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## Clonal Repeatabilities and Clone-Site Interactions in *Pinus radiata*

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### Introduction

This paper covers some results of a 12-year-old clonal replication trial with *Pinus radiata* in which clones were replicated within and between four different sites. It is concerned with growth vigour in general, the frequency of branch clusters on the stem, and tree form and stem straightness. Several clonal replication trials with *Pinus radiata* have been reported (FIELDING, 1953; FIELDING and BROWN, 1961; NICHOLLS, 1967; PAWSEY, 1960) which have demonstrated considerable variation between clones for a wide range of characters. In none of these trials, however, was the replication extended to more than one site.

Clonal replication trials can give estimates of the magnitudes of total genetic and environmental variation, from which predictions may be made of the genetic gain to be expected from improvement Programmes based on vegetative propagation. If such trials are extended to several sites they can give estimates of clone-site interactions, and will help to ascertain the range of sites over which a selection of clonal or seedling stock can be profitably planted.

### Procedure

#### *Establishment and Design of Trial*

The trial was initiated and established by G. C. WESTON. In 1950 open-pollinated seed was sown from nine parent trees, which had been chosen for a variety of distinctive morphological features. In 1953 two seedlings were chosen from each of the nine progenies for replication as being representative of their respective progenies. It is clear, then, that the 18 clones are far from being a random population sample.

From 6 to 25 plantable cuttings (ramets) were obtained from each of these seedlings, giving a total of 224. They were planted out in 1955 at 9 ft X 9 ft spacing on four sites: Glenbervie, Whakarewarewa (Whaka), Gwavas and Berwick. Where there were too few ramets of a clone to permit replication within all four sites it was omitted from one of the sites. As far as possible equal numbers of ramets of a clone were planted on each site where it was represented, and with this restriction the ramets were allocated at random to the respective sites. The unbalanced structure was accentuated by some mortality and by the partial felling of the Whaka plot (Clones 59 to 63 inclusive) in 1961. The lack of complete surround plantings, the suppression of some trees, and the lack of a randomised lay-

out at Whaka, further complicate the analysis and interpretation of data.

#### *Particulars of the Sites*

Glenbervie State Forest, Lat.: 35° 35'; Alt.: C 500'; Rainfall: c 65 in.; Slope c 20°; Aspect: N, sheltered; Soil: clay, shallowly rooted with tree growth indicating a fertility gradient within plot.

Whaka State Forest, Lat.: 38°; Alt.: 950'; Rainfall: c 55 in.; Flat ground slightly exposed; Soil: pumice, sandy loam, freely rooted.

Gwavas State Forest, Lat.: 39° 15'; Alt.: c 1200'; Rainfall: c 50 in. (probable evapo-transpiration deficit in summer); Slope 15–20°; Aspect: NE, exposed; Soil: gravelly sandy loam, freely rooted.

Berwick State Forest, Lat.: 46°; Alt.: 200'; Rainfall: c 28 in.; Slope c 20°; Aspect: N, sheltered; Soil: loess — derived clay loam, with good root penetration in spite of compactness. Two of the last three seasons had been abnormally dry on this site.

The soil in the Glenbervie plot is representative of clay soils in that district which have previously carried kauri (*Agathis*) forest and which are known to be of low fertility. Results of foliage analyses and fertilizer trials (WESTON, 1956) indicate that low phosphate status is by far the most important factor which limits the growth of *P. radiata* on such sites. The other soils in this trial are generally considered to be of high fertility for growing conifers.

#### *Measurement of Trial*

In the winter and early spring of 1967 all plots were felled and measured in detail. In connection with this paper the following observations were recorded for each tree:

- (1) Total height (to top of annual growth stage, summer 1967).
- (2) Breast height diameter over bark (d.b.h.o.b.).
- (3) Any growth abnormality.
- (4) Incidence of forking.
- (5) Visual assessment of stem straightness.
- (6) Total number of branch clusters on main stem.

The visual assessment for stem straightness was made by three independent observers, using a 1 to 9 scale, 1 being extremely straight and 9 extremely crooked. Sinuosity or "crook" or "kink" was the only form of crookedness considered; butt sweep, bole sweep, and lean were ignored as far as possible (cf. SHELBOURNE and STONECYPHER, in press; BANNISTER, MS in preparation).

For purposes of counting branch clusters, cones or aborted female strobili were treated as branches (cf. BANNISTER, 1962).

## Analysis of Results

Analyses of variance were performed for each metric character, site by site. Combined analyses for all four sites were not attempted because of the unbalanced structure of the experiment and also the obvious magnitude of the clone-site interactions; these factors could have made the analyses difficult and then only of limited value when completed. The test for the significance of differences between clones is automatically a test for clonal repeatability. Repeatability is given by the ratio  $V_c/(V_c + V_E)$  where  $V_c$  is the variance between clones and  $V_E$  is the variance between ramets of clones, within one site. In this trial repeatability cannot be regarded as a broad-sense heritability, because the clones are few in number and are not a random selection from the population. The components of variance are calculated from the analysis of variance (see SNEDECOR, 1956, 10.6). The square root of  $V_E$  gives a pooled standard deviation of ramets within clones, although this must be treated with some caution because of some undoubted heteroscedasticity, or differences in between-ramet variance, among clones.

For stem straightness, which was assessed by three independent observers, the analysis is more complex. If the scores for the ramets are summed over the three observers, and no account taken of the observers in the analysis of variance, the expected mean square for within-clone variation is equal to  $3V_{R:C} + V_{OR:C}$ , where  $V_{R:C}$  is the variance between ramets within clones and  $V_{OR:C}$  is the residual variance. In this event a repeatability estimate is of the form  $3V_c/(3V_c + 3V_{R:C} + V_{OR:C})$ . However there are indications that  $V_{OR:C}$  can be treated purely as observer error (BANNISTER, MS in preparation); so when account is taken of observer effects in the analysis  $V_{OR:C}$  can be partitioned off, and an adjusted estimate of repeatability may be obtained by treating it as the ratio  $V_c/(V_c + V_{R:C})$ . The analysis of subjective assessments for straightness is being treated comprehensively by BANNISTER and will not be considered in further detail here.

Results for the different characters are tabulated as arithmetical means for each clone on each site, the number of ramets being listed in brackets. Because of the unbalanced structure of the experiment and the large clone-site interactions no satisfactory expression of site means can be obtained. However, listing the values for individual clones in order of ranking does permit some overall comparison between sites. Individual clone-site interactions or comparisons between particular clones can be roughly evaluated on inspection by considering the pooled standard deviations ( $\sqrt{V_E}$ ) in conjunction with the numbers of ramets involved.

Certain ramets were discarded from the analyses. For assessing height and diameter growth all dead trees were omitted and also any trees in which suppression had resulted from slow establishment. In assessing height growth trees which had been affected by appreciable leader breakage were discarded if possible. Where the calculated mean height is necessarily an underestimate of the growth potential of a clone through wind breakage, leader dieback or suppression, a plus sign is written beside the figure.

## Results and Discussion

### Growth Vigour

Results for height and diameter growth are presented in Tables 1 and 2. The effects of sites, clones within sites and clone-site interactions are large.

At Glenbervie the reduction in growth was caused almost certainly by phosphorus deficiency, of which the spindly, thin-crowned appearance of the trees, some leader dieback, some mortality without crown suppression, and the occasional individual showing needle fusion, are typical stand symptoms (WESTON, 1956). Foliar analyses, which are still in progress give very strong support to this view.\*) Growth at Gwavas was probably restricted by several factors, including summer drought, winter temperatures and exposure. At Berwick it appears to have been limited mainly by summer drought and winter temperatures. On the whole, height growth at Berwick was about 10 ft less than at Gwavas and a preliminary study of successive annual height increments predicts this difference resulted entirely from a combination of slow initial growth and the effects of two particularly dry seasons.

The clonal repeatabilities for height were generally higher than those for diameter, particularly at Whaka and Gwavas where the within-clone variance for diameter was inflated by edge effects. At Glenbervie the within-clone variances for height and diameter growth were doubtless inflated by the fertility gradient within the plot; that for height was further inflated by some leader dieback. Glenbervie and Whaka showed much greater between-clone variances than the other sites. At Whaka this resulted largely from the partial suppression of clones 67 and 70. From a study of the establishment records there was no indication that clonal differences had resulted from initial ramet size effects.

It must be emphasised that height and diameter growth are two aspects of overall vigour, which itself is a somewhat indeterminate character. When comparing sites, or clones within a site, diameter growth appears to give a clearer indication of poor vigour than does height growth, even though height growth is far less influenced by edge effects. The general unkriftness of the trees at Glenbervie was reflected more in stem diameter than in total heights. In comparing clones within sites, differences in height growth can often reflect habit of growth rather than overall clonal vigour; e.g., clones 65, 66 and 69 were undoubtedly tall-growing, while clones 64, 71 and 72 were relatively squat, at least up till the age of felling.

The clone-site interactions were very striking and they mainly reflected the inability of certain clones to thrive at Glenbervie. With the evidence from foliar analyses that low soil phosphate status is by far the main factor to limit growth on this site, it is almost certain that these clones performed poorly because of a greater susceptibility to phosphorus deficiency. All clones showed more or less normal vigour at Gwavas and Berwick, but at Glenbervie there were several namely 59, 60, 61, 62, 67, and possibly 69, in which diameter growth was severely depressed. All three ramets of clone 66 which had been planted there died naturally, although one which survived for several years had made reasonably rapid growth. At Whaka clones 67, 68 and 70 all showed poor diameter growth, although height growth was normal in clone 68. Unfortunately, the other clones which performed poorly at Glenbervie were not represented at Whaka.

That most of the clone-site interactions for vigour have, in this trial, arisen from clonal differences in ability to tolerate low available phosphate is evident. At Whaka, clones 67 and 68 showed evidence of phosphate deficiency, which was rather unexpected; however, on this site boron

\*) They will be reported in another paper together with the results of soil analysis.

**Table 1. — Mean Total Heights (Feet)**  
(Clones, in Order of Ranking, Within Sites)

GLENBERVIE				WHAKA			GWAVAS			BERWICK		
Ranking	Clone	Height	Ramets	Clone	Height	Ramets	Clone	Height	Ramets	Clone	Height	Ramets
1	65	59.7	(2)	66	73.3	(3)	66	65.5	(1)	69	55.2	(4)
2	58	56.2	(2)	69	71.7	(4)	65	62.0	(1)	66	53.3	(3)
3	64	55.5	(2)	65	70.9	(3)	68	61.2	(2)	61	50.2	(2)
4	71	52.3	(4)	73	66.8	(6)	69	60.9	(2)	70	49.4	(3)
5	72	50.9+	(4)	68	65.9	(1)	61	60.7	(1)	68	48.5	(4)
6	69	50.2	(4)	72	64.7	(3)	67	59.5	(4)	59	48.1	(2)
7	73	49.5+	(5)	74	61.7	(1)	71	58.6	(3)	62	47.8	(5)
8	70	47.5	(2)	71	60.5	(4)	74	58.5+	(2)	67	47.3	(5)
9	59	47.2	(3)	64	56.4	(2)	73	58.3	(2)	60	46.1	(2)
10	57	46.94-	(2)	70	47.2+	(3)	63	47.2	(2)	73	45.9	(5)
11	63	46.64-	(2)	67	42.2+	(6)	58	57.7	(2)	72	45.8	(4)
12	60	43.9	(2)	Other Clones			70	55.0+	(1)	63	44.8	(2)
13	74	43.84-	(2)	felled in 1961			62	54.8+	(6)	71	44.7	(3)
14	61	34.5	(2)				59	53.5+	(3)	57	40.8+	(2)
15	62	32.4	(3)				64	53.1	(2)	Other Clones not represented		
16	67	23.74-	(5)				72	51.8+	(2)			
17	66	died naturally					57	48.0+	(2)			
18	68	missing					60	47.3+	(1)			
$V^c$			92.68		114.3			(28.3 <sup>+</sup> )	13.03		10.09	
$V_E$			41.86		24.63			(5.72 <sup>+</sup> )	8.25		8.17	
Repeatability			0.96***		0.82***			(0.83****)	0.62***		0.55***	
SD (ramets)			6.47		4.96			(2.39 <sup>+</sup> )	2.87		2.86	

+ clones 67 and 70 omitted

NS denotes Not significant,  $P > 0.05$

\* denotes  $P < 0.05$

\*\* denotes  $P < 0.01$

\*\*\* denotes  $P < 0.001$

**Table 2. — Mean Diameter Growth (d.b.h.o.b., in inches)**  
(Clones, in Order of Ranking, Within Sites)

GLENBERVIE				WHAKA			GWAVAS			BERWICK		
Ranking	Clone	Diameter	Ramets	Clone	Diameter	Ramets	Clone	Diameter	Ramets	Clone	Diameter	Ramets
1	72	10.8	(4)	69	14.3	(4)	72	13.9	(4)	61	10.9	(2)
2	63	9.3	(2)	64	13.8	(2)	70	13.6	(1)	69	9.9	(4)
3	71		(4)	74	13.3	(1)	63	13.2	(2)	62	9.8	(5)
4	57	9.1	(2)	65	12.5	(3)	74	12.3	(2)	71	9.1	(3)
5	58		(2)	71	12.4	(4)	65		(2)	73		(5)
6	65	8.9	(2)	66	12.1	(3)	71	11.7	(3)	66	8.7	(3)
7	64	8.8	(2)	73	11.1	(6)	61	11.6	(3)	79	8.7	(3)
8	73	8.7	(5)	72	10.3	(5)	69	11.1	(3)	72	8.3	(4)
9	74	7.3	(2)	67	6.8	(6)	73	11.0	(5)	68	7.8	(2)
10	70	7.1	(2)	68	6.7	(1)	67	11.0	(4)	63	7.7	(2)
11	69	6.3	(4)	70	4.3	(3)	60	10.8	(1)	59	7.7	(2)
12	59	5.3	(3)				62	10.7	(6)	57	7.6	(2)
13	60	4.7	(2)				57	10.3	(2)	67	7.5	(5)
14	61	4.5	(2)				66			60	7.2	(2)
15	67	4.1	(5)				58	10.2	(2)			
16	62	3.0	(3)				64	9.9	(2)			
17							68	9.3	(2)			
18							59	8.5	(4)			
$V^c$			5.22		6.67			0.170			0.789	
$V_E$			2.51		6.54			3.91			0.959	
Repeatability			0.68***		0.50***			0.04 NS			0.45**	
SD (ramets)			1.583		2.558			1.978			0.978	

deficiency could also be involved, because there is reason to believe that phosphorus and boron can interact in nutrition (LUDBROOK, 1942), and there are strong indications of widespread boron deficiency on pumice soils (BANNISTER and BURDON, 1968, unpublished report). There are only two obvious clone-site interactions which cannot readily be

explained in terms of phosphate deficiency. They reflect the relatively poor height growth of clone 71 at Berwick, and the very low ranking of clone 70 at Whaka, in spite of its moderate growth at Glenbervie.

The symptoms of the presumed phosphate deficiency were remarkably varied, although all clones with severely

reduced growth had thin and unthrifty-looking crowns. Clone 67 showed extreme needle fusion and repeated leader dieback at Glenbervie, needle fusion being classically, although perhaps not exclusively, a symptom of phosphorus deficiency (LUDBROOK, 1942; WESTON, 1956; STONE and WILL, 1965). It showed the same symptoms to a lesser degree at Whaka, even though early height growth was quite normal. Clone 68 showed slight needle fusion at Whaka and even had it survived release cutting at Glenbervie it would almost certainly have performed poorly there. In contrast with clone 67, clone 62, although showing extreme depression of growth and some mortality at Glenbervie, showed practically no leader dieback or needle fusion. On the other hand, clones 63 and 73, although maintaining reasonable growth rates at Glenbervie, were subject to frequent dieback and resinosis on this site, while other clones such as 64 and 65 were free from these troubles. The complete mortality of clone 66 at Glenbervie was very likely a phosphate deficiency effect. This very complex picture accords well with the results of FIELDING and BROWN (1961).

Abnormal Growth Behaviour

The incidence of terminal hypertrophy (syn. "foxtail") is listed in Table 3. This condition was taken to include

Table 3. — Incidence of Terminal Hypertrophy

Site	Clone	Certain Cases	Possible Cases	Total Press
Whaka	59*)	2	1	4
Whaka	72	0	1	5
Gwavas	59	5	0	5
Gwavas	60	0	1	1
Gwavas	72	1	2	4
Berwick	59	2	1	3
Berwick	72	2	1	4

\*) Information abstracted from G. C. WESTON'S records. Two of the affected trees of clone 59 had died.

any tree in which the leader was unbranched over a length appreciably greater than one year's usual height growth, although the presence of "epicormic" shoots arising from proliferated fascicles sometimes made diagnosis uncertain. It did not occur at Glenbervie and only two clones were definitely affected.

Soil fertility is more likely to account for the site effect than climate. The prevalence of "foxtail" in low-latitude plantings of *P. radiata* (ANON, 1962; KUMMEROW, 1962; LANNER, 1966), particularly in the absence of a dry season, is hardly consistent with a climatic effect operating within this trial. There is other evidence that high soil fertility may be a predisposing factor (LLOYD, 1914). Although some of the cases were "true foxtails" by LANNER'S definition the affected parts of the leaders still showed discernible growth rings near the pith.

Fasciation had occurred repeatedly in both ramets of clone 57 at Berwick during the last three years. There was no other fasciation in the entire trial, although it was observed in some trees in a neighbouring progeny trial at Berwick. Thus, there appear to be both clone and site effects.

Tree Form and Stem Straightness

A visual evaluation of tree form involves branch diameter, branch angle, incidence of malformation and stem straightness. General tree form, with a notable exception

Table 4. — Incidence of Forking (Expressed as Total Forks / No. of ramets, Within Sites).

Clone	Glenbervie	Whaka	Gwavas	Berwick
57	0/2	—	0/2	0/2
58	0/2	—	1/2	—
59	0/3	—	0/5	0/3
60	0/2	—	1/1	0/2
61	0/2	—	1/3	0/2
62	0/6	—	5/6	2/6
63	0/2	—	0/2	0/2
64	0/2	4/2	4/2	—
65	0/2	0/3	3/2	—
66	0/1	1/4	0/2	1/3
67	NA	NA	1/5	0/5
68	—	0/1	0/2	0/2
69	0/4	0/4	1/3	0/4
70	0/2	1/3	2/3	1/3
71	0/4	0/4	0/3	0/3
72	0/4	2/5	0/4	1/4
73	0/5	1/6	2/5	0/5
74	0/2	0/2	0/2	—
Totals	0/45	9/34	21/54	5/46

Note: Ground level forks not included.

in clone 67, appeared to be best at Glenbervie, and appreciably better at Berwick than at Gwavas or Whaka.

Forking: Data for forking are presented in Table 4, a fork being deemed to include any persistent fork that originated either spontaneously or through only minor leader damage. At Glenbervie there was no forking at all, although there had been frequent minor dieback of leaders. However, many of the upper crowns were deteriorating. On the other sites some clones, such as 62 and 64, showed frequent forking. Clone 62, with its steep-angled branches as well as its forking was particularly subject to wind breakage. At Glenbervie clone 64, although growing vigorously, gave no indication of its general poor form when planted on other sites. Clone 72, also acceptable at Glenbervie, was of very poor form elsewhere, it being crooked, sometime forked, and very subject to wind breakage.

Straightness: Results, presented in Table 5, show significant clonal effects on all sites. Comparisons between sites are not strictly valid because of the arbitrary scale used to measure straightness on each site. However, real differences between sites are almost certainly underestimated, because visual assessments tend to be made largely in relation to neighbouring trees. Between sites there appears to be an inverse relationship between overall mean vigour and overall mean straightness, although this relationship does not emerge so clearly at the level of individual clones.

When adjusted for observer effects the estimated repeatabilities are quite high, being upwards of 0.48. The high repeatability shown at Berwick is largely attributable to the behaviour of clone 72. At Glenbervie a significant observer — clone interaction ( $F_{32,62} = 1.91$ ;  $P < 0.05$ ) indicates basic disagreement among observers as to criteria of straightness, but this almost certainly arose through having to compare trees of widely differing sizes. Between sites, some clones such as 60 and 66 behaved very consistently, while others, such as 67 and 71 showed large site interactions. These interactions are almost certainly genuine, to some degree, but it must be appreciated that with the method of assessment used, the apparently erratic be-

**Table 5. — Mean Stem Straightness Scores**  
(Clones, in Order of Ranking, Within Sites)

GLENBERVIE				WHAKA			GWAVAS			BERWICK		
Ranking	Clone	Mean	Ramets	Clone	Mean	Ramets	Clone	Mean	Ramets	Clone	Mean	Ramets
1	66	1.33	(1)	67	3.33	(6)	68	2.17	(2)	71	2.11	(3)
2	57	2.17	(2)	66	3.83	(4)	65	2.33	(2)	57	2.33	(2)
3	69	2.33	(4)	70	3.89	(3)	67	3.33	(5)	66	2.33	(3)
4	64	2.50	(2)	68	4.67	(1)	66	3.78	(3)	68	2.33	(2)
5	67	2.53	(5)	69	4.75	(4)	73	3.80	(5)	70	2.83	(3)
		2.67	(2)	73	4.83	(6)	69	3.89	(3)	73	3.33	(5)
			(2)	65	4.89	(3)	64	4.17	(2)	63	3.83	(2)
8	72	2.83	(4)	71	5.00	(4)	74		(2)	62	3.87	(5)
9	59	3.00	(3)	74	5.67	(2)	71	4.33	(4)	59	4.00	(2)
10	62	3.08	(4)	72	6.00	(5)	61		(3)	69	4.33	(4)
11	70	3.17	(2)	64	6.17	(2)	62	4.44	(5)	61	4.83	(2)
12	73	3.60	(5)				70		(3)	67	4.93	(5)
13	74	3.67	(2)				57	4.67	(2)	60	6.00	(2)
14	60	4.00	(2)				58	5.50	(2)	72	7.42	(4)
15	63	4.83	(2)				63		(2)			
16	58	5.00	(2)				59	5.58	(4)			
17	71	5.67	(4)				60	5.67	(1)			
18							72	6.33	(4)			
$V_c$												
$3V_c/(3V_c + V_E)$												
SD (ramets)												
$V_{R:c}$												
$V_{OR:c}$												
+) Repeatability												
$\sqrt{V_{R:c}}$												

+) In this case  $V_c/(V_c + V_{R:c})$

**Table 6. — Mean Branch Cluster Frequency ("Mean Internode Length", in Feet)**  
(Clones, in Order of Ranking, Within Sites)

GLENBERVIE				WHAKA			GWAVAS			BERWICK		
Ranking	Clone	Mean	Ramets	Clone	Mean	Ramets	Clone	Mean	Ramets	Clone	Mean	Ramets
1	66	1.24	(1)	70	1.38	(3)	63	1.57	(2)	68	1.35	(2)
2	62	1.29	(4)	68	1.50	(1)	68	1.65	(2)	63	1.47	(2)
3	60	1.30	(2)	65	1.56	(3)	60	1.68	(1)	66	1.47	(3)
4	61	1.44	(2)	66	1.57	(4)	70	1.71	(3)	73	1.56	(6)
5	70	1.47	(2)	72	1.60	(5)	66	1.76	(3)	57	1.57	(2)
6	64	1.50	(2)	73	1.64	(6)	73	1.87	(5)	61	1.60	(2)
7	74		(1)	69	1.67	(4)	61	1.80	(3)	60	1.61	(2)
8	63		(2)	64	1.68	(2)	64	1.85	(2)	67	1.69	(5)
9	67	1.52	(5)	67	1.72	(6)	65	1.87	(2)	70		(3)
10	69		(4)	74	1.89	(2)	62	1.89	(6)	69	1.71	(4)
11	59	1.55	(3)	71	2.13	(4)	57	1.93	(2)	62	1.79	(5)
12	65	1.61	(2)				72	1.95++	(4)	71	2.28	(3)
13	57		(2)				58	1.97	(2)	72	2.33++	(4)
14	73	1.62	(6)				67	2.04	(5)	59	2.86++	(3)
15	72	1.66	(4)				69		(4)			
16	58	1.67	(2)				74	2.06	(2)			
17	71	2.24	(4)				71	2.28	(4)			
18							59	2.73++	(5)			
$V_c$												
$V_E$												
Repeatability												
SD (ramets)												

+) Clone 59 omitted

+++) Clone showing terminal hypertrophy

haviour of a clone could reflect consistent performance in the face of a strong site effect shown by the other clones.

### Branching Frequency

Results for branching frequency are expressed as "mean internode length" in Table 6. For each tree the total height was divided by the total number of branch clusters and within each site the mean of these means was calculated for each clone. Where a tree had two or more leaders of approximately equal height the mean heights and mean numbers of branch clusters were used for calculating the branching frequency of that tree.

The frequency was highest on the phosphate-deficient Glenbervie site, but it differed appreciably among the other sites. At Berwick the frequency had apparently been affected by the recent drought years, while at Whaka the more rapid development had evidently brought the trees into a growth phase in which branching frequency is inherently greater (see BANNISTER, 1962).

Within sites the clonal repeatabilities were generally high, and, when one highly anomalous clone (clone 59) was omitted, the within-clone and between-clone variances were fairly similar over the four sites. The repeatabilities may have been depressed by several factors, including the incidence of leader injury, and the effects of exposure on a plot margin at Gwavas.

Clone-site interactions were again evident. While some clones such as 68, 71 and 73 behaved very consistently, others were rather erratic. In general, the clones which suffered the worst phosphorus deficiency showed the greatest increase in branching frequency at Glenbervie, but there were exceptions, such as clone 64.

### General Discussion

The appreciable clonal repeatabilities which were shown within sites are consistent with general expectations. Some relatively low repeatabilities for diameter growth can be explained. Narrow-sense heritabilities can be expected to be considerably lower, because part of the genotypic variance is non-additive and because with the non-random selection of clones the between-clone variance may be greater than the normal genotypic variance within the population. It is of interest to compare the results of a 14-year-old open-pollinated progeny trial with *P. radiata* (BANNISTER, MS in preparation), although any such comparison between the two trials must be very tentative. Estimated narrow-sense heritabilities for height and diameter growth were much lower, c 0.20 and c 0.15 respectively, but as high as 0.53 for stem straightness. Thus there is some indication that on any one site non-additive genetic variation is appreciable for growth rate characters, but very small for stem straightness.

However, the real interest in this trial lies in the clone-site interactions. They demonstrate clearly a principle which has long been appreciated: that the behaviour of different genotypes relative to one another could vary greatly between sites. But until recently there has been very little concrete evidence as to which out of many possible site factors (viz. rainfall, latitude, altitude, temperature, edaphic factors, etc.) contribute mainly to genotype-site interactions. Without this evidence there can be no real basis for drawing up a code of practice for seed transfer within the country, or for regionalising intensive tree improvement Programmes. The interesting point is that among these very diverse sites, one factor — phosphate status of

soils — should apparently be paramount as a cause of interactions. The importance of phosphate status in this respect has already been demonstrated in ACT, Australia, by FIELDING and BROWN (1961).

Where a single site factor is near the physiological limit of a species, genetic differences between trees in tolerance to that factor will tend to be manifested by large differences in growth. This doubtless happened to some extent with phosphate requirement in this trial and in that of FIELDING and BROWN. However it is probable that in addition, the genetic differences in phosphate requirement are large compared with genetic differences in a character such as nitrogen requirement. In the writer's experience stands of *P. radiata* grown on nitrogen-deficient sites do not show the large tree-to-tree differences in growth which are found on phosphate-deficient sites. As yet there is no indication as to what extent the genetic differences in phosphate requirement are additive.

In selecting parent trees from which to propagate stock for afforesting phosphate-deficient sites it is necessary to choose between two different approaches; the first would be to accept the cost of generous topdressing, in order to ensure that phosphate would be adequate for almost all trees that may be planted; in this case selection would be based largely on ability to produce good tree form under high nutrient status, so pumiceland selections might be quite appropriate. The second would be to select trees of proven tolerance to low soil phosphate levels and so minimise the cost of topdressing, but such selections would need to be screened, either by progeny tests or by clonal tests, for their ability to produce good tree form on the more fertile microsites.

### Conclusions

1. At any one site clonal repeatabilities in *P. radiata* appear to be high for height growth, branching frequency, and stem straightness.
2. Depending on competition effects and on the site clonal repeatability for stem diameter can range from high to very low.
3. Within *P. radiata* there appears to be considerable clone-to-clone variation in tolerance of low phosphate status.
4. The symptoms of the apparent phosphorus deficiency vary greatly from clone to clone.
5. The performance of a clone growing on a fertile site seems to be no guide to its vigour where phosphate is deficient.
6. In some clones phosphorus deficiency may mask a tendency towards extreme bad tree form.
7. Among the sites studied clone-site growth rate interactions not involving phosphorus deficiency appear to be relatively small, but not altogether absent.
8. Considerable clone-site interactions can occur for branching frequency and stem straightness; these can be largely but not entirely secondary to phosphorus deficiency effects.
9. Where sites are phosphate deficient, and are to remain so, it would appear that tolerance of low phosphate status must be the main criterion for selection within *P. radiata*.

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## Summary

In 1955 a total of 224 cuttings of *Pinus radiata*, derived from 18 juvenile clones, was planted on four widely separated sites in New Zealand. The clones were replicated within and between sites. One of the sites was severely deficient in available soil phosphate. In 1967 a final destructive measurements was made. Considerable site effects were evident for growth rate, stem straightness, incidence of malformation, and frequency of branch clusters on the stem. Within sites, clonal repeatabilities were high (mostly between 0.50 and 0.75) for total height, stem straightness, and frequency of branch clusters, but very variable (0.04 to 0.69) for stem diameter. Some drastic clone-site interactions appear to have resulted almost entirely from genetic variation between clones in their ability to tolerate low soil phosphate status. The symptoms of the apparent phosphorus deficiency varied greatly from clone to clone, but in some it masked a tendency towards extreme bad tree form. There were also marked clone-site interactions for branching frequency and stem straightness, which appeared to be largely, but not entirely, the consequence of phosphorus deficiency. These results argue strongly for some regionalisation of seed collection and tree improvement Programmes within New Zealand and indicate that in this connection phosphate status should be a prime consideration.

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# Variations in esterase zymogram patterns in needles of *Pinus siivestris* from provenances in northern Sweden

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Electrophoretic patterns of enzymes (zymograms) show a wide range of variation in natural populations of many organisms, both animals and plants. These patterns have sometimes been found to vary between different stages of development in the same individual and also between individual at the same stage of development. This latter type of variation is genetically determined, and most populations seem to be polymorphic for electrophoretic patterns in at least some enzyme systems.

This paper is a preliminary report from an investigation concerning the enzyme pattern variations in forest tree populations, aiming at a fast and reliable method for evaluation of genetic variation.

The esterase enzyme system was found to show a considerable variation between individual trees. In order to find out if these patterns were genetically determined and stable, or if they were influenced by different environmental factors, the following test was performed. Zymograms were produced from a material in which a collection of mother trees were represented by clonal grafts grown at different localities. The investigators did not know the origin of the samples and it was our task to combine genetically identical samples with guidance of the zymogram patterns, thus testing both the specificity of the pattern and its stability.

## Material and methods

The test material consisted of 96 samples. These had been collected by the staff at The institute for forest improve-

ment, northern district, Umeå. 16 mother trees from different provenances were included. Their place of origin is shown in Fig. 1. Each mother tree was represented by clonal grafts planted at three different plantations. The locations of these, five in all, are also shown in Fig. 1. Four of them are situated near the coast, whereas the fifth — Sundmo — is in the inland. Of each clone two samples from different grafts were taken at each plantation, giving a total of  $16 \times 3 \times 2 = 96$  samples. Each sample had been given a random consecutive number before being delivered to the laboratory.

Needles provided the material for the zymograms, and were all sampled from one year old branches on the south side of the trees. The zymograms were produced with electrophoretic migration on starch gel according to POULIK (1957). Because of the high content of resin, special pre-treatments were necessary to obtain a good separation and clearly stained bands.

The pine twigs were collected in October and sent to the laboratory in plastic bags. Needles taken from the twigs were stored, for at a maximum, another seven days in darkness at  $\pm 0^\circ$  C and were exposed to light for 24 hours before the analysis.

2 g of needles and 4 ml of 0.2M Tris-HCl buffer, pH 8.5, supplied with 0.001 M EDTA, 2% polyvinylpyrrolidone (PVP) according to BOUDET (1965) and 0.7% 2-merkaptoetanol according to BHATIA and NILSON (1969), were ground in a high speed laboratory grinder (JANKE, KUNKEL type A 10). The dispersed material was freeze-dried and thawed two times in