FOLIAR MACRONUTRIENT CONCENTRATIONS AND FOLIAGE RETENTION IN RADIATA PINE CLONES ON FOUR SITES

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ABSTRACT

Foliage of radiata pine (**Pinus radiata** D. Don) clones on four sites, at Glenbervie, Whakarewarewa (Whaka), Gwavas and Berwick State Forest, was analysed for N, P, K, Mg and Ca. Foliage longevity was recorded and crown density scored visually.

At Glenbervie P deficiency was confirmed, and Ca deficiency was possible. Mg was just adequate at Whaka. Otherwise, available macronutrients appeared abundant.

Clonal differences in concentrations of individual nutrients occurred within sites rather than persisting over several sites.

Among clones, foliar nutrient concentrations were independent of growth rates; in particular, differences in P content were unrelated to large differences in tolerance of P deficiency. Hence foliar analysis, although reflecting average nutrient status of a population, appears less reliable for individual genotypes.

Tree-to-tree correlations within clones between different nutrients showed few clear patterns, but there was a general positive association betwen P and K levels.

Foliage was retained much longer at the sites which were drier and had no evident nutrient deficiency. Foliage longevity although differing between clones was unrelated to crown density or growth rate, except at Glenbervie.

INTRODUCTION

Foliar analysis is a well accepted method of assessing nutrient status in tree crops (Leyton, 1958; Gessel, 1962). Relatively little work has, however, been done on tree-to-tree genetic variation in foliar nutrient concentrations. Hence there remains the question of whether foliar analysis accurately reveals the nutrient status of an individual tree. In practice, diagnostic foliage sampling is normally made from 10 or more trees as a precaution against both genetic and non-genetic variation between individuals in nutrient concentrations.

Apart from the nutrient concentrations of foliage the longevity of foliage could influence the nutrient economy because of its obvious influence on nutrient turnover. Moreover, the longevity of foliage should influence the total foliage in the crown. This in turn has a potential influence on productivity.

An earlier paper (Burdon, 1971), describing the growth of radiata pine (*Pinus*

radiata D. Don) clones planted on four sites, reported large clonal differences in tolerance of adverse soil conditions at one site, Glenbervie. This paper is concerned with the differences between clones and sites in foliar nutrient concentrations, and with confirming the critical factors limiting growth at Glenbervie. Clonal relationships between nutrient concentrations and growth rates are considered, as are the general interrelationships between concentrations of different nutrients. The paper also covers the longevity of foliage among clones and sites, and its relationship to other characters.

MATERIALS AND METHODS

The experiment has been described in detail earlier (Burdon, *loc. cit.*). Eighteen young seedlings were replicated as cuttings within and between four contrasting sites, at Glenbervie, Whakarewarewa (Whaka), Gwavas, and Berwick State Forests. Not all clones were represented on all sites, while the number of cuttings (ramets) per clone at a site ranged from one to six.

Among sites Glenbervie and Whaka have the highest rainfall and Berwick the lowest. The soil at Glenbervie is infertile clay, typical of the region, where soils are characteristically deficient in available phosphate. The soils at Whaka, Gwavas and Berwick are a pumiceous sandy loam, a gravelly sandy loam, and a loess-derived clay loam respectively.

Twelve years after planting, during a destructive assessment, a foliage sample was collected from each live and unsuppressed tree. Sampling was done at Glenbervie in mid-June, at Gwavas in early July, at Whaka during August, and at Berwick in mid-October. Mature first-year foliage was taken from second-order branches in the free-growing crown, all aspects being represented. Samples were analysed for N, P, K and Ca, using methods of Knight and Will (1971).

The number of years' foliage retained on each tree was recorded by the author, for the leader, the upper crown, and the lower crown, separately. If almost all foliage of a given age n years, was retained, but practically no older foliage, a value of n would be recorded. According to whether a regular sprinkling, most, or almost all the foliage aged $(n + 1)$ years was retained, the recorded value would be $(n + 1/3)$, $(n + 2/3)$ or $(n + 1)$. This procedure was necessarily somewhat subjective, and was imprecise insofar as some foliage of one year would be shed before all from the preceding year had fallen. The resulting errors of assessment, however, were clearly small in relation to differences that existed.

Crown density was scored visually by the author for each tree, using a 1 to 6 scale, 1 being very sparse and 6 very dense. Each tree was scored purely in relation to others within the stand, so the scores formed no basis for comparing sites.

RESULTS

At Glenbervie the trees showed the poor growth, thin crowns, spindly form, and some needle fusion and crown dieback, which characterise growth on phosphate deficient soils in the region. However, clones differed strikingly in vigour and in the amount of dieback. Needle fusion although severe was confined to a single clone (67). At Whaka growth was generally very vigorous. Even so, a few clones showed poor vigour there. Clone 67 had severe needle fusion and dieback as well, although not as

badly as at Glenbervie. Another clone, 68, which was missing at Glenbervie, had very slight needle fusion. At Gwavas growth was somewhat slower than at Whaka, and at Berwick it was slower still. At these two sites, however, all clones showed satisfactory vigour and no nutrient deficiency was evident. Detailed results for growth have been presented earlier (Burdon, 1971).

Table 1 shows site means for nutrient concentrations and foliage retention. The means represent either averages of clonal means or overall means, depending on whether or not clones differed significantly. With calcium, which had appreciably skewed distributions, the values are root mean squares. One outlier value for calcium (which was associated with relatively low nitrogen and phosphorus and high magnesium) suggested that the sample in question included some second-year foliage. Records showed abnormal crown development (terminal hypertrophy, or "foxtail") in the particular tree, which would appear to have caused difficulties in applying the specified sampling procedure. All data for the sample from this tree were therefore discarded.

TABLE 1—Mean foliar concentrations of individual macronutrients, and mean foliar retention, by sites

Site	Foliar concentration					Foliage retention (yr)	
	N	P	K	Mg	Ca	leader	lower crown
Glenbervie	1.95a	0.110c	0.76c	0.117b	0.18c	1.4b	2.6c
Whaka	1.75a	0.188ab	1.29a	0.064c	0.23b	1.3b	2.4c
Gwavas	1.85a	0.212a	1.11b	0.127b	0.28a	1.6b	3.4b
Berwick	1.96a	0.176b	0.71c	0.150a	0.28ab	1.9a	5.3a

Reading down columns, values with a letter in common do not differ significantly at the 1% probability level.

Note: Values for Ca are root mean squares. Arithmetic means are greater by approximately 0.01 at each site.

With the highly unbalanced classification, differences between sites were tested individually, using paired t-tests. The pairs of values represented the means, at the respective sites, for each clone that was common to both sites. Hence the site means used in the tests did deviate very slightly from the values in Table 1. Such tests are only approximate, so $P < 0.01$ was adopted as the criterion of statistical significance for site differences.

The concentrations of all nutrients except nitrogen differed significantly between sites. Of note were the low phosphorus level at Glenbervie (S.E. $< 0.003\%$), the low magnesium level at Whaka, and the lowish calcium level at Glenbervie. Foliage was retained longest at Berwick, followed by Gwavas, and then Glenbervie and Whaka. Foliage was retained longer, with greater differences between clones, in the lower crown than on the leader. Upper crown foliage was generally intermediate in both respects. Further results on this character are only presented for the lower crown. It may be noted that there are no satisfactory estimates of the actual amounts of foliage.

Clonal repeatabilities for nutrient concentrations, foliage retention, crown density scores, and breast height diameter over bark (d.b.h.o.b.) are listed for individual sites in Table 2. Clonal repeatability was calculated as $V_C/(V_C + V_E)$, where V_C and V_E were between-clones and (between-ramets-) within-clones variances respectively, as estimated from analysis of variance (Burdon, *loc. cit.*). The statistical significance of clonal differences is identical to the significance of a clonal repeatability. This repeatability represents broad-sense heritability if the clones are a random sample* from the population and if clonal differences are purely genetic.

TABLE 2—Clonal repeatabilities of foliar macronutrient concentrations, foliage retention (lower crown), crown density, and d.b.h.o.b., by individual sites

Site	Foliar concentration N	P	K	Mg	Ca	Foliage retention	Crown density	D.b.h.o.b.†
Glenbervie	0.39*	0.46**	0.40*	0.40*	0.36*	0.47**	0.80***	0.68***
Whaka	0.00 NS‡	0.00 NS‡	0.48**	0.11 NS	0.03 NS	0.76***	0.89***	0.50***
Gwavas	0.62**	0.20 NS	0.40**	0.25 NS	0.17 NS	0.39**	0.64***	0.04 NS
Berwick	0.00 NS‡	0.26*	0.39**	0.37*	0.24 NS	0.54***	0.72***	0.45**

NS denotes not significant, $P > 0.05$
* denotes significant, $P < 0.05$
** denotes highly significant, $P < 0.01$
*** denotes very highly significant, $P < 0.001$
† from Burdon (1971)
‡ when clonal differences give $F \leq 1$ in analysis of variance, V_C is assumed to be zero

Clones differed significantly ($P < 0.05$) in levels of all nutrients at Glenbervie. Clonal differences in potassium were significant on all sites. Otherwise there were relatively few significant clonal differences in nutrient levels. Highly significant ($P < 0.01$) clonal differences were observed for foliage retention and crown density score throughout, and for d.b.h.o.b. at all sites except Gwavas. Repeatabilities are presented for stem diameter as it appeared a better index of clonal vigour than height (Burdon, *loc. cit.*).

Table 3 shows the between-clone, within-clone and phenotypic coefficients of variation for individual characters at each site. The coefficients represent $\sqrt{V_C} \div S$, $\sqrt{V_E} \div S$ and $\sqrt{(V_C + V_E)} \div S$ respectively, where S is the mean for the site in question.

The within-clone coefficients, which are subject to comparatively small sampling errors, differed strongly between sites for nitrogen, phosphorus and calcium. In these cases there is between-site heterogeneity of within-clone variance which cannot be overcome by any customary transformation of data (e.g. logarithm or square root). The low phosphorus levels at Glenbervie were associated with low within-clone variability, but

* The clones actually represented two individuals from each of nine wind-pollinated progenies. With no selection for the character in question the expected variance of the clones is similar to that if they were chosen at random.

TABLE 3: Between-clone, within-clone, and phenotypic coefficients of variation (%) for foliar macronutrient concentrations, foliage retention (lower crown), and d.b.h.o.b. by individual sites

Coefficient	Site	Foliar concentration					Foliage retention	D.b.h.o.b.*
		N	P	K	Mg	Ca		
Between-clones	Glenbervie	12	8	13	16	7	20	31
	Whaka	0	0	8	7	3	11	24
	Gwavas	7	7	9	8	3	11	4
	Berwick	0	10	9	10	7	6	10
Within-clones	Glenbervie	14	8	14	19	11	14	22
	Whaka	9	19	9	20	15	8	24
	Gwavas	5	14	11	14	7	11	18
	Berwick	12	17	12	13	13	6	11
Phenotypic	Glenbervie	18	11	19	24	14	24	38
	Whaka	9	19	12	21	15	14	34
	Gwavas	9	16	14	16	8	16	18
	Berwick	12	20	15	16	15	8	15

* derived from Burdon (1971)

no other such relationship was evident. The phenotypic coefficients of variation for nutrients typically ranged from 10 to 20 percent. At Glenbervie there were very large clonal differences in both diameter growth and foliage retention.

Correlations between sites, of clonal means, for concentrations of individual nutrients and for crown density and foliage retention, are noted in Table 4. The correlations for nutrient concentrations were generally weak, although mainly positive. Only for nitrogen were any correlations statistically significant, which suggests that this is the only nutrient for which any clonal differences are consistent from one site to another. With potassium, which showed clonal differences within sites but no real correlations between sites, there appear to be considerable clone-site interactions. The strong correlations for crown density suggest that interactions are subordinate to clonal differences over all sites. The weaker correlations for foliage retention suggest some interactions. Rigorous tests, in two-way analyses of variance, for clonal differences over all sites and for all interactions, were generally impracticable, because of between-site heterogeneity of residual error variance.

At each site correlations were calculated between the clonal means of nutrient concentrations on one hand, and the means of d.b.h.o.b. and foliage retention on the other. These correlations were generally too weak and too inconsistent among sites to appear meaningful. This applied even for phosphorus content and stem diameter at

TABLE 4—Between-site correlations of clonal means, for foliar macronutrient concentrations, crown density, and foliage retention (lower crown), by individual sites

Sites	Foliar concentration					Crown density	Foliage retention
	N	P	K	Mg	Ca		
Glenbervie/Whaka	-0.32	0.15	0.21	0.43	0.42	0.65	0.03
Glenbervie/Gwavas	0.53*	-0.28	0.17	0.11	0.32	0.73*	0.37
Glenbervie/Berwick	0.24	0.34	0.26	0.06	0.29	0.49	0.45
Whaka/Gwavas	0.69*	0.10	-0.14	-0.20	0.20	0.80*	0.73*
Whaka/Berwick	0.44	0.35	-0.02	0.34	0.03	0.85*	0.57
Gwavas/Berwick	0.28	0.22	0.12	-0.17	0.03	0.62*	0.33

* denotes significant, $P < 0.05$
Other correlations not significant, $P > 0.05$

Glenbervie ($r_{14_{d.f.}} = 0.21$, $P > 0.4$), despite strong clonal differences for both characters. The occasional significant correlation could be attributed to random chance. For the corresponding relationships between nutrient levels and foliage retention the situation was similar.

The prevalence of dieback in individual clones at Glenbervie showed no clear relationships with foliar nutrient levels there. There were no significant correlations of clonal means between foliage retention and d.b.h.o.b., and between foliage retention and crown density. Only at Glenbervie was there a significant correlation between crown density and stem diameter ($r_{14_{d.f.}} = 0.85$, $P < 0.001$).

Within-clone "correlations" (R) between different nutrients, derived after fitting pooled or average within-clone regressions for each site, are listed by sites in Table 5. Results are presented only for pairs of nutrients which appeared to be appreciably correlated, although all combinations were calculated.

TABLE 5—Within-clone "correlations" (R) between different nutrients, by sites. R values calculated after fitting pooled or average within-clone regressions

Nutrients	Site			
	Glenbervie	Whaka	Gwavas	Berwick
N/P	-0.27 NS	0.04	0.44*	0.66***
N/K	-0.19 NS	0.44*	0.45*	0.36*
P/K	0.57**	0.45*	0.74**	0.49**
P/Ca	0.26 NS	-0.55**	-0.28 NS	-0.41*
K/Ca	-0.28 NS	-0.07 NS	-0.36*	-0.34 NS
Mg/Ca	0.36 NS	0.65**	0.36*	0.28 NS

NS denotes not significant, $P > 0.05$
* denotes significant, $P < 0.05$
** denotes highly significant, $P < 0.01$
*** denotes very highly significant, $P < 0.001$

Phosphorus and potassium and, to a lesser extent, magnesium and calcium, were positively associated throughout. Potassium and calcium appeared to show a general negative association. For nitrogen and potassium, and possibly nitrogen and phosphorus, the association was positive except at Glenbervie. Glenbervie appeared to be the exception, also, to a negative association between phosphorus and calcium. Rigorous between-site comparisons of these relations were prevented by heterogeneities of variance.

The corresponding correlations (r) of clonal means between different nutrients had fewer degrees of freedom, and were mainly non-significant ($P > 0.05$). In general, they did not indicate gross disparities between within-clone and between-clone relationships. True clonal or genotypic correlations were not pursued; the repeatabilities were generally too low and the trees too few to give worthwhile estimates.

DISCUSSION

Comparisons between sites were necessarily confounded with some differences in dates of sampling. However, available evidence (Mead and Will, 1972) indicates that this latter effect was minor.

At Gwavas and Berwick the foliar levels of all the nutrients exceeded the accepted thresholds (Adams, 1970, p. 148) of fully adequate supply.

At Glenbervie tree growth must have been limited, at least in large measure, by phosphorus deficiency. Phosphorus levels there were at the accepted threshold of acute deficiency (Will ,1965) and below the level (0.13%) regarded as necessary for optimal growth (Mead, 1972). Calcium deficiency possibly occurred as well, in which case it would probably have caused dieback rather than slow growth. Calcium levels were not notably low (cf. Adams, *loc. cit*), but the foliage was almost a year old and calcium accumulates progressively as needles get older (Will, 1957; Mead and Will, 1972). Since calcium is not effectively remobilised in the tree foliar analysis need not reflect short-term deficiencies arising in the meristems. Moreover, calcium deficiency in radiata pine has been observed to cause meristem necrosis rather than retarding growth (Purnell, 1958). Phosphorus deficiency in radiata pine in the presence of abundant calcium has been associated with slow, spindly growth, but no dieback (D. J. Meads, pers. comm.). Hence calcium deficiency, if present, was evidently superimposed on phosphorus deficiency. The absence of an exclusive effect of calcium deficiency is further indicated by the ineffectiveness of a lime application (Weston, 1956) on a soil similar to that of Glenbervie plot.

Despite the possible calcium deficiency it is considered that the gross clonal differences in growth rate must have resulted from differential responses to phosphate deficiency. Dieback and growth rate were not correlated among clones, and if the dieback did reflect calcium deficiency there must also have been clonal differences in degree of calcium deficiency.

At Whaka the low magnesium levels were not accompanied by visual deficiency symptoms. Since growth is only reduced by this deficiency when visual symptoms are obvious (Will, 1961), it appears that no actual deficiency existed. Unexplained is the needle fusion in two clones, which was associated with frequent dieback in one of them. Needle fusion has been corrected by superphosphate, and less effectively, by boron application (Ludbrook, 1942). Yet phosphorus levels in the Whaka foliage were

consistently high, while boron deficiency although occurring on some pumice soils (Will, 1971), seems unlikely on that site. Needle fusion has also been associated with copper deficiency (Will, 1972), but copper levels appear generally adequate on pumice soils (Knight, 1970). A nutrient imbalance rather than a deficiency *per se* might have been involved. Occasional trees with needle fusion have been observed by the author on a pumice soil despite topdressing with borated sulphur superphosphate.

Particularly interesting is the fact that large clonal differences in the degree of phosphorus deficiency at Glenbervie were not reflected in foliar phosphorus concentrations. A similar situation has been observed with magnesium deficiency (G. M. Will, pers. comm.). It may be noted that in ryegrass clonal differences in nutrient levels could not be related to growth rate (Butler *et al.,* 1962), at least with relatively high nutrient status.

Clonal repeatabilities for foliar nutrient levels were generally much lower than those observed for wood density (Burdon and Harris, 1973), branching frequency and tree height (Burdon, 1971), and cone characters (Burdon and Low, 1973). Thus, although clones frequently differed in foliar nutrient levels there was apparently considerable tree-to-tree variation within clones. The phenotypic coefficients of variation were, however, consistent with the results of Mead and Will (1972) and Raupach (1967) for radiata pine. A more precise specification of sampling positions would probably help, but it appears that foliage nutrient concentrations in this species can vary erratically. Moreover, Forrest and Ovington (1971) demonstrated large clonal differences in the within-crown distribution of phosphorus. Furthermore, it appears that different positions and different times of the year are appropriate for diagnostic sampling for different nutrients (Raupach *et al.,* 1972; Mead and Will, 1972). With these factors it appears impossible to develop a satisfactory all-purpose sampling procedure. In this particular trial there was the complication of having to accept some trees in the lower crown classes. This last factor, however, derived very largely from clonal differences in tolerance of edaphic conditions. In any event, it appears essential that diagnostic sampling be done from a number of trees.

The apparent clone-site interactions for potassium levels have arisen when this nutrient has been plentiful. This suggests that the propensity of a genotype, relative to others, to accumulate a nutrient is influenced by the supplies of other nutrients (c.f. Walker and Hatcher, 1962).

The within-clone correlations between levels of different nutrients may partly reflect tree-to-tree differences in effctive sampling position. For instance, nutrients that are distributed similarly within the crown would tend to show positive correlations.

The differences between sites in the longevity of foliage were large. The quicker turnover at Glenbervie and Whaka was associated with higher rainfall and some low foliar nutrient levels. It is not known which if either of these factors was decisive, although a nutritional effect is suggested by the positive correlation between foliage retention and stem diameter at Glenbervie. The immediate cause of needle fall might have been infection by *Naemacyclus minor,* which itself could be influenced by environment. At Whaka the rapid growth might have increased turnover through early suppression of foliage.

In general, it appears that neither foliage longevity nor crown density greatly affected growth rates. This accords with the finding (Whyte, 1968) that radiata pine

can withstand 25 percent defoliation before growth is appreciably reduced. The weak or non-existent clonal correlations between foliage longevity and visual crown density suggests that the amount of foliage may be governed largely by branching behaviour and the distribution of foliage on the branches. A dense crown may therefore result from the production of more branchlets, or from more foliage being produced on individual branchlets, or from both factors.

CONCLUSIONS

1. Foliar macronutrient concentrations indicate that phosphorus deficiency was the main factor limiting growth at Glenbervie.
2. This, together with very large clonal differences in vigour at Glenbervie, supports the earlier postulate that genotypes of radiata pine differ widely in tolerance of soil phosphate deficiency.
3. Although foliage analysis can reflect average nutrient status of a stand, if accepted sampling procedures are followed, it appears much less reliable for diagnosing the nutrient status of an individual or even of a clone.
4. Although clones frequently differ in foliar concentrations of individual nutrients at any one site, these differences may not be maintained over several sites.
5. Longevity of foliage, although differing between sites, appears to have had little effect on crown density or growth rate.

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