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VARIATION OF NUTRIENTS IN FOREST TREE FOLIAGE

- A REVIEW -

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ABSTRACT

Variation in nutrient content of forest trees is discussed using the data from literature plus data collected by the authors. Sections are included on sampling and methods of expression of nutrient content. The emphasis is on possible causes of variation, which involves nutrient variation between years, within the year, and during the day, as well as effect of tree age and of foliage age. The effect of variation between tree species, crown classes, position on the tree, branch aspect, foliage exposure, presence of fruit, presence of pathogens, nutrient variability, geographical location, soils differences, and management practice are also discussed. Not all of the literature found is included in the discussions but all items are given in the References and Reading List.

INTRODUCTION

Our own studies, together with those in the literature, provide a picture of variation in foliar nutrient concentrations. In this review the variation has been broadly divided into factors arising from time and age, tree physiology and morphology, factors of tree location and environment, and management practice. A section on nutrient variation due to handling and sampling is also included. Some guidelines on sampling have been discussed (Newbould 1967, Rennie 1966, Lavender 1970), but they have neither described nutrient variation nor attempted to ascribe the causes. This review will not define sampling guidelines but only discuss the variations.

The above-mentioned general factors causing nutrient variation are shown in more detail in Table 1. Many potential causes of variation are listed, but no data were available.

Table 1. Detail of classes of nutrient variation.

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1. Variation caused by handling and sampling of tissue
 2. Methods of expression of nutrient content
 3. Nutrient variation
 - 3.1. Time and age
 - 3.1.1. Nutrient variation between years
 - 3.1.2. Nutrient variation during the year (seasonal)
 - 3.1.3. Nutrient variation during the day
 - 3.1.4. Nutrient variation due to tree age
 - 3.1.5. Nutrient variation due to foliage age
 - 3.2. Tree physiology and morphology
 - 3.2.1. Nutrient variation between tree species
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 - 3.2.4. Nutrient variation due to branch aspect
 - 3.2.5. Nutrient variation due to foliage exposure
 - 3.2.6. Nutrient variation due to presence of fruit
 - 3.2.7. Nutrient variation due to pathogens
 - 3.2.8. Nutrient variation due to genetic variability and provenance
 - 3.3. Tree location and environment
 - 3.3.1. Nutrient variation due to geographical location (altitude, distance from coast or equator)
 - 3.3.2. Nutrient variation due to differences in soils (site quality)
 - 3.4. Effect of management practice on nutrient concentration
 4. Discussion and conclusions

The biochemical characteristics of elements within the tree can be expected to account for additional variation (e.g., K is mobile and Ca

is immobile within the plant). The elemental concentration may also be influenced by the nutritional status (e.g., luxury consumption may lead to accumulation, or deficiency may cause more intensive internal redistribution).

Subdivisions in Table 1 are also related, thus differences shown in foliage age (3.1.5) may be considered as an integration of the seasonal variation (3.1.2).

1. VARIATION CAUSED BY HANDLING AND SAMPLING OF TISSUE

Procedures of sampling and handling can cause variation in nutrient concentration mistakenly attributed to sample differences. This section describes some of the possible errors.

Most researchers recommend removing and drying or killing the foliage as soon as possible after sampling to minimize dry-weight changes and ion migration out of the leaves. White (1954) presented data that indicated drying of *Pinus resinosa* Ait. foliage on the branch introduces serious errors in nutrient concentrations of the foliage. Sample foliage material allowed to dry slowly on the branch was found to undergo a decrease in dry matter content and thus a percentage increase in nutrient concentration. When analyses were expressed in absolute amounts of elements per fascicle (i.e., gram per fascicle rather than percent dry weight), no nutrient losses were indicated. Tamm (1951) obtained data for the N, P, K, and Ca contents of *Betula* leaves that were removed immediately from branches as opposed to leaves allowed to dry on the branches. No differences were found.

Forrest (1966) found that branchlets of *Pinus radiata* D. Don stored at room temperature or cooled lost up to 8% of initial dry weight presumably because of respiration. Branchlets could be stored for seven days at room temperature and up to 17 days at 7°C with losses of less than 2%. Dry weights estimated at 105°C were 2% less than those estimated at 70°C. Similar results on drying were found by the authors using Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco), and further analyses found no difference in N concentration as a result of storage and drying.

The presence of dust and aerosols on foliage and branches can potentially alter analytical results. Their presence is an obvious contamination (Tamm and Troedsson 1955), but attempts at removal by washing could conceivably result in a greater percentage error for some elements through leaching losses (Mason 1952). Unless excessive contamination is expected, cleaning should be limited to gentle brushing of the foliage (Ward and Johnston 1962). Raupach et al. (1972) analyzed *P. radiata* foliage for Si, Al, Fe, and Ti to determine dust contamination, found it to be negligible, and hence did not consider it necessary to wash the samples. Situations when there may be excessive contamination are generally predictable, e.g., near roads (Pb), factories (SO₄), or the ocean (NaCl). Karschon (1958) found mineral Na, K, or Cl contamination in his studies of *Eucalyptus camaldulensis* Dehn. in Israel but advised against washing.

Robinson and Freeman (1967) studied a series of plant species including *Pinus patula* Schlecht. et Cham., and attempted to partition the errors involved in foliar sampling and chemical analysis. The nutrients for which analyses were carried out were N, P, K, Ca, Mg, Na, Mn, Fe, and Zn. The largest single source of error was in the field sampling of material, and this involved the subjective selection of plant material (between individual plants and on a given plant). The next largest error was in the preparation and handling, while the analytical errors were comparatively small. The estimation of macronutrients involved a coefficient of variation of not more than 15%, of which 5% was attributable to analysis. Micronutrients are more variable, especially Mn. Care in field sampling was advised but duplicate chemical analysis did not seem justified. However, our own recommendation is to also run duplicate analyses if for nothing else than to prevent gross errors.

2. METHODS OF EXPRESSION OF NUTRIENT CONTENT

There are several alternative ways to express the nutrient concentration of tissue and the method selected should be the optimum for the subject under study. The most common method is the expression of percent oven-dry weight, and because of the large amount of data available it may be valuable always to express results on that basis for comparison, while including other methods under specific circumstances. This method is also necessary for quantitative estimates such as establishing the nutrient distribution in nutrient cycling studies.

The use of percent oven-dry weight can have a masking effect so that apparent changes in nutrient concentration may in fact be losses or gains in organic matter. To overcome this, alternative methods of expression

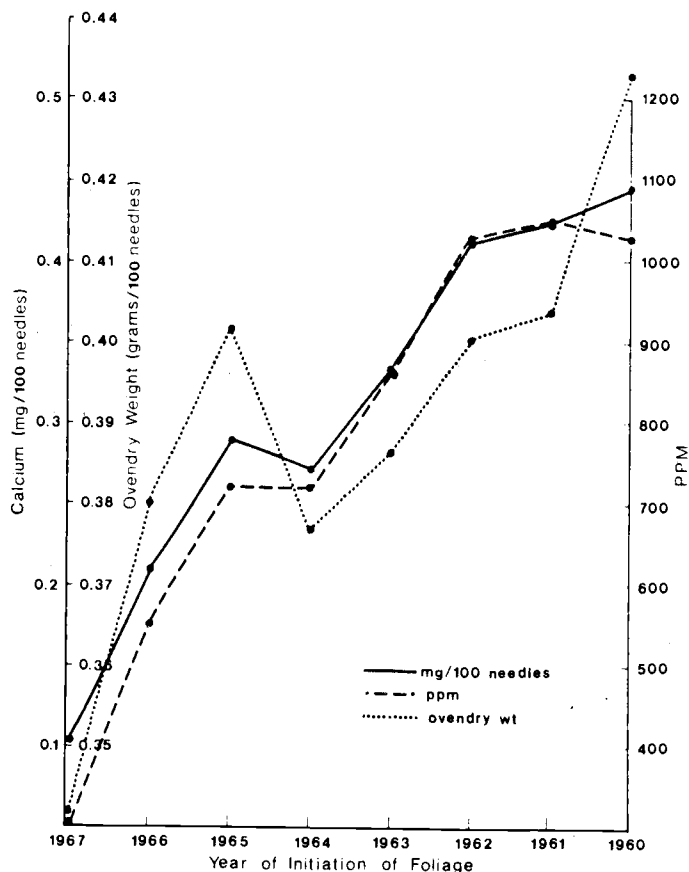


Figure 1. Calcium concentration, absolute calcium, and needle weights for the 1954 whorl of a codominant Douglas-fir.

have been devised such as using leaves as a basis (i.e., milligrams per 100 leaves or milligrams per 100 centimeters of needle length). The degree to which concentrations are related to changes in organic matter content can be shown by calcium content of Douglas-fir foliage in Figure 1. Several workers have used milligrams per 100 needles to overcome concentration effects especially when nutrient changes with time are to be monitored. Leaf et al. (1970) and Leaf (1973) used several methods of expression. Tamm (1955) discusses the seasonal trends in terms of carbohydrate storage and change (i.e., the effect on weight change), showing significant changes that will affect nutrient concentration.

A further method, probably more applicable to the study of changes in highly mobile nutrients (K, Cl), is that of expressing nutrients on the basis of sap concentration as proposed by Cassidy (1966), and previously suggested by Olsen (1948). This method of expression may be useful for certain types of study, but it involves a great deal more sample handling. As pointed out in the following discussion some apparent elemental inconsistencies may be the result of the method of expression of nutrient concentration, rather than of actual biological differences.

3. NUTRIENT VARIATION

3.1. Time and Age

3.1.1. Nutrient variation between years

Variation between years with respect to concentrations in the same age foliage and other tissues could be due to factors such as climatic variability, disease, or minor disturbance. Climatic variability would include variation in all factors bearing directly upon the tree, such as rainfall causing depth fluctuations of the water table.

Humphreys et al. (1972) studied annual variation in concentrations of N, P, K, S (total), SO₄, Ca, Mg, Al, Na, Mn, Fe, and Cl in 12 *Pinus radiata* trees in New South Wales, Australia, over a nine-year period. Annual foliar nutrient variation had been noticed previously on this site, but no definite reason for the variation had been suggested (Humphreys and Lambert 1965, Gentle and Humphreys 1968). It was found that N, S, and Cl were related to the number of wet days per year, where wet days per year are defined as the number of days that rainfall occurred from one dormant period of the tree growth to the next. The K, Ca, and Mn concentrations were related to the total rainfall that occurred in the year, and Na, Fe, and Al were related to the rainfall per wet day; P and Mg were not significantly related to any studied climatic factor. In the case of P, this was understandable as there was no significant difference between years in the foliar concentration.

In the case of Cl, a further study for *P. radiata*, *P. elliotii* Engelm., and *Eucalyptus pilularis* Sm. (Turner and Kelly 1973) indicated that between-year chloride concentration variation in the tree foliage could be related to yearly rainfall, the number of wet days, or both, and this

was apparently related to a supply factor from the rainfall as there was very little soil storage of chloride.

Humphreys and Kelly (1962) showed highly significant annual variation in P levels in the foliage of *P. elliotii* but no cause was suggested.

Annual nutrient variation was monitored in 160 trees of red pine (*Pinus resinosa*) for six years (Leaf et al. 1970). For the first three years of the study no treatments were carried out, while for the following three years the plots were treated as controls and were fertilized, irrigated, or both. Needles were measured for length and dry weight and analyzed for ash content, N, P, K, Ca, and Mg. The results were expressed as either percent dry weight or milligrams per 100 needle fascicles. Significant differences were found in every case between years and in most cases the results could be grouped showing the effect of treatment. On the control plot there was significant variation between years for all variables studied, and significant correlations with an expression of precipitation assumed to be important for red pine growth were found between years for all variables studied. Correlations were listed, but the method of expression of chemical content (i.e., percent dry weight or milligrams per 100 fascicles) changed the level of significance.

Cannon et al. (1960b) followed the seasonal foliar fluctuations in *Gleditsia triacanthos* L., *Quercus palustris* Muench., and *Crataegus phaenopyrum* Haw. for a period of years. In all species the K, Ca, and Fe varied annually but N, P, Mg, and Mn remained fairly constant. In a study of *Pinus taeda* L., Miller (1966) found that foliar concentrations of N, P, and K were relatable to average maximum and average minimum temperatures for certain periods preceding the sampling date.

It is concluded that annual variation is significant and often relatable to climatic or supply parameters, but this varies with species, location, and experimental treatment.

3.1.2. Nutrient variation during the year (seasonal)

Elemental variation during the year could be due to: factors of the environment, the nature of tree growth, nutrient accumulation, translocation or redistribution within the plant, and leaching from the foliage. Some seasonal changes are accentuated or masked by dry-weight changes, as previously discussed (sec. 2). Certain trends appear consistently in the literature and indicate that some nutrients have distinctive seasonal patterns that hold true for most tree species studied (Table 2). Calcium, Fe, and Mn concentrations and contents (absolute contents) appear to increase during the growing season while N, P, and K generally decrease. While total nutrient content may show one trend, fractionation of the nutrient may indicate changing patterns of the nutrient increase in the soluble fraction. An example of S fractionation can be shown from Kelly and Lambert (1972) in Figure 2.

A study of foliar nutrient trends during the growing season sometimes reveals periods when the levels are stable and therefore allow a relatively long time for comparative sampling. Stable periods are generally

Table 2. Foliar nutrient changes during the growing season.

Species	Form of expression	Changes during growing season			Reference
		Increase	Decrease	Stable	
<i>Abies amabilis</i>	%	Ca, Mn	N, K	P, Mg	Turner (present study)
<i>Acer platanoides</i> L.	%	Ca, Mn, Fe	N, K	P, Mg, Cu, B	Davidson (1960)
<i>A. pseudoplatanus</i> L.	% & mg/leaf	Ca, Mn, B, Si,	P	Mo, K	Guha & Mitchell (1966)
	%	Sr, Ba, Mg, Fe,			
		Pb (Co, Ni, V, Ti, Cr, Al, Zn, Na either peaked or decreased in the growing season)			
<i>A. rubrum</i> L.	%		K		Walker (1955)
<i>Aesculus hippocastanum</i> L.	% & mg/leaf	Ca, Fe, V, Ti, Cr, Pb, Al, B, Si, Co, Ba, Na	Cu, P, K	Sr, Ni, Mg, Mo	Guha & Mitchell (1966)
		(Mn & Zn either peaked or decreased)			
<i>Alnus rubra</i> Bong.	%	Ca, Mn	N, P, K	Mg	Turner (present study)
<i>Betula Britton</i>	mg/leaf	Ca, Mg, K, N, S		P	Hoyle (1965)
<i>B. verrucosa</i> Ehrh.	%	Ca	N, P, K, S		
<i>Crataegus phaenopyrum</i>	%	Ca	N, P, K		Tamm (1951)
<i>Euonymus alatus</i> Maxim	%	Ca, Mn, Fe, Mg	N, P, K		Cannon et al. (1960a)
<i>E. fortunei</i> Maxim	%	Ca, Mn, Fe	N, K	P, B, Cu, Mg	Davidson (1960)
<i>Fagus sp. L.</i>	%	Ca	N, P, K		Davidson (1960)
<i>Fagus sylvatica</i> L.	% & mg/leaf	Ca, Fe, V, Pb, Al, Si, Co, Sr, Na	Cu	Ni, Mn, Mg, P, Zn, K	Henry (1908)
		Ba, Mo either peaked or decreased)			Guha & Mitchell (1966)
<i>F. sylvatica</i>	%	Ca, Mn, Fe, Mg	N, P, K		Olsen (1948)
	mg/leaf	Ca, Mn, Mg, Fe, N, P, K			
<i>F. grandifolia</i> Ehrhart	% & mg/leaf	Ca			Chandler (1939)
<i>Gleditsia triacanthos</i>	%	Ca, Mn, Gm, Fe	N, P, K		Cannon et al. (1960a)
<i>G. triacanthos</i>	%	Ca, Mn, Fe	N, K	P, B, Cu, Mg	Davidson (1960)
<i>Juniperus chinensis</i> L.	%	Ca, Mn, Fe	N, K	P, B, Cu, Mg	Davidson (1960)
<i>J. virginiana</i> L.	% & mg/leaf	Ca			Chandler (1939)
<i>Larix sp.</i> Adans.	%	Ca	N, P, K		Henry (1908)
<i>Magnolia acuminata</i> L.	% & mg/leaf	Ca			Chandler (1939)
<i>Picea sp.</i>	%	K	P	N, Ca	Touzet et al. (1969)
<i>Picea sp. A.</i> Dietr.	%	Ca	N, P, K		Henry (1908)
<i>Picea abies</i> Karst	%	Ca	N, P, K		Tamm (1955)
<i>P. abies</i>	%	Ca, K	N, P		Touzet et al. (1969)
<i>P. mariana</i>	%	Ca, Mg	N, K	P	Lowry & Avard (1965)
	mg/leaf	Ca, Mg, K	P	N	
<i>Pinus radiata</i>	%			B	Windsor & Kelly (1972)
<i>P. radiata</i>	%	Ca			Will (1957a)
<i>P. radiata</i>	%	N, S(total), S(organic)	SO ₄		Kelly & Lambert (1972)
		N, P, K			
<i>P. radiata</i>	%				Raupach (1967)
<i>P. resinosa</i>	%		N, K	P	White (1954)
<i>P. strobus</i>	% & mg/leaf	Ca			Chandler (1939)
<i>P. strobus</i>	%			N, P, K	Touzet et al. (1969)
<i>P. strobus</i>	%		K		Walker (1955)
<i>P. strobus</i>	%		N, K	P	Tamm (1955)
<i>P. sylvestris</i>	%	Ca	N, K	P	Tamm (1955)
<i>P. taeda</i>	%	Ca, Mg	N, K	P	Wells & Metz (1963)
	mg/leaf	Ca, Mg		N, P, K	
<i>P. taeda</i>	%		K	N, P	Miller (1966)
<i>P. virginiana</i> Mill.	%		K		Walker (1955)
<i>Populus tremuloides</i> Michx.	% & mg/leaf	Ca	N, P, K		Chandler (1939)
<i>Pseudotsuga menziesii</i>	%	Ca, Mg, N, P, K			Lavender & Carmichael (1966)
<i>P. menziesii</i>	%	Ca, K	P	N	Lavender (1970)
<i>P. menziesii</i>	%	Ca, K		P, N	Turner (present study)
<i>Quercus sp. L.</i>	%	Ca	N, P, K		Henry (1908)
<i>Quercus sp.</i>	%	Ca	N, P, K	Mg	McVickar (1949)
<i>Q. gambelii</i> Newb.	mg/leaf	Ca, K, P			Sampson & Samisch (1935)
	mg/in ²	Ca, K, P			
<i>Q. kelloggii</i> Newb.	mg/leaf	Ca, K, P			Sampson & Samisch (1935)
	mg/in ²	Ca	K, P		
<i>Q. palustris</i> Muench.	%	Ca, Mn, K, Fe, Mg	N, P		Cannon et al. (1960a)
<i>Syringa vulgaris</i> L.	%	Ca, Fe, Mn	N, K	P, B, Cu, Mg	Davidson (1960)
<i>Taxus cuspidata</i> Sieb. et Zucc.	%	Ca, Fe, Mn	N, K	P, B, Cu, Mg	Davidson (1960)
<i>T. media</i> L.	%	Ca, K, Mn, Mg	N, P, B, Fe		Boonstra et al. (1957)
<i>Ulmus pumila</i> L.	%		N		Chapman (1941)
Hardwoods	%	Ca, Si	N, P, K		McHargue & Roy (1933)
<i>Acer, Betula</i>	% & mg/m ²	Ca, Mg, Na	Si		Likens & Bormann (1970)
<i>Fagus</i>	% & mg/m ²		Ca, Mg, K		Likens & Bormann (1970)

used for taking of samples for diagnostic purposes. The dormant seasons are generally recommended for most sampling purposes, but the practice is not adequately documented in relation to stability of nutrient concentrations. There is reported to be little change in foliar N, P, and K during the dormant seasons for *Pinus resinosa* (White 1954), *Pinus contorta* Dougl. [ex Loudon], and *Pseudotsuga menziesii* (Beaton et al. 1965b) as long as foliage is not senescing. Likens and Bormann (1970) indicated not only seasonal differences in Ca, Mg, K, and Na for three deciduous species but also showed a seasonal difference between sun and shade leaves.

3.1.3. Nutrient variation during the day

While very few data for daily nutrient variation in trees were found, it is possible that changes could occur under some conditions, for example, K under extremes of water stress. Khashes (1972) found that daily and seasonal variation of K concentration in trees was related to transpiration patterns. How this would affect nutrient distribution and diagnostic work is not known.

3.1.4. Nutrient variation due to tree age

Raupach et al. (1969), working on *Pinus radiata* in South Australia, showed foliar N percentage increases with tree age but no trend was found for P or K. F. R. Humphreys (pers. commun.), also working with *P. radiata*, found no age effect on nutrient concentration in trees growing in New South Wales, Australia. Analysis of young needles of *P. radiata* in New Zealand (Askew 1937) indicated that older trees had decreased concentrations of Ca, P, Na, and Cl and increased N, Mg, K, and Mn when compared with younger trees.

Emmert (1957) found that apple trees 16-25 years of age had higher Ca and Mg than did 9- to 16-year-old trees. No differences were found for N, P, or K.

An investigation of *Agathis australis* Salisb. revealed that foliar concentrations of K and Mn increase with increasing tree age while N, P, Ca, S, and Fe decrease (Peterson 1961). Hhne (1967), working with *Pinus sylvestris* L. in Germany, did not find any significant trends with age for N, P, K, Ca, Mg, Mn, and S in the age range 9-110 years.

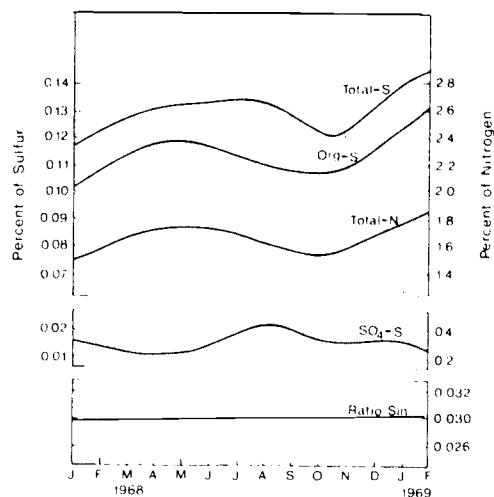


Figure 2. Mean variation of total S, sulfate S, organic S, and total N for nine trees of *Pinus radiata* throughout the growing season (from Kelly and Lambert 1972).

It appears that age of tree does affect the concentration of nutrients in foliage, but no physiological basis within the tree has been substantiated. Instead of a physiological effect, the change, if there is one, could be hypothesized due to increasing or decreasing availability of nutrients within the soil as the stand ages, because of immobilization of N, Ca, and Mn, in the forest floor organic matter (Turner 1975, Heilman 1966) or because of the presence of species with high leaching potential.

3.1.5. Nutrient variation due to foliage age

Difference in nutrient concentration with foliage age is a major source of variation in the sampling of foliage of some tree species. Many nutrients have characteristic patterns showing similar trends toward seasonal differences. Such variation is to be expected as the difference in age classes could be viewed as an integration of seasonal

Table 3. Foliar nutrient variation in relation to age of foliage.

Species	Form of expression	Elemental change with increasing foliar age.			Reference
		Increase	Decrease	Stable	
<i>Abies amabilis</i>	%	Ca, Mn	N, P, K	Mg	Turner (present study)
<i>A. amabilis</i>	%	Ca	N, P, K	S, Mg	Beaton et al. (1965a)
<i>A. lasiocarpa</i> (Hook.) Nutt.	%	Ca	N, P, K	S, Mg	Beaton et al. (1965a)
<i>Acer saccharum</i>	% & % ash mg/leaf	Ca, ash	N, P, K, Mg		Leaf (1973)
<i>Agathis australis</i>	%	Ca, Na, S, Fe, Mn	N, P, K,		Peterson (1961)
<i>Juniperus virginiana</i>	% & mg/leaf	Ca			Chandler (1939)
<i>Picea abies</i>	%	Ca	K		Heiberg & White (1951). Tamm (1955)
<i>P. abies</i>	%	Ca	N, P, K		
<i>P. abies</i>	%	Ca, Mn, Si	N, P, K	Mg	
<i>P. engelmannii</i> Parry	%	Ca, Mg	N, P, K, S		Beaton et al. (1965a)
<i>P. glauca</i> Moench.	%	Ca	K		Heiberg & White (1951)
<i>P. mariana</i>	% & mg/leaf	Ca	N, P, K, Mg		Lowry & Avard (1965)
<i>P. sitchensis</i> (Bong.) Carr.	%	Ca	N, P, K, S		Beaton et al. (1965a)
<i>Pinus contorta</i>	%	Si, Al, Fe, Mn	Zn	B, Co, Mo, Cu	Beaton et al. (1965b)
<i>P. contorta</i>	%	Ca, Mg	N, P, K, S		Beaton et al. (1965a)
<i>P. elliotii</i>	%		P		Humphreys & Kelly (1962)
<i>P. halepensis</i> Mill.	%	Ca	K		Oppenheimer & Halfon- Meiri (1961)
<i>P. nigra</i> Arnold	%	Ca	N, P, K, Mg	Na	Wright & Will (1958)
<i>P. radiata</i>	%	Ca, Cl	N, P, Mn	K, Mg, Fe	Askew (1937)
<i>P. radiata</i> upper crown	%	Ca, Na	N, P, K	Mg	Will (1957a)
<i>P. radiata</i> lower crown	%	Na	N, K	P, Mg, Ca	
<i>P. radiata</i>	%		N, P, K		Hall & Raupach (1963)
<i>P. resinosa</i>	%	Ca	K		Heiberg & White (1951)
<i>P. resinosa</i>	%	Ca, Mg	N, P, K		Jurgensen & Leaf (1965)
<i>P. resinosa</i>	%	Ca	N, P, K, Mg	Na	Madgwick (1964b)
<i>P. strobus</i>	% & mg/leaf	Ca			Chandler (1939)
<i>P. strobus</i>	%	Ca	K		Heiberg & White (1951)
<i>P. sylvestris</i>	%	Ca	N, P, K		Leyton & Armson (1955)
<i>P. sylvestris</i>	%	Ca, Mg	N, P, K	Na	Wright & Will (1958)
<i>P. sylvestris</i>	%	Ca, Mg, Mn, Si	N, P, K		Höhne (1967)
<i>P. sylvestris</i>	%	Ca	N, P, K		Tamm (1955)
<i>Pseudotsuga menziesii</i>	%	Si, Al, Fe, Mn		B, Co, Mo, Cu	Beaton et al. (1965b)
<i>P. menziesii</i>	%	Ca, P, S	N, K	Mg	Beaton et al. (1965a)
<i>P. menziesii</i>	%	Ca	N, K, Mg	P	Lavender & Carmichael (1966)
<i>P. menziesii</i>	%	Ca, Mn	N, P, K, Mg		Turner (present study)
<i>Tsuga heterophylla</i> (Raf.) Sarg.	%	Al, Mn, Fe		B, Co, Mo, Cu, Zn	Beaton et al. (1965b)
<i>T. heterophylla</i>	%	Ca, P, S	K	N, Mg	Beaton et al. (1965a)

trends. Nitrogen, P, and K have been observed to decrease with increasing foliage age while Ca and Mn increase. Table 3 presents a summary of this variation, taken from the literature.

Dice carried out a detailed analysis of foliage on one co-dominant Douglas-fir and produced data on variation with foliar age. All branches from each whorl of the tree were brought to the laboratory for careful separation into age classes. All foliage in a given age class was composited for each whorl to include all parts of all branches present. Figure 3 shows the increase in foliar Ca with increase in foliage age for whorls 2 through 11 as counted from the top of the tree. This indicates a continued accumulation of Ca in all whorls, and the buildup has proceeded for seven years in whorl 11. Comparable patterns were also found for N. A similar distribution with foliage age is shown for the same whorls (Figure 4). At each level in the tree, the one-year-old foliage has the highest N concentration, with the level gradually diminishing toward the bole. The repetition of pattern in successive whorls is striking.

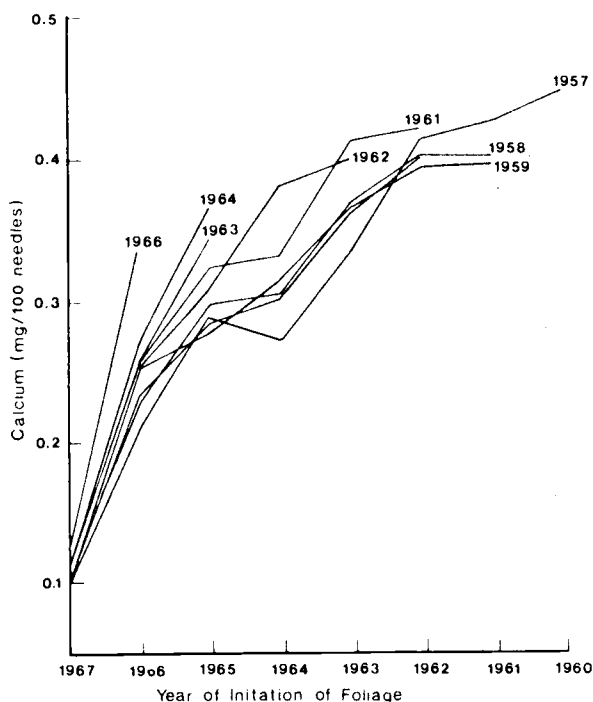


Figure 3. Increase in foliar calcium with foliage age by whorls.

Similar work was carried out by Turner (present study) in Douglas-fir and Pacific silver fir (*Abies amabilis* [Doug.] Forbes). The study for Douglas-fir was in a poor quality 30-year-old stand deficient in N. Needle retention time was shorter than in the study of Dice. While the patterns of N concentration were generally the same, the decrease with the age of the needles was much more rapid. The concentrations to which the N decreased in the older needles were also much lower--down to 0.6% in the oldest needles. Probably the trends are the same in most Douglas-fir trees but, depending upon the nutritional status of the tree, the rates of change and the absolute values vary. The results with the Pacific silver fir (from Findley Lake in the Cedar River watershed) indicated a general decrease in foliar N concentration with increasing age of the foliage similar to that found in the Douglas-fir. The trees were 175 years old (three trees used) and needle retention was up to 15 years. Rates of change in N (%) were very slow, and there was a very obvious effect of good and poor years in terms of length of growing season. Very poor years had a marked decline; while the trends were similar to those of Douglas-fir, there were marked differences arising from the harsher environment.

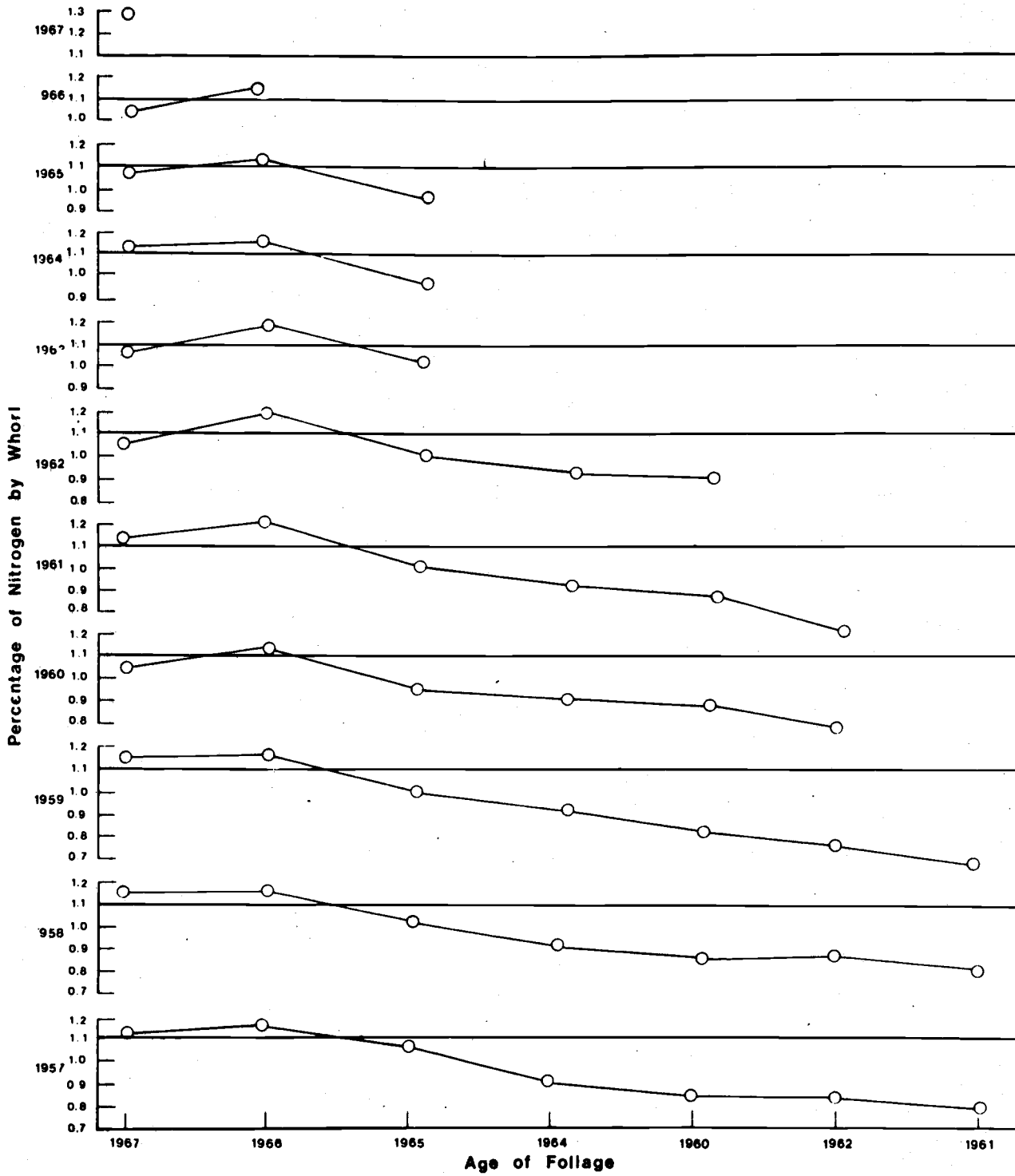


Figure 4. Foliar nitrogen content for tree C-12 by age and whorl.

3.2. Tree Physiology and Morphology

3.2.1. Nutrient variation between tree species

That tree species differ in their nutrient requirements and accumulation patterns is well known. Other than some possible generalizations, such as that conifers are lower in alkali metals than are hardwoods, most of the variation must be termed random. Differences in data for many studies are not attributable to differences in species because there was also a simultaneous change in one or more of the other variables such as soil, location, tree age, sampling time, method of collection, and so on.

Some idea of different nutrient contents of species can be obtained from various summaries of Bengston (1968). A study by Beaton et al. (1965a,b), shown in Table 4, on different species growing in British Columbia makes

Table 4. Summary of foliar nutrient concentrations (%) of tree species growing in British Columbia (from Beaton et al. 1965a).

Species	No. of locations	N	P	K	Ca	Mg	S
<i>Abies amabilis</i> older	1	0.9	0.16	1.20	0.80	0.08	0.12
<i>A. lasiocarpa</i> seedlings	3	1.05-1.85	0.18-0.26	0.70-1.08	0.29-0.44	0.07-0.11	0.12-0.16
<i>Picea engelmannii</i> seedlings	3	1.26-1.72	0.21-0.29	0.71-0.80	0.44-0.58	0.13-0.15	0.13-0.19
older	3	0.92-1.08	0.20	0.70-0.88	0.28-0.33	0.11-0.12	0.12-0.14
<i>P. sitchensis</i> older	1	1.15	0.18	0.82	0.42	0.09	0.14
<i>Pinus contorta</i> seedlings	3	1.18-1.77	0.09-0.12	0.35-0.39	0.15-0.16	0.08-0.12	0.09-0.11
older	3	0.97-1.12	0.12-0.22	0.38-0.70	0.16-0.44	0.07-0.18	0.14-0.25
<i>Pseudotsuga menziesii</i> older	7	0.88-1.37	0.12-0.22	0.38-0.70	0.16-0.44	0.07-0.18	0.14-0.25
<i>Thuja plicata</i> older	1	0.73	0.13	0.52	1.16	0.10	0.07
<i>Tsuga heterophylla</i>	3	0.86-1.17	0.11-0.19	0.28-0.57	0.18-0.27	0.08-0.12	0.10-0.15

it apparent that the accumulation of nutrients in foliage varies considerably between species. Examples are the relatively high levels of Ca in the foliage of *Thuja plicata* Donn and the higher K concentration of *Abies amabilis*. Also noticeable are the higher nutrient concentrations in seedlings compared with older trees. Groups of trees planted in arboreta give some basis for comparison as most variables are held constant. From a small amount of data available from New South Wales (F. R. Humphreys pers. commun.), certain tree species accumulate specific nutrients. For example, *Pinus radiata* accumulated Al and *Pseudotsuga menziesii* accumulated Mn. Likens and Bormann (1970) gave estimates of ash (%) in five different tree species from the Hubbard Brook Ecosystem. These are shown in Table 5. Species differences are very obvious. It could be expected that this is a general trend of specific nutrient accumulation through all tree species.

Table 5. Amount of insoluble ash, as percent of sample dry weight in tissues of tree species at Hubbard Brook (from Likens and Bormann 1970).

Component	<i>Acer saccharum</i>	<i>Betula alleghaniensis</i>	<i>Fagus grandifolia</i>	<i>Acer spicatum</i>	<i>Picea rubens</i>
Leaves	0.99	0.31	0.87	0.34	0.40
Current twigs	0.06	0.07	0.14	0.05	0.05
Branches	0.04	0.02	0.30	0.02	0.13
Bark	0.10	0.03	0.59	0.12	0.18
Light wood	0.009	0.004	0.032	0.003	0.009
Dark wood	0.002	0.128	0.009	0.029	
Roots	1.52	0.73	1.44	0.68	0.41

3.2.2. Nutrient variation due to crown class

Lavender (1970) showed (Table 6) that foliar N concentrations decreased from dominant to suppressed trees. Wright and Will (1958) indicated that for needles, branches, bark, and wood there is little difference between dominant and suppressed trees for N and Na, while P, K, and Mg are higher in suppressed trees and Ca is lower. Carter and White (1971) working on *Populus deltoides* Bart. found no great differences between suppressed and dominant trees in N, P, K, Ca, and Mg. Ash (%) was higher in suppressed than in dominant trees.

Lowry and Avard (1968a), in a study on black spruce (*Picea mariana* [Mill.] B.S.P.), found no significant differences between crown classes for N, P, and Ca but with K the order was suppressed > intermediate > codominant > dominant; the order was reversed for Mg.

Dice has noted that one source of variation was the differing date of budbreak in the different crown classes. It was noted that the suppressed and intermediate trees began extension growth first and the dominants last. Trees growing along roads or adjacent to stand openings began growth before trees farther in the stand. Sampling during the early spring period of growth indicated that the different crown classes are in different stages of growth--a cause for different nutritional regimes.

While there are (or may be) differences in nutrient concentration between crown classes within a stand, there also are differences between trees within the same crown class. Thus for sampling purposes it must be borne in mind that there will be a range in nutrient concentrations in the trees even when all sampling procedures are held constant. This can be shown from the work of Morison (1970) indicating a typical normal curve in the stand N distribution (Figure 5).

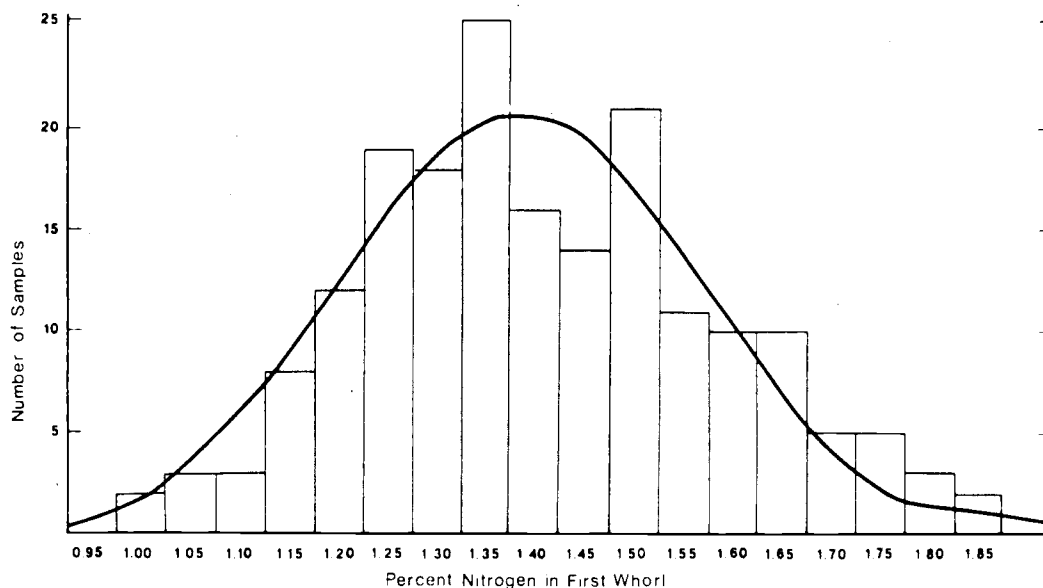


Figure 5. Range and frequency of foliar nitrogen percentage in the first whorls from 188 trees (from Morrison 1970).

Table 7. Foliar nutrient variation in relation to position in the tree.

Species	Trend with tree height					Reference
	Increase toward top	Decrease toward top	Stable	Max. in midcrown	Min. in midcrown	
<i>Abies alba</i> Mill.						
healthy		Ca	N	P	K, Mg	Nemec (1940)
dying	P	Ca, N	K, Mg			
<i>Acer saccharum</i>		N	P, K, Ca			Wallihan (1944)
<i>Agathis australis</i>	P	K, Ca, Mn, Fe	N	Na	S	Peterson (1961)
<i>Cryptomeria japonica</i>	N, K	Ca	Mg, P			Harada et al. (1972)
<i>Picea abies</i>	N		P, K, Ca, Mg			Swan (1962)
<i>P. abies</i>			P, Ca, Mg	N	K	Strebel (1961)
<i>P. glauca</i>	Mg	K	N, P, Ca			Swan (1962)
<i>P. mariana</i>	N					Gagnon (1964)
<i>P. mariana</i>	N, Mg	K	P	Ca		Lowry (1970)
<i>Pinus banksiana</i> Lamb.			P, N, K, Ca, Mg			Swan (1962)
<i>P. elliotii</i>			P			Humphreys and Kelly (1962)
<i>P. nigra</i>	N, P, K, Ca, Mg, Na					Wright and Will (1958)
<i>P. radiata</i>	N, P, K, & needle wt					Hall & Raupach (1963)
<i>P. radiata</i>		Ca, K, P	N, Mg, Na			Will (1957a)
<i>P. resinosa</i>	N	K	P, Ca, Mg			Swan (1962)
<i>P. resinosa</i> good site	Mg	K, Ca	N		P	Madgwick (1964b)
<i>P. resinosa</i> poor site	N		P, K, Ca, Mg			
<i>P. resinosa</i>	K					White (1954)
<i>P. strobus</i>	K					White (1954)
<i>P. sylvestris</i>	N	K	P, Ca, Mg			Swan (1962)
<i>P. sylvestris</i>	N, P, Mg		K, Ca, Na			Wright & Will (1958)
<i>Populus deltoides</i> Bart.	N, P, K,	Ca, Mg, ash				Carter & White (1971)
<i>Pseudotsuga menziesii</i>	N, P, K, Mg	Ca				Lavender & Carmichael (1966)
<i>P. menziesii</i>	N	P				Brackett (1964)
<i>Taxus baccata</i> L.		Ca, Mg			K, P	Nemec (1947)

3.2.3. Nutrient variation due to position on tree

In the past the principal reason for studying nutrient variation with regard to position was to find the position on the tree most sensitive to the nutritional status of the forest stand. Table 7 presents the results from the literature on the subject. Generalizations are difficult to make, but foliar Ca is frequently observed to decrease in concentration with increased sampling height within the tree, while foliar N shows the reverse. Nemec (1940) and Madgwick (1964a) had different results, as site and tree vigor produced different elemental variation within their sample trees.

The data of Dice from Cedar River presented in sec. 3.1.5 are also applicable to this section. Figures 3 and 4 show Ca and N levels in the top eleven whorls of a codominant Douglas-fir. Nitrogen concentrations are remarkably uniform between whorls when comparable foliage ages are considered. Calcium levels are not quite as uniform as N. Sample location within branches constitutes another source of variation with position in the tree. Nutrient levels within branches exhibit a distribution dictated by such influences as foliage age, year of foliage initiation (a poor year versus good year), distance from the main branch, distance from the bole, and foliage exposure. Brackett (1964) studied the N and P variation in the foliage of one branch of an open-grown Douglas-fir (Table 8). Arranged in growth sequences similar to those of Duff and Nolan (1953), Brackett's data showed a maximum foliar N and P level two years from the tip along the main branch, and two to three years from the tips of the laterals. Nutrient concentrations then progressively decreased with distance from the tips of both the main branch and the laterals.

Table 8. Nutrient variation within a single Douglas-fir branch (from Brackett 1964).

Internodes from main branch along laterals	Year						
	1958	1959	1960	1961	1962	1963	
<u>Nitrogen (%)</u>							
7	1.52						
6	1.34	1.55					
5	1.27	1.60	1.43				
4	1.14	1.48	1.32	1.31			
3	1.09	1.38	1.46	1.35	1.33		
2	1.03	1.16	1.28	1.52	1.32	1.31	
1		1.16	1.13	1.16	1.52	1.57	1.54
<u>Phosphorus (ppm)</u>							
7	2968						
6	3699	3074					
5	3699	3710	2873				
4	3371	3392	3095	2735			
3	2810	3318	3497	3497	2809		
2	2862	2650	3180	3498	3604	2544	
1		2390	2500	2767	3275	3381	2809

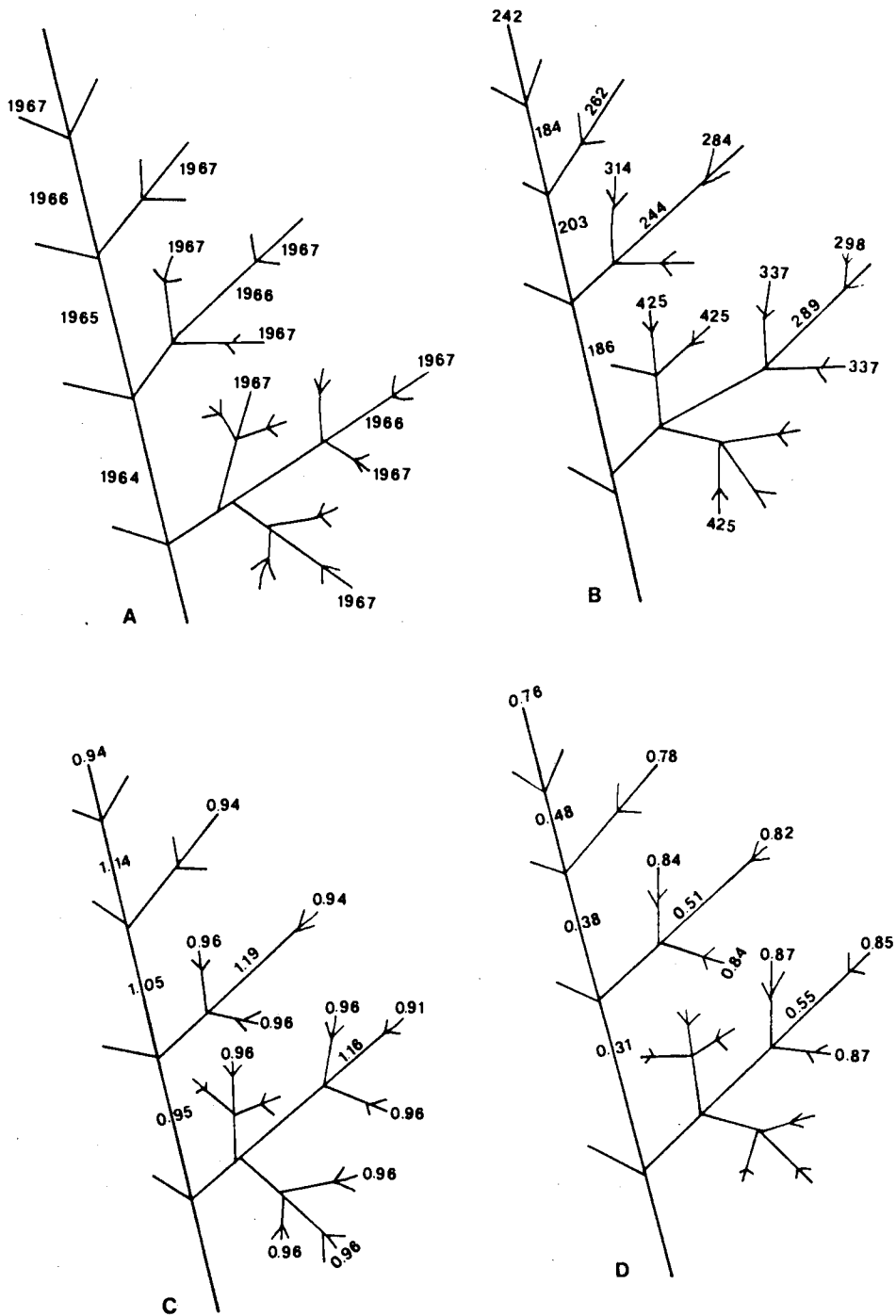


Figure 6. Within-branch nutrient variation for Douglas-fir: (A) year of initiation of branch segment; (B) number of needles per gram oven-dry weight; (C) percentage of nitrogen in foliage; (D) percentage of nitrogen in branches.

3.2.4. Nutrient variation due to branch aspect

Various researchers have found significant relations between aspect and foliar nutrient levels. *Agathis australis* was shown to have higher N and P on north-facing than on south-facing branches, while K had an opposite pattern (Peterson 1961). Oppenheimer and Halfon-Meiri (1961) found that the eastern and southern aspects of *Quercus ithaburensis* Mich. had higher P than other aspects. Tamm (1951) found that N levels were highest on the northern aspects of *Betula* foliage.

On the other hand, Wallihan (1944), studying *Acer saccharum* Marsh, found no relationship between aspect (side of tree) and the N, P, K, Ca, and Mg concentrations in the foliage. Similarly, White (1954) found no relationship between foliar K and aspect in *Pinus resinosa* and *P. strobus* L. Humphreys and Kelly (1962) found no effect of aspect for P in *Pinus elliottii* foliage. These findings were supported by studies on N and K in the Cedar River watershed on *Pseudotsuga menziesii*, in which no difference in concentration could be found in the cardinal directions.

It is concluded that there is no systemic, universal effect of foliage aspect on nutrient concentrations in tree foliage.

3.2.5. Nutrient variation due to foliage exposure

Variation with exposure may be due to different photosynthetic activity or to plant moisture relations associated with different light intensity and transpirational stress. Gutschick (1940) is reported to have found a higher Mn content in the shade needles of *Picea* and *Pinus* species as compared with the sun needles of the same tree. Succulent hardwood foliage was found to have higher N and lower Ca concentrations than non-succulent foliage (Plice 1943).

3.2.6. Nutrient variation due to presence of fruit

The effect of fruit on trees is a problem in sampling foliage in that some trees in the stand may have cones while others do not, thus creating a problem of deciding which is the most representative situation. Fruit crops on trees have been shown to result in alterations of concentrations in the foliage. Lower elemental concentrations are observed in foliage associated with fruit compared with similar foliage without fruit. Fletcher and Ochry-Meirych (1955) showed foliage of female trees of eastern redcedar to have higher P than male trees, while Ca was reversed, and different patterns occurred over seasons. There was no significant difference for K. Brackett (1964) found that *Pseudotsuga menziesii* foliage without cones had higher N and P concentrations than foliage subtended by cones. Figure 7 (from Gessel 1962) depicts N variation in foliage as a result of fruit.

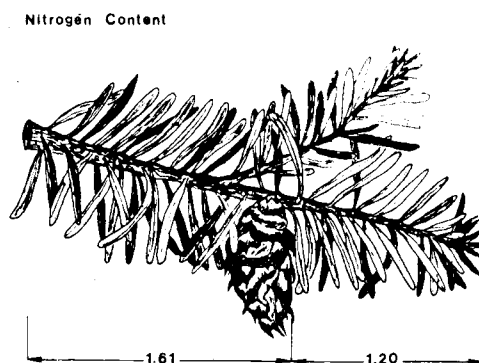


Figure 7. Change in nitrogen content of Douglas-fir foliage as a result of seed production (from Gessel 1962).

3.2.7. Nutrient variation due to pathogens

Nutrient variation due to pathogens has not been well investigated although it could be significant. Rennerfelt and Tamm (1962) investigated the foliar contents of spruce infected with *Fomes annosus* root rot but found no difference in the nutrient levels. While no evidence is available as to the effect of pathogens, their potential effect should be kept in mind.

3.2.8. Nutrient variation due to genetic variability and provenance

It is hypothesized that different provenances of a tree species have different nutrient uptake potentials and thus, in a given environment, different nutrient concentrations. Each of eight provenances of Douglas-fir (*Pseudotsuga menziesii*) from the Pacific Northwest were planted in three different locations in New South Wales. Nutrient analyses were carried out for P, Al, Ca, Mg, K, Na, and Mn. Manganese was found to be significantly different between provenances while no difference between provenances could be found for the other nutrients studied (F. R.

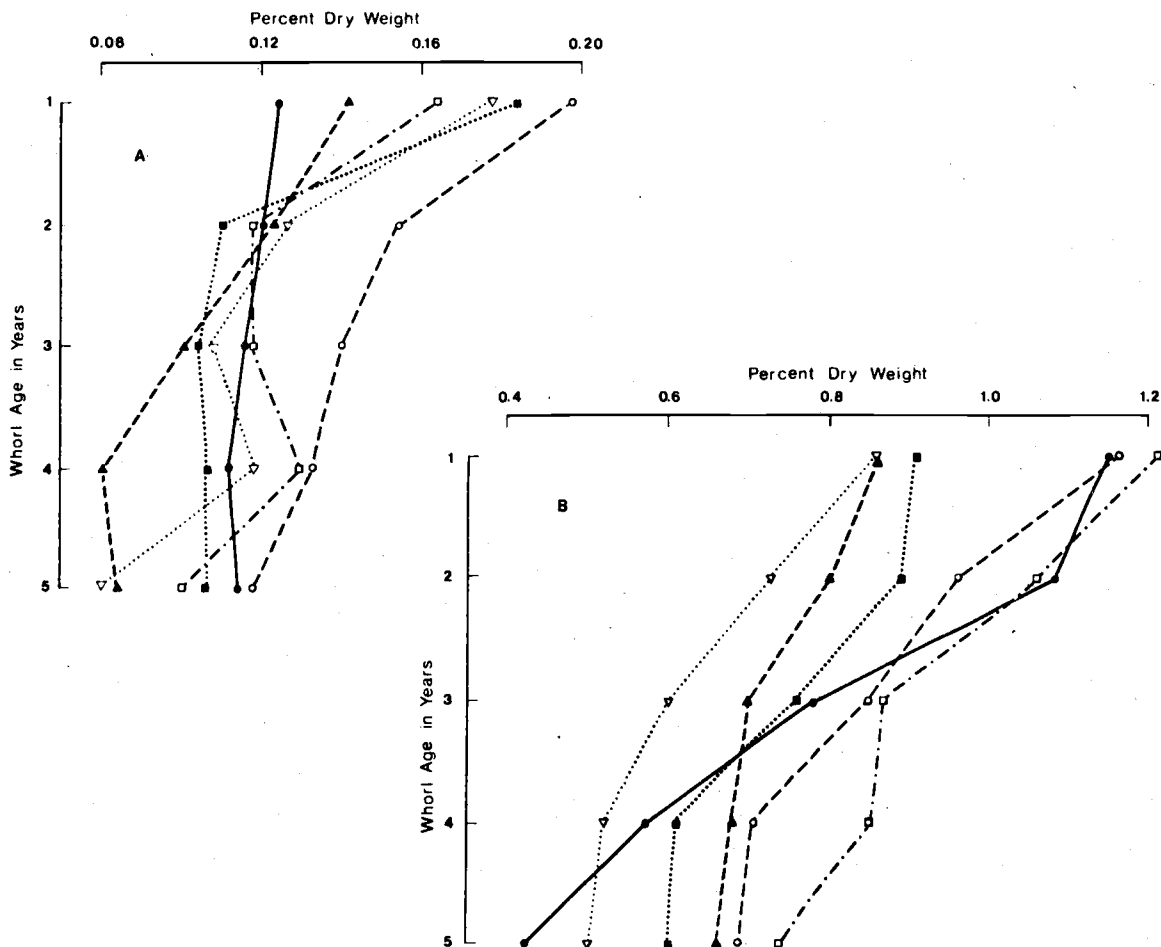


Figure 8. Average concentration of (A) phosphorus and (B) potassium through the crowns of trees for six *Pinus radiata* clones.

Humphreys pers. commun.). Van den Driessche (1973) studied nutrient concentrations of different provenances of Douglas-fir growing in Canada and found differences for N, P, K, Ca, and Mg. Comparable effects have been found by Steinbeck (1965, 1966), Giertych and Farrar (1962), Mergen and Worrall (1965), Pritchett and Goddard (1967), and Walker and Hatcher (1965). Forrest (1969) showed variation in different parts of the crown for P and K for six clones of *P. radiata* (Figure 8). The mean concentrations showed different clonal patterns, which should have a bearing on sample collection.

While it is understood from these studies that there are genetic differences, they must be treated as a random variable. An important significance is the potential selection for specific nutritional requirements.

3.3. Tree Location and Environment

3.3.1. Nutrient variation due to geographical location (elevation, distance from the coast or Equator)

The specific effect of a geographical location is essentially the proximity of a specific nutrient source. Turner and Kelly (1973) studied the effect of distance from the ocean on foliar chloride levels of various forest trees in New South Wales. For three species, *Eucalyptus pilularis*, *Pinus radiata*, and *P. elliottii*, the foliar chloride concentration decreased with increasing distance from the ocean. There were definite species differences. Turner (pers. files) found similar trends for Na, but the concentrations were not so high; that is, Na did not balance the Cl, indicating possible selective absorption.

In a study of the effect of elevation on the concentration of N, P, K, Ca, Mg, Mn, and Si in spruce, Höhne (1963) found the only effect was a decrease in the concentration of Si at higher elevations.

3.3.2. Nutrient variation due to differences in soils

Dissimilarities in nutrient concentration caused by soil differences are expected as a result of the different soil nutritional regimes. Safford and Young (1968) studied nutrient differences in red spruce growing on different soils. Significant differences were found between soil series for P, Zn, Mn, and B. Further differences in foliar nutrient levels were found within a soil series at different locations for P, K, Zn, Mn, and Al. Sukachev and Dylis (1964) discuss the relation between soils and nutrient content for various species, indicating that for most nutrients the concentration can be changed severalfold. Table 10, from Gentle and Humphreys (1968), compares soil type and foliar nutrient content for *P. radiata* indicating differences. Ito et al. (1972) give similar information for *Cryptomeria japonica* D. Don in Japan.

Table 10. Influence of parent material on soil and foliage nutrient concentrations from two adjacent sites at Belaglo State Forest, New South Wales, Australia (from Gentle and Humphreys 1968).

Parent material	Soil horizon	P (ppm)	Soil analyses					Foliage analyses (%)					
			Exchangeable bases (meq/100 g)					P	Ca	Mg	K	Na	Al
			Ca	Mg	K	Na	Al						
Basalt intrusion	A	306	1.36	1.14	0.49	0.14	1.18	0.153	0.126	0.244	1.174	0.010	0.073
	B	280	0.31	0.87	0.46	0.07	2.31						
Hawkesbury sandstone	A	71	0.92	0.46	0.31	0.03	0.58	0.085	0.131	0.189	0.380	0.025	0.060
	B	113	0.03	0.97	0.16	0.02	1.88						

3.4. Effect of Management Practice on Nutrient Concentration

Forest fertilization is aimed at specifically increasing the concentration of a specific nutrient or nutrients, as discussed in previous reviews (Gessel et al. 1965, Bengston 1968, Baule and Fricker 1970). The application of one nutrient and its subsequent increase may cause growth resulting in its dilution and therefore apparent decrease in other nutrient concentrations.

Thinning can cause either increases in nutrients as a result of greater availability or an apparent lowering due to dilution from extended growth. Hatch and Mitchell (1972) studied the effect of thinning on nutrient levels in *Pinus pinaster* Ait. stands in western Australia, and found that only K was affected (increased). On this site water was considered the main limitation to growth.

Burning, either accidental or as a controlled management procedure, potentially can volatilize nutrients and thus reduce quantities of available nutrients (Grier 1976).

While no great detail is given here on management effects on foliar concentration, the effect is systematic and must be considered in any sampling procedure.

4. DISCUSSION AND CONCLUSIONS

The main interest of the study was the causes of variability occurring in forest tree foliage. Some of these differences are very obvious (species, soil) and are usually explicitly or implicitly accounted for in any experimental design. An attempt has been made to divide the variation into a logical sequence and then, where data were available, define the difference as systematic or random.

Various tissues on a tree also differ in nutrient concentrations and this is summarized for N in a Douglas-fir tree in Figure 9.

Generally as foliage increases (mainly leaves, as they were the principal part studied) in age, either seasonally or yearly, predictable changes occurred. Thus mobile nutrients (K) generally decrease and immobile nutrients (Ca and Mn) increase. The yearly changes are the integration of seasonal changes.

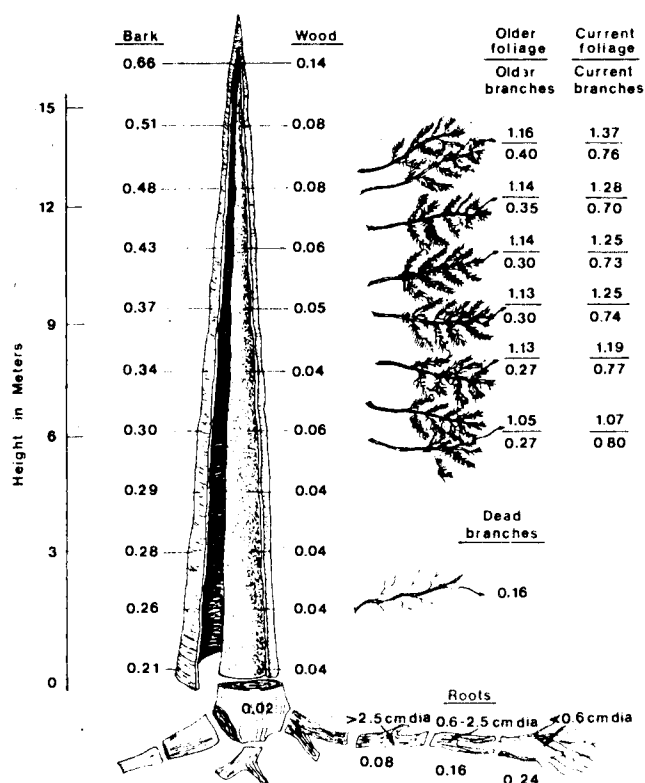


Figure 9. Generalized nitrogen variability within a mature Douglas-fir (nitrogen in percent).

Further differences can be related to environmental influences and soil nutrient content. Some annual differences can be related to climatic variability and some to geographical location, for example Cl in relation to the ocean and to rainfall.

Within the tree foliage there are changes and many of these (aspect, exposure) are related to the physiological activity of the tissue. The tissue sampled depends upon the type of study involved but, to lower variability, all samples should be taken within a short period of time and samples of comparable age and exposure should be taken.

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