INTERACTIONS OF SULFUR WITH NITROGEN IN FOREST STANDS

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ABSTRACT

Growth responses to nitrogen fertilization in Douglas-fir forests have been predicted with a high degree of success when due regard has been taken of their sulfur status. An index of sulfur availability has been determined using foliar analysis, a combination of soil nitrogen content and soil parent material, or both. Foliar sulfate-sulfur concentrations have been used to assess the sulfur/nitrogen status of conifers and it has been shown that in excess of 400 parts per million (ppm) is required to obtain growth responses to nitrogen fertilizers. Sulfur deficiency results in an accumulation of the amino acid arginine. For radiata pine a good relation has been found between sulfur deficiency and increased foliar disease susceptibility.

INTRODUCTION

Although it has been acknowledged for more than 100 years that S is an essential major plant nutrient, this element has received little attention in laboratory, greenhouse, and field research in comparison with that received by N, P, and K. This is partly because the use of N and P fertilizers containing S has masked a deficiency of S and also because of the comparative difficulty of analyzing this nutrient in biological materials.

Recent reports from different areas of the work suggest that the incidence of S deficiency in soils is increasing (Beaton et al. 1971, Blair 1979). Possible reasons are the increased use of high-analysis fertilizers with low S content, environmental protection legislation which has restricted the input of sulfur dioxide to the atmosphere from industrial processes, and a growing awareness of the importance of S as a plant nutrient.

The addition of N fertilizers to forests to increase productivity is common practice in northern Europe/ Scandinavia, New Zealand, and the Pacific Northwest of the United States either in the form of urea or ammonium nitrate, but it is a comparatively rare practice in Australia (Armson et al. 1975, Atkinson and Morison 1975, Pritchett and Smith 1975, Ballard and Will 1978). Treatment effects and growth response predictions have been inconsistent for Douglas-fir in the U.S. Pacific Northwest (Gessel et al. 1965, Miller and Williamson 1974) and it is necessary to take into account factors other than N status alone.

Balanced nutrition to obtain growth response and reduced disease susceptibility has been recognized by many workers, but few working hypotheses have been suggested to explain the mechanisms involved. The S status of trees and the relation between S and N nutrition have been suggested as one critical group of factors (Lambert and Turner 1977). The aim of this paper is to discuss S nutrition of trees, S interactions with N, disease susceptibility, and the relation between these nutrients and growth response after manipulation.

SULFUR RELATIONSHIPS IN PLANTS

Sulfur is required by plants for the synthesis of three amino acids—cystine, cysteine, and methionine—which are essential components of protein and which contain approximately 90% of the organic S found in plants; for the formation of chlorophyll; for the activation of certain enzymes and the synthesis of certain vitamins; for the formation of certain disulfide linkages associated with the structural characteristics of protoplasm (the concentration of sulfydryl [-SH] groups in plant tissues has also been shown to be related to increased cold and drought resistance in some species); the formation of ferredoxin, an iron-containing plant protein that functions as an electron carrier in photosynthetic processes; the formation of a ferredoxin-like compound that is involved in the fixation of N by root nodule bacteria and free-living, N-fixing soil bacteria; and the activity of ATP sulfurylase, an enzyme that functions in the metabolism of S (Anderson 1975).

A constant ratio of 0.030 has been found between organic S and total N in the foliage of *Pinus* spp. (Kelly and Lambert 1972) and Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco), the same ratio as that in their foliar protein. Unlike certain other plants, the foliar total N has always been found to be equal to organic N and there has been no evidence of nitrate-N even when S has been limiting. Apparently N is taken up only at the rate at which S is available and therefore protein formation is limited by the amount of S available.

When the S supply is adequate, the conifer accumulates as sulfate any excess S beyond that required to balance the N available, and protein formation proceeds at the rate at which N becomes available. The sulfate-S status of the foliage provides an indicator of the S status of both the tree and the site and is a much more sensitive and indicative measure than foliar

total S (Lambert and Turner 1977). Hence, the relationship between N and S can be summarized as shown in Table 1.

General S ratings based on foliage sulfate-S levels (winter sampling—dormant growth period) have been derived for *Pinus radiata* D. Don (Turner et al. 1977). That is, with less than 80 ppm sulfate-S the trees are S deficient; 80–200 ppm is marginal to adequate; 200–400 ppm is adequate to high, and over 400 ppm is high and probably N deficient. These levels indicate S storage concentrations that are readily available for immediate utilization and growth in spring. Modifications to these ratings based on site productivity are presented later.

SOURCES OF SULFUR

Three possible sources of S to meet plant requirements are soil, fertilizers, and atmosphere. The various chemical forms of S in soils (Williams 1975) include both organic and inorganic compounds and their amounts vary widely both between soil types and within the soil profile itself. The various chemical forms of S also differ greatly in their availability to plants.

Table 1. Relation between S and N in *Pinus radiata* foliage.

1.	There is nil inorganic-N in tree foliage
2.	Total-N = inorganic-N
3.	Total-S = organic-S + inorganic-S (SO_4-S)
4.	N and S are biochemically related (protein and amino acids)
5.	$\frac{\text{Organic-S}}{\text{Organic-N}} \times 0.437 = 0.030$ (on a gram-atom basis)
6.	Sulfate-S is accumulated in excess of that S required to balance the N in protein formation
7.	Sulfate-S is an indicator of foliage S and N status

In the surface horizons of most well-drained soils, sulfate concentrations are generally low but considerable seasonal fluctuations in the amounts of soluble sulfate in the surface soil occur as a result of the mineralization of organic S, leaching of soluble sulfate, and its uptake by plants. The sulfate content of soils is also affected by the application of fertilizers and by the sulfate content of rain and irrigation waters. Soils vary widely in their capacity to adsorb sulfate. Many possess little or no sulfate adsorption capacity but in others adsorption plays an important part in the retention of sulfate against leaching and in determining its distribution in the profile.

Sulfate adsorption is greater in soils containing large amounts of aluminium and iron oxides, aluminium oxides usually being the more important. It is generally accepted that plants take up their S in the sulfate form and its availability is dependent upon the mineralization of soil organic S. Apart from fully available water-soluble sulfate, adsorbed sulfate has been shown to be available and to comprise a major source of plant-available S in many soils (Freney and Spencer 1960, Williams and Steinbergs 1964, Barrow 1967).

Wide areas of S deficiency have been reported in the United States (Beaton et al. 1971). The S status and S-supplying power of a range of Oregon soils were determined by Harward et al. (1962) in order to study soil properties and phenomena involving S, and their relation to plants to obtain a better basis for prediction to response to S fertilization (Table 2).

Table 2. Soil S status and percent growth response of alfalfa to added S as Na_2SO_4 (from Harward et al. 1962).

Parent material	Soil series	Organic -S (ppm)	Extractable SO_4-S (ppm)	Organic -C (%)	Relative growth[a]	Response to S[b]
Pumice	Deschutes	77	5	0.91	1	4.4
Basalt colluvium	Aiken	255	9	3.96	1.8	1.6
Basalt alluvium	Coker	113	8	1.63	2.6	1.6
Granitic alluvium	Medford	151	11	1.93	2.4	2.3
Granitic alluvium (old)	Barron	236	12	3.13	2.8	1.8
Alluvium (recent)	Chehalis	128	11	1.27	1.9	2.7
Alluvium (recent)	Powder	90	10	1.21	5.3	1.1
Alluvium (recent	Wingville	188	20	4.37	3.8	1.0
Alluvium (recent)	Sams	125	8	1.66	1.8	3.1
Water-deposited silts	Williamette	200	10	2.30	3.2	1.6
Alluvium (old)--gravelly	Baker	112	10	1.62	1.4	4.1
Alluvium (old)--silty	Knappa	765	19	10.63	1.7	1.1
Alluvium (old)--silty	Quillayute	692	16	10.23	1.1	1.0
Sedimentary	Astoria	408	20	7.42	2.5	1.0

[a]Growth of control plots compared with plot with lowest growth (i.e., pumice); e.g., growth of Aiken/growth of Deschutes = 1. [b]Comparison of growth of S-treated plots with control plot for each soil; e.g., at Aiken, growth of S-treated plot/growth of control = 1.6.

Sulfur is closely associated with C and N in soil organic matter and ratios of C:N:S = 140:10:1.3 have been recorded mainly for surface soils (Williams 1975). In Australian forest soils, the C:N:S ratio was found to be in the range 200:9:1 to 300:14:1 (J. Kelly, Forestry Commission of New South Wales, pers. comm. 1978). If N and S are released in these ratios during organic matter mineralization, then larger quantities of N are released than required to balance S; this S deficit in most situations is made up from the soil inorganic S reserves.

In the atmosphere the principal S compounds are sulfur dioxide, hydrogen sulfide (probably together with other reduced S species), and sulfate aerosols and mists. Removal of S from the atmosphere takes place by precipitation processes (involving mainly sulfate) and by dry deposition (principally of sulfur dioxide). The natural sources of atmospheric S include geothermal emissions, sea spray, and biogenic sources, while the major manmade sources of S emission into the atmosphere are from principal industrial sources, which include the combustion of coal and petroleum, petroleum refining, and the smelting of nonferrous ores.

Forest trees are extremely efficient at trapping S compounds in their foliage (Smith 1974). Clearly, evergreen trees act as filters all through the year, while deciduous trees, including such conifers as larch, intercept far less sulfur dioxide during the winter and early spring. Elements reach a forest canopy not only in bulk precipitation but also in aerosols and gases that are trapped from the atmosphere by impaction or adsorption onto the surfaces of the trees. This additional input can then be washed down in subsequent rain.

With living vegetation, unlike other inert vertical surfaces exposed to the wind, there are two further processes, foliar uptake and crown leaching, the first of which removes elements from the rain and the second adds elements to rain. Thus the element loading in rainwater beneath trees differs from that in bulk precipitation by an amount that is the sum of trapped input plus crown leaching minus foliar absorption, this amount being the gain of that particular element (Miller et al. 1976).

The sulfate-S status of conifer foliage provides an indicator of the S status of both the tree and the site (discussed earlier), and a relation has been found (Table 3) between the distances from S emitting sources and foliar sulfate-S concentrations (all foliage sampled at a standard position in the tree crown in autumn/winter at the end of the growing season; Lambert and Turner 1978).

SULFUR DEFICIENCY IN TREES

In contrast with P and N there do not appear to be any unequivocal demonstrations of growth responses to S by trees in the forest situation, although they have been demonstrated in culture solution and pot experiments for many commercial species. Beaton (1966) reported an S response in the greenhouse on pumice soils for *Pinus ponderosa* Laws., and found some evidence of a response in the field. Ingestad (1963) showed that there was a clear relationship between growth and S for *P. sylvestris* L. in culture solution.

In *P. radiata*, moderate S deficiency is associated with overall winter yellowing, especially on cold, exposed sites. When severe deficiency occurs, 1–2 m of the leading shoot, or sometimes merely the terminal buds, die back often with spectacular brownish red or red orange colorations. Needle bases are frequently much yellower than the remainder of the needle and this appears to be the best visual diagnostic symptom available in *P. radiata* (Lambert and Turner 1977).

Increased susceptibility to fungal disease can be demonstrated. In Australian *P. radiata* plantations, S deficiency does not appear to cause a direct reduction in primary productivity. There appears to be a high correlation between S deficiency and foliar pathogen infection (Lambert and Turner 1977), however, and associated with this are stem malformations with subsequent losses in merchantable productivity and volume. Sulfur deficiency produces a metabolic malfunction that leads to apical bud resinosis (hence facilitates the entry of fungus into the shoot) and also leads to an accumulation of particular amino acids favorable for the rapid growth of fungus.

Symptoms of S deficiency are sometimes confused with those of N deficiency, but have been variously described for tree species (Will 1961) to include pale greenish yellow foliage, reduced growth, and very fine branching. Within the foliage tissue, soluble N compounds are reduced in quantity.

Table 3. Comparison of S levels in *Pinus radiata* foliage from forests in close proximity to or distant from atmospheric S sources in Australasia.

Form of S	Distance from S source (km)	Soil type	Foliar sulfate-S (ppm) Mean	Range
H_2S[a]	0.1	Pumices	755	305–985
SO_2	2	Quarternary sands	1115	380–1840
SO_4	5–40	Quarternary sands	520	270–850
SO_2	5	Permian sediments	355	120–740
SO_2	18	Triassic sandstone	250	100–525
SO_2	25	Silurian	210	0–445
H_2S[a]	30	Pumices	190	80–310
SO_2	>28	Quarternary sands	125	50–250
SO_2?	>100	Tertiary basalt	45	0–120
SO_2?	>100	Diorite	30	0–110
SO_2?	>100	Basic extrusives	15	0–95

[a]New Zealand.

NITROGEN AND SULFUR UTILIZATION

The precise relation discussed previously between N and S in foliage allows for estimations to be made of the relative utilization of these nutrients. Growth responses to applied N fertilizers are dependent upon N uptake and incorporation into amino acids, which in turn is dependent upon adequate available S. Based on the constant ratio between organic S and total N, theoretical calculations have been made of the quantity of sulfate-S required to utilize added concentrations of N (Turner et al. 1979b). For every 0.1% increase in foliage N concentrations, 0.0065% S (65 ppm S) should be utilized. These theoretical calculations were calibrated (Table 4) using a Douglas-fir fertilizer trial in the Pacific Northwest where foliage S concentrations had been estimated (Turner 1977, Turner et al. 1979a).

The application of N at the rate of 220 kg/ha increased the mean foliar N concentration by 0.81% which corresponded to the theoretical utilization of 0.053% S (530 ppm S; Turner and Lambert 1979). The actual utilization was 0.074% S, the excess being attributable to needle expansion and retention. The calculations indicated that in order to obtain a response from N fertilization without inducing absolute or even marginal S deficiency, high foliar sulfate-S levels were required. Based on calculations from a typical case in Douglas-fir regrowth, it was shown that a minimum of 400 ppm sulfate-S was required to obtain a growth response to applied N fertilization. This minimal concentration of foliar sulfate-S was used as a predictive index (Table 5) for response in a series of Pacific Northwest Douglas-fir N fertilizer trials (26 stands).

Table 4. Calculated and actual foliage utilization of sulfate-S in a Douglas-fir fertilizer trial in western Washington.

Treatment	Before treatment	After treatment		
		Increase in	SO_4-S utilization	
	N concn. (%)	N concn. (%)	actual (ppm)	calcd. (ppm)
220 kg/ha N	0.94	0.61	790	395
880 kg/ha N	0.94	1.00	870	650

Table 5. Soil, foliage, and stand data for the control plots in the Pacific Northwest Douglas-fir fertilizer installations grouped according to growth response.

Location	Age (yr)	Site index (m)	Elevation (m)	Foliage N (%)	Foliage SO_4-S (ppm)	Foliage B (ppm)	N in profile (kg/ha)	Soil parent material
High growth response to urea application								
Black Rock[a]	45	38	530	1.24	760	38	7 720	igneous
Mineral Creek[a]	26	33	560	0.88	540	13	4 670	igneous
Skykomish[a]	45	32	100	0.92	740	26	5 440	igneous
Dollar Road[a]	31	32	530	0.94	690	32	4 200	sediments
Hood Canal[a]	59	37	60	1.11	1040	16	2 700	sandstone/glacial
Rhode Lake[a]	35	37	230	1.75	600	21	7 450	glacial
Matlock North[a]	42	33	185	0.83	420	14	4 070	glacial
Lake Nawatzel[a]	49	33	125	0.94	520	19	1 760	glacial
Cedar River[a]	42	26	60	0.99	550	9	2 800	glacial
Wonder	34	19	100	1.21	490	29	2 835	marine sediments
Marys Peak				1.21	450			
Old Gonyea				1.25	425			
				1.45	400			
Low or no response to urea application								
Mill Creek[a]	40	26	945	1.44	30	46	2 300	pumice
Rogue River[a]	52	26	835	1.36	50	51	1 360	pumice
Cummins Ridge[a]	38	35	435	1.70	0	26	10 300	basalt
Hamiltons Creek[a]	32	43	500	1.62	740	37	12 300	basic igneous
Deep Creek[a]	32	35	155	4.76	0	15	10 500	sediments
Camp Grisdale[a]	28	39	200	1.19	90	10	15 400	sediments
Hunger Mountain[a]	29	40	540	1.06	110	17	11 500	sandstone
Colton	29	38	370	1.20	480	18	4 570	sandstone
Elks Creek		48		1.42	50		5 960	sandstone
Satsop[a]	28	37	75	1.01	230	8	8 150	glacial
Eatonville[a]	49	33	245	1.18	470	19	4 330	glacial
Matlock		42		1.28	245		8 150	river outwash

[a]Source: Turner and Lambert (1979).

All stands responding to N applications had in excess of 400 ppm sulfate-S but not all the nonresponding stands had less than 400 ppm sulfate-S (Figure 1). Seventy-five percent of the nonresponders had less than 400 ppm sulfate-S and 60% had less than 200 ppm. Thus, for stands with less than 400 ppm foliage sulfate-S, a 100% correct prediction of nonresponse would have been made. For stands with foliage sulfate-S concentrations in excess of 400 ppm, however, the correct prediction would have been made for 80% of the stands.

Two related aspects have been studied in more detail. The first was to ascertain whether parameters other than foliar sulfate-S, which has not been routinely analyzed by the Regional Fertilization Project, could be used as predictive indexes of response to N fertilization. The second was to determine other nutritional limitations to growth response. Based on previous experience from relation between foliage S concentrations and soil types in Australia (Lambert and Turner 1978, Turner and Lambert 1979), soil parent materials were selected as a primary category.

In New South Wales, Australia, soil types had been divided into basic extrusives, granites, and sediments, with the sediments further subdivided according to age. At the first approximation, the soil parent material can be considered to reflect the possible soil nutrient reserve. Together with this an availability factor should be considered and, as most S in most soils becomes available from mineralization of organic matter, the quantity of soil organic matter was selected as this gross factor. Data were available on growth response, soil parent material, and soil organic matter for 62 Douglas-fir installations in the Pacific Northwest and they were used to ascertain the applicability of the stated parameters to the predicted growth response to N fertilization.

Various reported studies have indicated that the soil parent materials have varying S and N status and hence provide a basis for grouping into different soil types. Pumice soils in Oregon have been studied (Harward et al. 1962, Will and Youngberg 1978, Youngberg and Dyrness 1965). The results indicated that the S status of these soils was low and that when N was applied it was desirable to apply S simultaneously. Harward et al. (1962) have indicated differences in S availability for Oregon soils derived from varying parent materials (Table 2) together with the relation between extractable S concentrations and percentage growth response of alfalfa to S applications (Figure 2). Will and Youngberg (1978) showed that S additions gave further growth responses to added N in field-grown *P. ponderosa* and *P. radiata*.

Figure 2. Relation between growth response of alfalfa to added S for a series of Oregon soils (from Harward et al. 1962). The soil parent materials were: pumice = p; basalt derived = b; granite derived = g; recent alluvium = r; old alluvium = o; sedimentary = s; silt = w; loess = l (Y = 295.15 S, r = 0.66, n = 14 where Y = percent growth response and S = soil sulfate + S [ppm]).

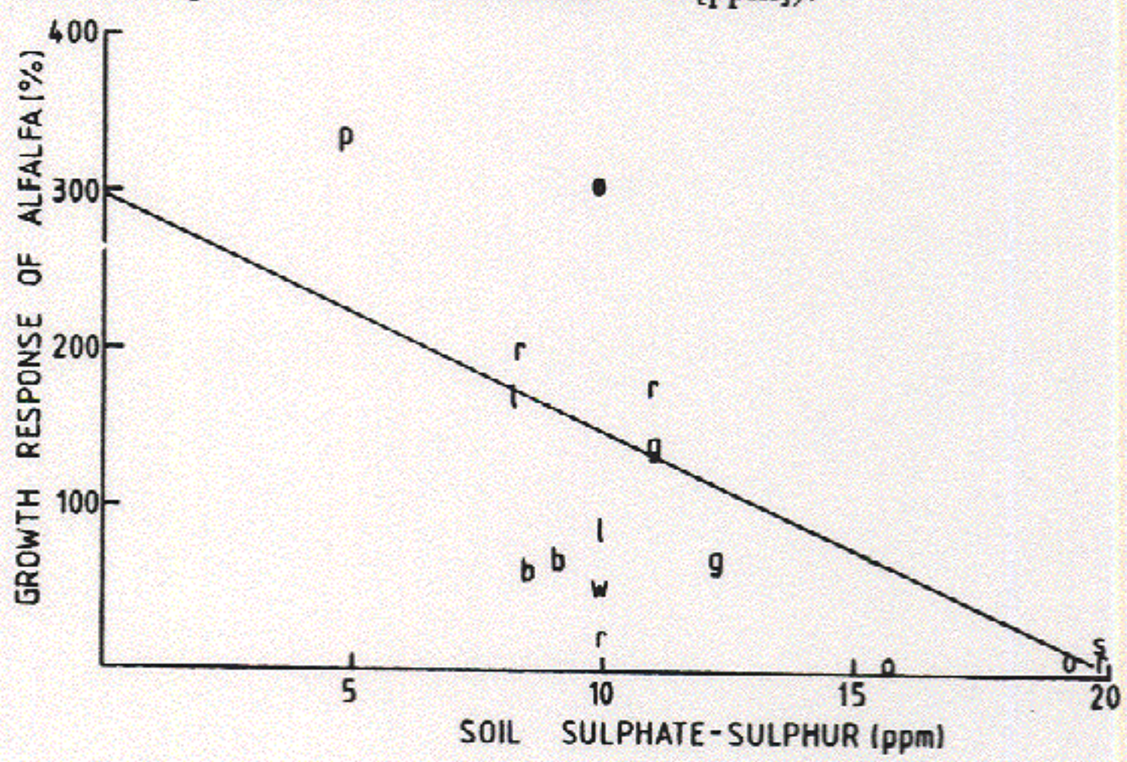
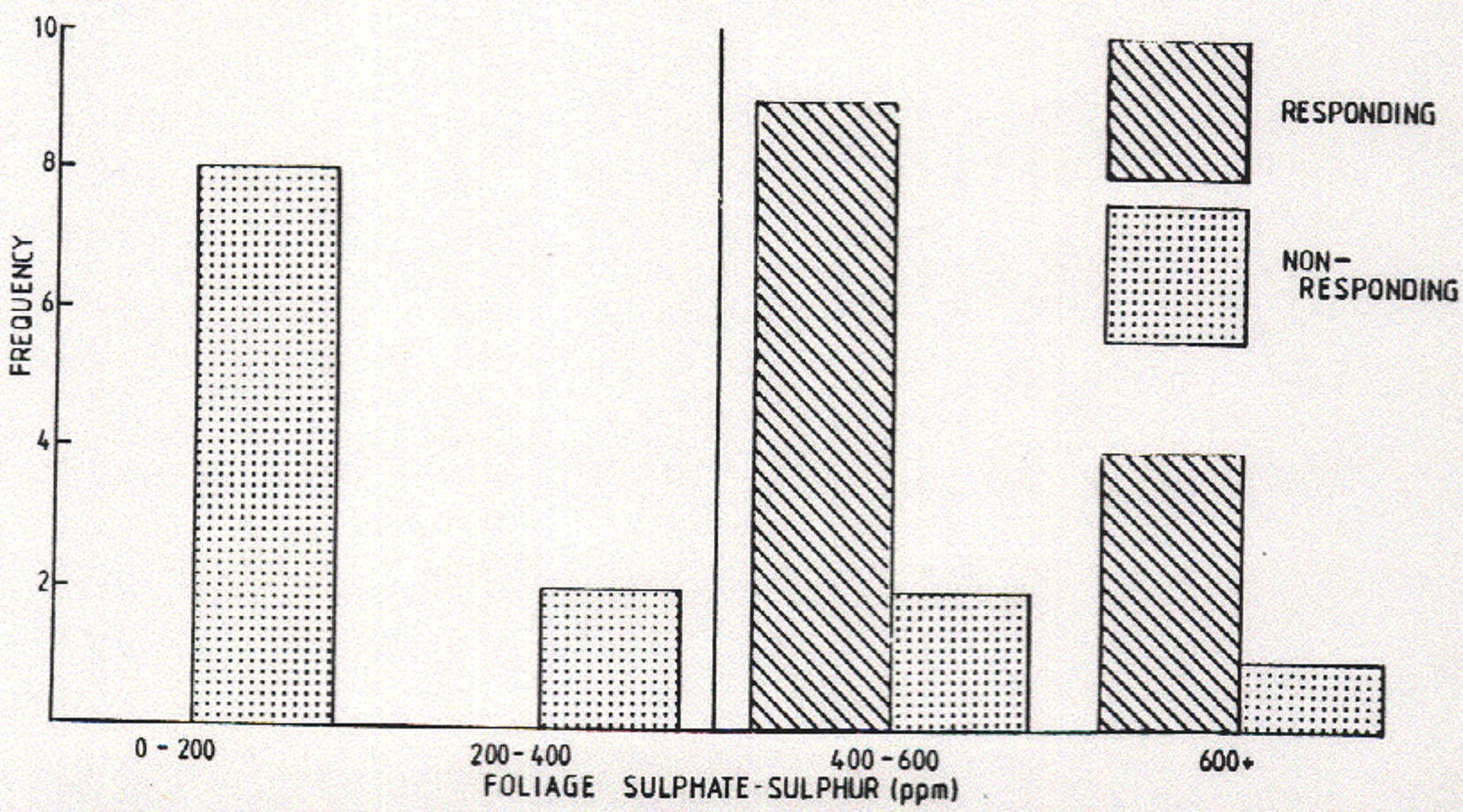


Figure 1. Frequency of response or lack of response for Pacific Northwest Douglas-fir stands in relation to foliar sulfate-S concentrations.



The soil parent materials represented in the Pacific Northwest installations were grouped in eight categories (Figure 3):

1. *Pumice soils*—Low response to N fertilization was obtained. The foliar sulfate-S two installations located on this soil type 30 and 50 ppm, respectively, hence response to N not expected.

2. *Soils derived from basalt and basic intrusives*— Eleven installations were located on this soil type and, since the presence of large quantities of organic matter (probably in excess of 200 000 kg/ha) would inhibit S mineralization, the response level was assessed in relation to the quantity of organic matter. On this basis, the correct response was made for 10 of the 11 installations since only one of the low responders had less than 200 000 kg/ha organic matter. There was a further relation between increase in plot elevation and decrease in soil organic matter quantity (Figure 4), so that all the responding plots were at the highest elevations.

3. *Soils derived from igneous (acid) parent materials*—All these installations had soils with less than 200 000 kg/ha organic matter and with two exceptions all responded.

4. *Soils derived from sedimentary parent materials*—Responses on these soils, which were divided into "old" sediments, sandstone, river outwash, and "other" sediments (including an "old marine" sediment), were variable. Subdivision provided an improved prediction for the river outwash and other sediments where a low response was obtained for all installations. For the old sediments, it appeared that there was a reverse relation to the basalts in that responses occurred with high organic matter accumulation. The sandstone group had no definite trend. For all subgroups, there was no relation with elevation.

5. *Soils of glacial origin*—The properties of these soils were similar to those derived from igneous parent materials and, using a similar assumption of expected response when the roganic matter content was less than 200 000 kg/ha, a correct prediction was made for 10 of the 14 installations. (Most of the early responses to N fertilization were obtained on these soil types [Beaton et al. 1964, Gessel and Shareef 1957, Gessel and Walker 1956]).

To determine further whether soil parent materials were a logical division in terms of growth parameters, other measured factors have been assessed. By pooling all the data for foliar N and site quality from the installations, no relations to explain response were found, but when the data were stratified according to soil parent materials relations were obtained (Figure 5). The soils derived from sedimentary parent materials formed a group with the following relation:

Site index (m) = 17.69 N(%) + 19.44 (r = 0.78, n = 9)

The soils derived from glacial and acidic igneous origins could not be distinguished from each other and so were pooled:

Site index (m) = 16.21 N(%) + 14.42 (r = 0.87, n = 16)

When the data from Shumway and Atkinson (1978) were

Figure 3. Relation between growth response from urea application to Douglas-fir and the parameters of soil parent materials and soil organic matter. *Low* response represented growth responses between 0% and 20%.

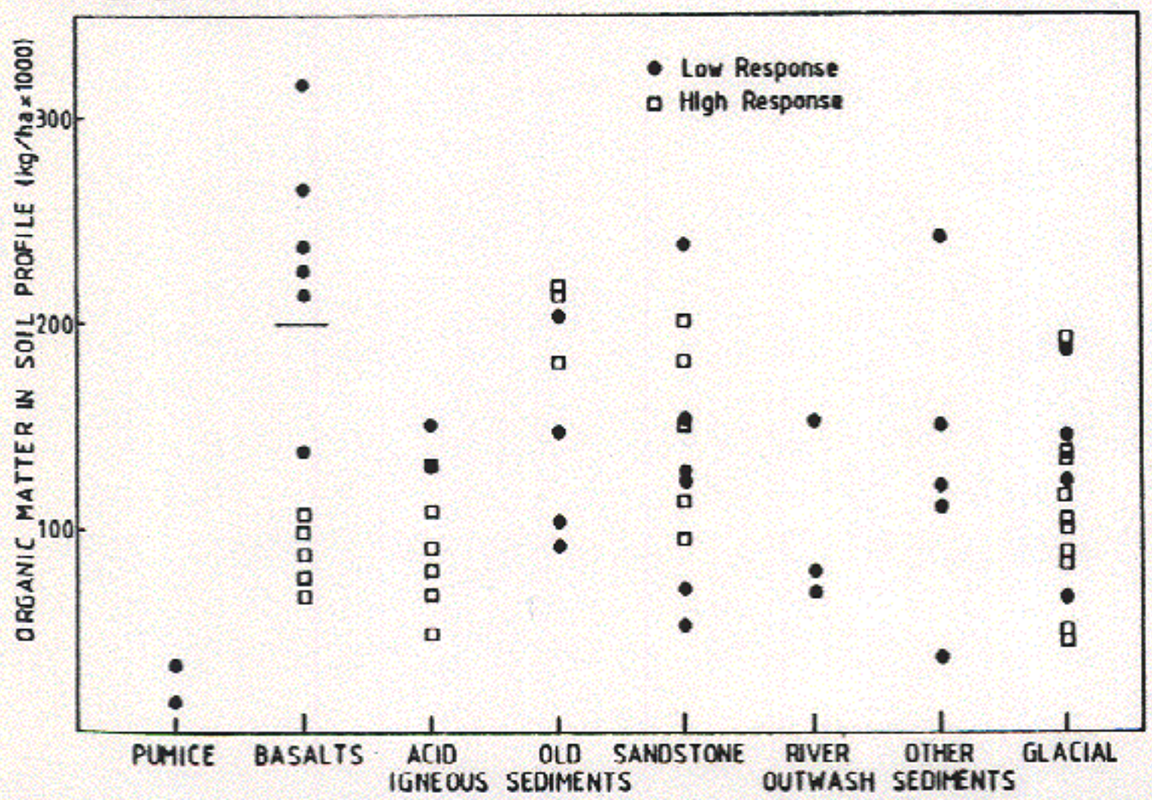


Figure 4. Relation between elevation and soil organic matter for soils derived from basalts and basic igneous parent materials. (Soil organic matter [kg/ha] = 315656 - 276 elevation [m]; r = 0.70, n = 8.)

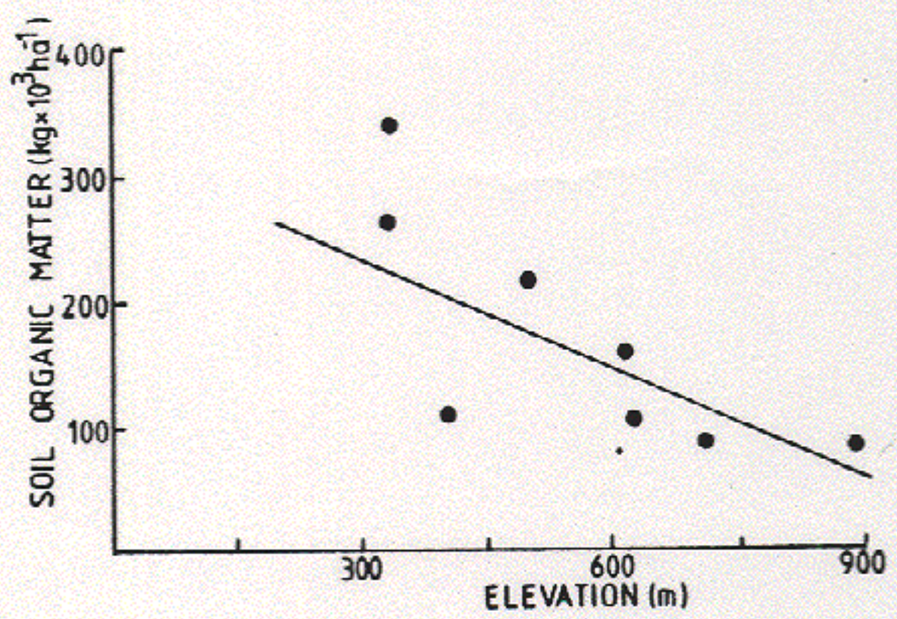
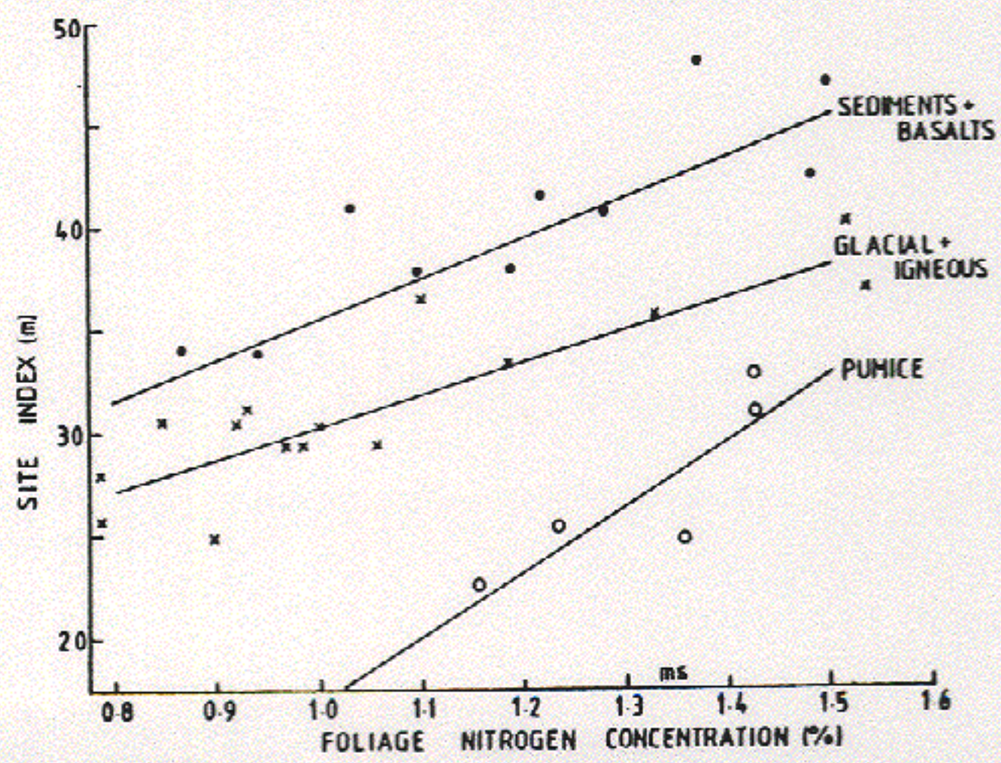


Figure 5. Relation between foliage N concentrations and site index for Douglas-fir. grouped into soil parent materials.



plotted according to their parent material groupings (Figure 6), there were indications that, depending on the concentration of mineralizable N, a greater response could be expected for soils derived from basalts than from sandstones.

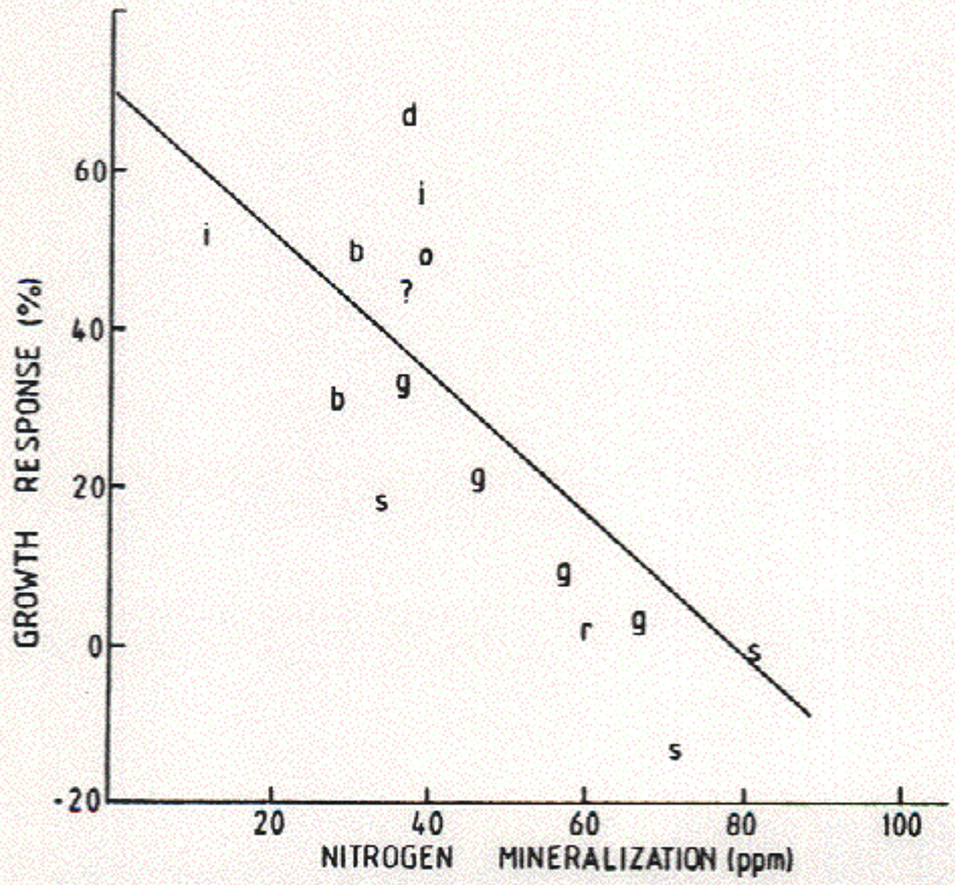
The installations that did not respond to N applications but had sufficient foliar sulfate-S, were assessed in greater detail to determine other potential nutritional limitations. By applying the B nutritional requirements of *P. radiata* (Lambert and Turner 1977) to the Douglas-fir data (Turner et al. 1977), it appeared that B was a potentially limiting nutrient on some sites, however it was not possible to determine the critical limiting concentration for this nutrient.

M. J. Lambert (Forestry Commission, New South Wales, pers. commun. 1979) has indicated that there is a relation between climatic factors and B deficiency levels such that trees growing in cooler moister locations require less B (<6 ppm B) compared with areas with higher moisture stress (12–15 ppm B). It has also been reported that applications of N have been found to reduce B concentration in *P. radiata* foliage and that dieback has been induced (Lambert and Turner 1978). Data for Douglas-fir grown in Australia has indicated that this species has higher nutrient demands than *P. radiata* (Table 6). The high nutrient demands of Douglas-fir have also been noted by other workers (Van Goor 1970).

The Diagnosis and Recommendation Integrated System (DRIS) developed by Beaufils (1973) and investigated by Sumner (1977, 1978) was applied to the data from the Douglas-fir installations in order to obtain preliminary concentrations of foliar nutrient adequate (Truman, Forestry Commission, New South Wales, pers. commun. 1978). The DRIS analysis attempts to characterize a range of nutritional and environmental parameters to develop norms used to calculate indexes that indicate nutrient imbalance. The system has been modified to determine limiting nutrient concentrations for Douglas-fir foliage. Preliminary investigations have indicated that the deficiency levels for N, B, and P are in the vicinity of 1.0%, 14 ppm, and 1500 ppm, respectively. Preliminary data have indicated a high probability that the nonresponding plots with sufficient S in the Douglas-fir installations (Table 4) required P additions.

In summary, it appears that in order to obtain growth responses, fertilizer types must be selected on the basis of soil type. On some sites urea alone would be the most appropriate, but on other sites N-S fertilizers (e.g., S-coated urea), N-P (e.g., urea-superphosphate or ammonium phosphate), or even further mixed fertilizers (e.g., urea-boronated superphosphate) may be required.

Figure 6. Soil N mineralization and tree growth response to urea application for a series of Pacific Northwest Douglas-fir stands (Shumway and Atkinson 1978). The soil parent materials were: glacial origin = g, sandstone = s, acidic igneous = i, basalt = b, old sediments = o, river outwash = r, basic igneous = d. ($Y = 48.92 - 0.92\ N + 211\ 361.69\ [1/S]^2$, where Y = percent diameter growth response, N = mineralizable N (ppm), S = percent normal stocking calculated for $S = 100$).



SULFUR DEFICIENCY AND FUNGAL SUSCEPTIBILITY

In field trials with *P. radiata*, Turner and Lambert (1979) found that the non-S-containing amino acid arginine accumulated in high concentrations in the foliage of S-deficient trees. Steward et al. (1959) also reported that high accumulations of amino acids, in particular arginine, were an indication of S deficiency in *Mentha piperita*. Despite the functional relation between S and N, the amino acid composition in plants is affected differently by a deficiency of either element. For example, N deficiency in *Mentha piperita* resulted in relative increases in comparison with the control in glutamic acid and serine, decreases in alanine, Y-amino butyric acid, and aspartic acid, and a disappearance of leucine.

Sulfur deficiency resulted in large increases in arginine and asparagine, decreases in valine, alanine, serine, glutamic acid,

Table 6. Comparison of foliar nutrient concentrations in *Pinus radiata*, *P. ponderosa* and *Pseudotsuga menziesii* growing in N.S.W., Australia, arboretums.

Location		Species	N (%)	P (ppm)	Ca (ppm)	B (ppm)	SO_4-S (ppm)
Nundle	-I	*P. radiata*	1.88	1410	2190	23	10
		P. ponderosa	1.60	1540	2310	22	5
		P. menziesii	1.87	2260	3910	35	30
	-II	*P. radiata*	1.75	1705	830	10	5
		P. menziesii	2.03	3080	3020	39	160
Barrington Tops		*P. radiata*	1.71	2150	3480	11	200
		P. ponderosa	1.82	3750	3880	25	55
		P. menziesii	2.04	3860	6610	42	230

and aspartic acid, and a disappearance of leucine. It appeared that N deficiency resulted in an increase in the quantity of free amino acids with high C:N ratios, while with S deficiency the free amino acids had lower C:N ratios. The total soluble N content of S-deficient plants was increased while Ndeficient plants it was decreased.

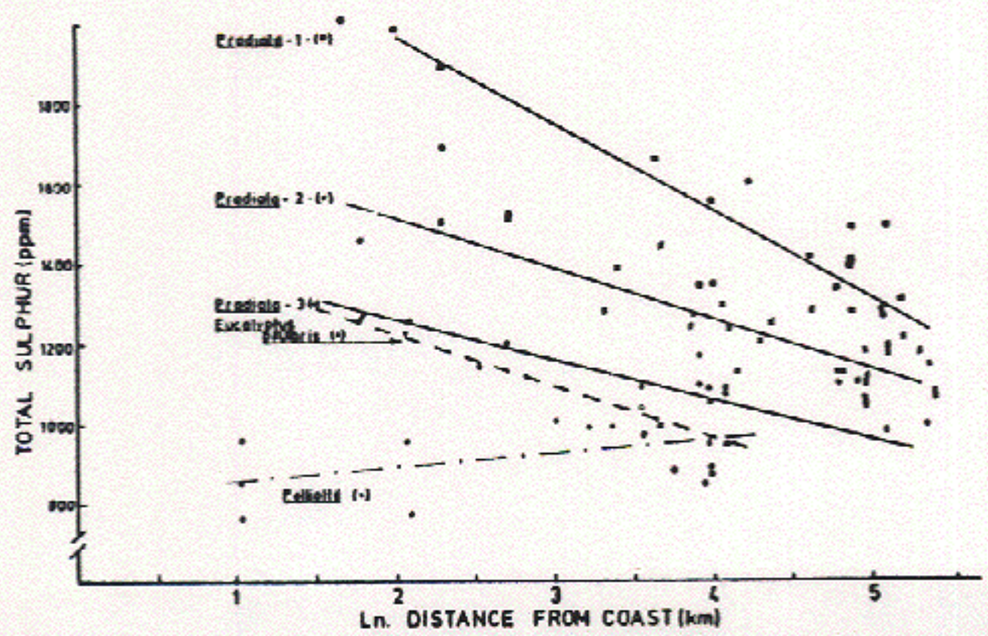
Arginine accumulation in *P. radiata* foliage has been found to be related to susceptibility to fungal disease (Turner and Lambert 1979). Infection by *Diplodia pinea (Desm.)* Kickx can be initiated in a number of ways, but it appears that the ability of a tree to limit the entry and development of the fungus is strongly influenced by its S status. The accumulation of particular amino acids (e.g., arginine) in the foliage of S-deficient *P. radiata* has been shown to be favorable for the rapid growth of the fungus (Edwards, Forestry Commission, New South Wales, pers. commun. 1977).

A field fertilizer trial with *P. radiata* was established in an N-rich/S-deficient environment to determine the effects of N and S fertilizers on the concentrations of these nutrients in the foliage and to relate any differences to tree growth and health (Turner and Lambert 1979). The treatments consisted of control (untreated), gypsum and two levels of N (100 and 400 kg/ha N as ammonium nitrate).

The results for the foliar S concentrations indicated that the most striking changes occurred in the plots where N fertilizer had been applied. Within 3 mo after treatment, S deficiency was induced and has persisted to the present. The foliar sulfate-S in the Ntreated plots had been utilized with a corresponding increase in the total concentrations of free amino acids, particularly arginine. It was further noted that *Dothistroma septospora* (Dorog.) Morelet infection, a severe needle cast fungus, was highest in the N-treated plots, with the degree of infection depending upon the intensity of S deficiency.

There is a high probability that similar foliar arginine accumulations can occur in other coniferous species as a result of induced S deficiency. van den Driessche and Webber (1977) found that applications of 0, 224, and 448 kg/ha N to a Douglas-fir stand resulted in 0.3, 5.4, and 26.1 μmol/g arginine, respectively, even 14 months after application, but there were no significant changes in needle N concentrations (foliage S concentrations were not assessed). In an attempt to improve cone production, Barnes and Bengtson (1968) induced increases in arginine concentrations in *P. taeda* L. needles with N applications. It has been suggested that such increases in arginine concentration will increase tree susceptibility to fungal and insect attack (Durzan 1974).

Figure 7. Relation between foliar total-S and log of the distance from the coast for *P. radiata, P. elliottii,* and *E. pilularis* (from Lambert 1979).



SPECIES AND PROVENANCE DIFFERENCES IN SULFUR UTILIZATION

Comparisons between tree species based on foliage nutrient concentrations from field situations often present problems and these are exacerbated when interacting nutrients are being assessed. In situations where S is adequate, foliar sulfate-S is a good comparative index, but if S is deficient or the N availability is variable, foliar total-S may provide an improved index. Lambert (1979) compared S uptake between coniferous species using a series of arboretums and trial plantings in New South Wales, Australia. The sources of S available to these trees were the soil and atmosphere which specifically involved oceanic inputs.

In the case of *P. raidata* (for which most data were available), foliar total-S concentrations decreased with increasing distance from the coast. There was an effect from soil fertility in that trees on the most fertile soils (usually basalt derived) had the highest S accumulations, whereas trees on the nutritionally poor sedimentary soils (Triassic, Permina, and Devonian sediments) had the lowest S accumulations. Lambert (1979) also showed that other coniferous species reacted differently (Table 6, Figure 7). For example, *P. elliottii* Engelm. did not appear to accumulate S even near the coast. Douglas-fir (from the small amount of data available) had very high S accumulations. These data suggested that species native to coastal situations (e.g., *P. radiata*), when planted near the coast, can accumulate higher concentrations of S.

Inland these species had low concentrations of total S, the lowest concentrations being where inputs were very low (i.e., the tablelands). Species native to inland locations (e.g., *P. ponderosa*) had a pattern of foliar total S accumulation independent of their geographical location. This indicates that inland species are adjusted to uptake of S from the soil and in areas of higher atmospheric inputs they cannot efficiently utilize this additional source.

Pinus radiata located on very fertile soils, and hence with high productivity, had higher foliar N utilization during spring than lower productivity stands, and therefore had a higher foliar sulfate-S requirement (Lambert 1979). On this basis sul-

fate-S requirements for adequate growth have been reassessed as shown in Table 7.

Various species and provenances differ in their ability to utilize nutrients (van den Driessche 1974), and hence potential responses to fertilizer applications will probably be different. Provenance differences have been obtained from a field experiment involving provenances of Pacific Northwest Douglas-fir located on a fertile basalt-derived soil at Canobolas, N.S.W. The average site quality was 47 m based on the system of King (1966), but there were no provenance growth differences. The provenances were found to differ in foliage total N, total S, and B concentrations (Table 8). These results indicate that if an area is to be restocked and the nutrient status of the site has been altered from the first crop (either by elevated inputs or fertilizer additions), then those provenances that are more efficient at utilizing the limiting nutrients or those giving better responses to fertilizer additions should be considered.

Table 7. Suggested deficiency and sufficiency sulfate-S levels in *Pinus radiata* foliage revised from Turner et al. (1977) to take site productivity into account.

Sulfur status	Foliar sulfate-S levels (ppm) (from Turner et al. 1977)	Revised productivity: Low	Medium	High
Deficiency to incipient deficiency	0–80	0–50	0–90	0–120
Marginal to adequate	80–200	50–100	90–120	120–240
Adequate to high	200–400	100–250	200–400	240–500
High (possible N deficiency)	400+	250+	400+	500+

Table 8. Mean foliar nutrient concentrations for provenances of Pacific Northwest Douglas-fir age 15 yr, grown on basaltic soil in N.S.W., Australia.

Provenance	N (%)	Total-S (ppm)	SO_4-S (ppm)	B (ppm)	Mean growth: dbh (cm)	ht (m)
Darrington	1.00	855	170	30	15.5	11.7
Ashford	1.04	930	210	24	15.0	11.1
Baker	1.17	930	125	16	15.0	11.4
Santian	1.31	1170	265	22	14.3	11.2
Pe-ell	1.34	1040	120	28	15.3	11.2
Cowlitz	1.40	1105	145	22	14.3	11.0
Mololla	1.50	1095	70	26	15.5	11.2
Vader	1.51	1285	245	22	15.1	11.2
$L.S.D._{0.05}$[a]	0.30	240	n.s.[b]	1.7	n.s.	n.s.

[a] $L.S.D._{0.05}$ = least significant difference at the 5% level. [b] n.s. = not significant.

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