mg, and K. This wet digestion technique is not only less time-consuming but also tends to give less variable results for Ca, Mg, and K compared to dry ashing<sup>21</sup>. Using a Caro's acid digest would have probably allowed seasonal analysis of Ca, Mg, and K. However, dry ashing was the standard technique in the forest ecology lab at the time of the study. Equipment for Caro's acid digestion was not available.

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<sup>21</sup>Pers. comm. from Dr. P. Pang, Canadian Forest Service, Victoria, B.C. and Mrs. B. Hermann, Pacific Soils Analysis Ltd., Vancouver, B.C., November, 1981.