THE EFFECT OF MATURATION ON THE GROWTH AND FORM OF VEGETATIVE PROPAGULES OF RADIATA PINE

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ABSTRACT

This paper reports the assessment, three yr after planting, of a trial designed to examine the effect of the age of parent ortets of radiata pine (**Pinus radiata** D. Don) on the growth of vegetative propagules taken from them. Seedlings were compared with grafts made from ortets aged 6, 15, 25, 43 and 66 yr, and cuttings rooted from ortets aged 6, 10, 19, 23 and 43 yr at the start of the trial.

A number of parameters were assessed and, after necessary covariance adjustments, it was shown that juvenile propagules (seedlings, and grafts and cuttings from six-yr ortets) differed widely in both growth rate and form from mature propagules (grafts or cuttings from ortets aged 19 yr and upwards). There were significant differences between the juvenile groups, and there were intermediates between the juvenile and mature groups; but there were few differences between the mature propagules. These data are interpreted to suggest that the process of maturation or phase change occurs progressively during the early years, but is a finite process which does not continue through the life of the tree.

The implications of these findings to a programme of plantation establishment with cuttings, combined with genetic improvement, are examined; and it is concluded that, at least in the early stages of the rotation, the use of vegetative propagules may mean a loss in stem volume of up to 40% compared with seedlings. This must be offset against improvements resulting from the reduction of defects associated with the juvenile habit.

INTRODUCTION

In many species of perennial plants there are clear differences between juvenile and adult individuals in appearance and growth behaviour (*see* e.g. Schaffalitzky, 1959). Wareing (1959) has pointed out that some of the changes associated with the adult habit are due to stable changes in the apical meristem (called maturation or phase change) while superimposed on these are changes in the nutrient status of the plant due to the effect of its increasing size and complexity. These latter are called ageing changes.

When a mature plant is propagated sexually the resultant progeny are, of course, juvenile; when it is propagated vegetatively, however, the resultant propagules differ from seedlings in a number of criteria. While changes due to ageing are reversed by vegetative propagation those due to maturation are normally not, and the differences

between a seedling and a vegetative propagule are essentially those resulting from maturation changes in the apical meristem of the ortet* (Wareing, 1959). The literature on maturation and ageing has been reviewed by several workers (e.g., Robbins, 1957; Schaffalitzky, 1959; Wareing, 1959; Sax, 1962; Brink, 1962; Doorenbos, 1965) and will not be discussed in depth here. It is necessary, however, to discuss the importance of the subject to forestry and to tree improvement procedures with radiata pine (*Pinus radiata* D. Don).

The case for using rooted cuttings of radiata pine in production plantations has by now been well made (Fielding, 1964, 1970; Thulin and Faulds, 1968; Libby *et al.*, 1972), and many of these published papers stress the advantages of coupling vegetative propagation with a genetic selection programme. The advantages for this have been summarised by Libby *et al.* (ibid.); briefly they are a reduction of defect associated with the juvenile habit, increased genetic gain from selection, improved uniformity of crop, and an increased ease of build-up of quantities of genetically improved material. These advantages must be weighed against some accepted disadvantages such as earlier and more frequent production of stem cones (Libby *et al.*, ibid.), and some potential disadvantages whose extent is as yet rather poorly defined. The most important of these concerns growth rate. While Fielding (1970) found little difference in growth rate between cuttings from young ortets and seedlings, his work did suggest, as did that of Sweet (1964), that the vegetative propagation of older ortets may result in a decline in growth rate.

It is not practicable in a genetic programme to make tree selection at too young an age, and Libby *et al.*, have pointed out that it takes some time after selection for testing and management recognition of good clones. During this time the normal processes of maturation are believed to be occurring. Thus by the time a clone is tested and accepted it is probable that it will be more mature than at selection, and that this process of maturation will continue. It is thus necessary to the sensible use of a vegetative propagation/genetic selection programme to understand the effects of maturation on the growth and form of vegetative propagules.

The experiment reported here was designed to provide information on that subject. The paper examines the effect of ortet age on the growth and form of cuttings and grafts of radiata pine three yr after establishment in the field, and compares the behaviour of these plants with seedlings. Such data have not previously been published from a well-replicated trial.

THE TRIAL

When plans were first made for the trial (in 1963) it was not possible to root large numbers of cuttings from ortets older than about 10 yr, and thus it was intended to establish the experiment with grafts. By 1966, however, suitable rooting techniques had been developed (Thulin and Faulds, 1968), and thus cutting material could be included. With recognition that the trial would provide much of the initial data on which to base decisions concerning the use of a vegetative propagation/genetic improvement programme in New Zealand, it was designed to have a useful life of *ca.* 20 yr.

* Ortet is defined as the one plant from which members of a clone were originally derived (Snyder, 1959).

The trial was established at Compartment (Cpt) 1350, Kaingaroa Forest, a site at the NE edge of the forest. The altitude is 420 m and the climate approximates to that at Kawerau. For the first two years of the experiment meteorological data were: mean annual temperature 14°C (mean maximum 20°C, mean minimum 8.9°C), mean annual rainfall 1772 mm, 26 days of ground frost annually with a minimum temperature of —3.5°C. The soil consists of some 60 cm of basaltic Tarawera lapilli over buried Kaharoa and Taupo ashes (Gibbs and Pullar, 1961). Detailed profiles and analyses of a comparable soil close by have been reported by Knight (1970).

Experimental Design

Two separate experiments were established on the same date, one containing cuttings and seedlings, the other grafts and seedlings. The design of each experiment was identical, allowing joint analysis, and the experiments were established on contiguous sites. Each experiment utilised a balanced incomplete block design with 25 blocks and nine units per block (Cochran and Cox, 1950). Within each experiment there were five ortet ages represented × five clones per ortet age × nine ramets per clone. Seedlings were planted between the vegetative propagules in the ratio of three seedlings to one clonal ramet. The initial plant spacing was 2.7 m × 2.7 m and this can be increased by thinning, first to 5.5 m × 2.7 m, and subsequently to 5.5 m × 5.5 m, without the removal of any clonal material.

Materials

1. The Experiment with Grafts

The initial graftings were made outside on line-sown rootstocks in March 1964, using a tip-cleft technique (Thulin, 1957). The scion material had the following origins:

Descriptive Code* Used in This Paper	Parent Stand
G 6	Seedlings sown in Rotorua Nursery in spring 1962.
G15	Cpt 1135, Kaingaroa Forest, planted 1955.
G25	Cpt 12, Whakarewarewa Forest, planted 1945.
G43	Grafted material from ortets planted in Kaingaroa Forest 1926-28, selected for a breeding programme and grafted repeatedly since 1953.
G66	Cpt 7, Kaingaroa Forest, planted 1904.

There is no satisfactory term in the literature to describe collectively the vegetative propagules made from a series of ortets of a given age. The people who would wish to use such a term are generally those interested in maturation, and to create an appropriate term requires a greater knowledge than we currently have of the way in which maturation changes occur, and are affected by factors such as repeated re-propagation. Ultimately such a term must be found, but as an interim measure this paper will use the term "group" specifically to meet this requirement.

Within each of the five ortet classes the selection of the ortets to be used in the

* The code has the following basis: G = graft, C = cutting, S = seedling. The numerical suffix is the age of the ortet in years from sowing, at the time when the trial was planted in the field in 1968.

experiment was at random, and on each ortet scion material was selected from the upper part of the crown. Due to the variable age of the ortets there was a difference in the size and nutritional status of the scions at grafting, and consequently in the growth of the grafts made from them. Thus, in March 1966 scion material was taken from each graft and regrafted onto stock from a population of full-sib seedlings, in an attempt to produce more uniform plants. Even so, complete uniformity between groups was not attained at planting (*see* Fig. 1a and Table 1). Planting was in June 1968. The seedling fillers in the trial (coded as "Group" S2 in this paper—*see* later) were raised in Kaingaroa Nursery from selected seed (selection of the best 25 trees per hectare), and were aged two years from sowing. Their quality was poor compared with the grafts, and their heights were low (Table 1).

2. The Experiment with Cuttings

The cuttings were set in May 1966, some in tubes and some open-rooted (*see* Thulin and Fauls 1968 for techniques). The material came from the following sources:

Descriptive Code Used in This Paper	Parent Stand
C 6	(Cuttings were set from) grafts made in 1964 from seedlings sown in Rotorua Nursery in spring 1962.
C10	Cpt 1293, Kaingaroa Forest, planted 1959.
C19	Cpt 1272, Kaingaroa Forest, planted 1951.
C23	Cpt 1099, Kaingaroa Forest, planted 1947.
C43	(Cuttings were set from) grafts made from ortets planted in Kaingaroa Forest 1926-28, selected for a breeding programme and grafted repeatedly since 1953.

Within each of the five ortet age classes the selection of the ortets to be used in the experiment was at random, except for the fact that clones with poor rooting ability were automatically excluded. In each collection, cutting material was selected from the upper part of the crown. Fig. 1b and Table 1 illustrate that the groups were not comparable in plant size or in quality of root system at the time of planting (June, 1968). The seedling fillers (coded S2) were from the same source as those used in the grafting experiment, and their mean height was smaller than that of any of the groups of cuttings. The cuttings in their turn were smaller than the grafts in the grafting experiments (*see* Table 1).

Characters Measured or Assessed

The following parameters were assessed on one or more occasions between 1968 and 1971.

1. Height (cm) measured with graduated poles from the ground to the tip of the highest shoot, 1968-71.
2. Relative height growth rate (RHGR — cm/cm/week). At a given moment of time RHGR (the change in height per unit of height per unit of time) $= \frac{dH}{dt} \cdot \frac{1}{H}$ where H = plant height and t = time. Over a period of time the mean RHGR $= \frac{\log e\ H2 - \log e\ H1}{t_2 - t_1}$ where H2 and H1 are heights at times

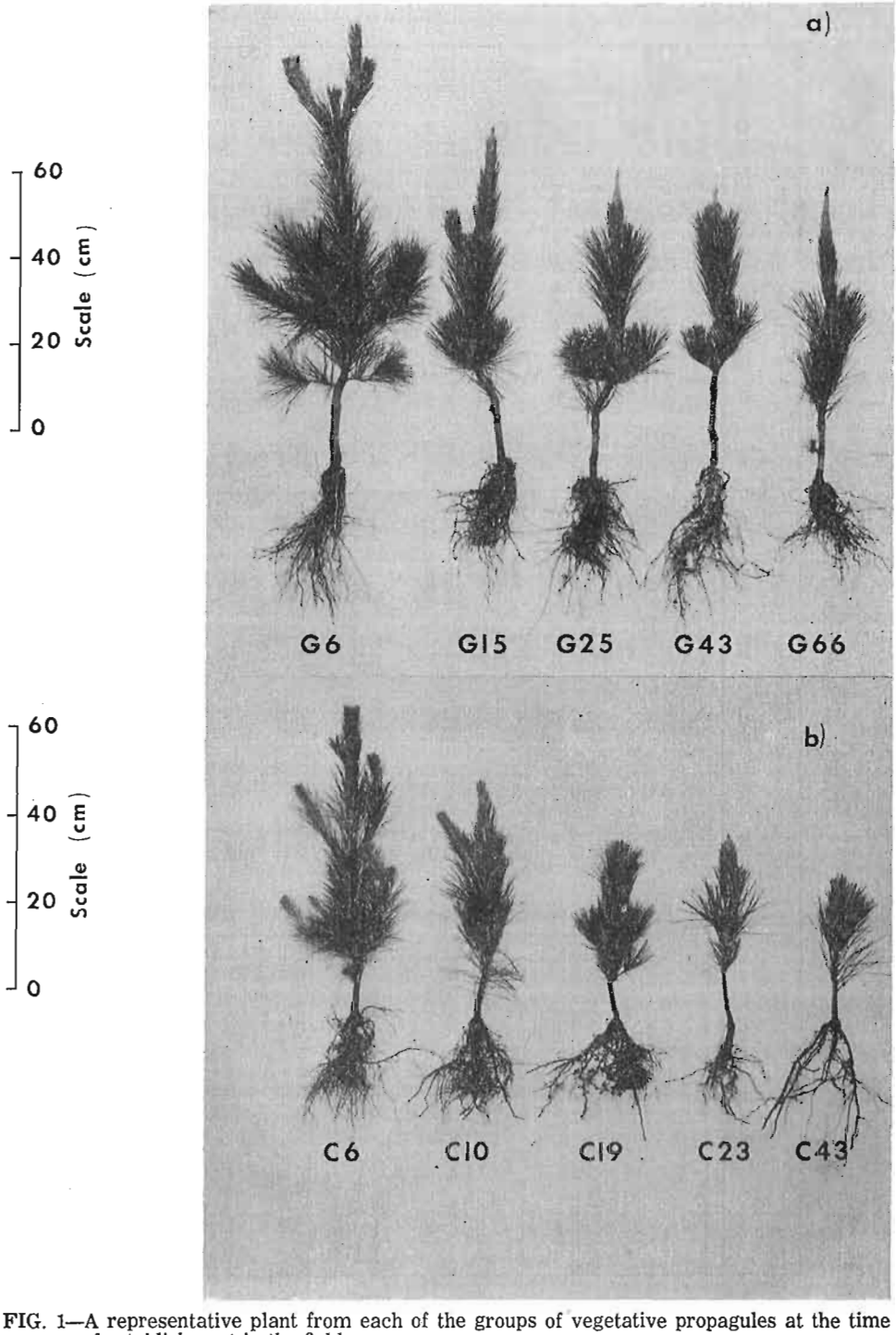

FIG. 1—A representative plant from each of the groups of vegetative propagules at the time of establishment in the field
(a) Grafts (b) Cuttings

TABLE 1—Assessment results

		Graft Experiment							Cutting Experiment						
		S2	G6	G15	G25	G43	G66	$G\bar{x}$	S2	C6	C10	C19	C23	C43	$C\bar{x}$
Tree height (cm)	Assessed data 1968	29.1	66.1	62.5	55.5	53.6	53.9	58.3	26.6	60.0	46.3	37.5	36.6	29.9	42.1
	Assessed data 1969	58.8	94.5	104.8	87.5	84.4	86.6	91.6	56.1	78.3	67.1	55.5	52.1	42.1	59.0
	Assessed data 1970	146.3	218.8	230.2	207.5	206.7	209.5	214.5	141.3	182.2	149.5	124.0	110.0	87.9	130.7
	Assessed data 1971	280.4	363.9	383.4	362.0	358.3	374.1	368.3	278.3	327.4	303.9	258.8	223.5	184.2	259.6
		cd	a	a	a	ab	a		cde	abc	bcd	de	ef	f	
Basal stem diameter (mm)	Assessed data 1971	72.8	92.8	80.9	70.6	68.4	72.2	77.0	69.3	83.2	62.5	50.2	44.8	34.7	55.1
	1971 data adjusted on 1971 tree height	77.6	83.0	67.8	61.2	59.6	60.7	66.4	74.4	79.8	63.2	58.7	59.5	56.3	63.5
		bc	a	d	ef	efg	efg		c	ab	e	fg	efg	g	
Form factor	Assessed data 1971	0.51	0.54	0.61	0.62	0.65	0.66	0.62	0.51	0.53	0.60	0.62	0.62	0.65	0.60
	1971 data adjusted on 1971 tree height	0.50	0.55	0.63	0.63	0.66	0.68	0.63	0.50	0.53	0.60	0.61	0.61	0.63	0.60
		e	d	bc	abc	ab	a		e	de	c	c	c	bc	
Stem volume (cc)	Assessed data 1971	4379	9625	8282	5997	5866	6837	7321	4053	6967	3951	2384	1629	986	3183
	1971 data adjusted† on 1971 tree height	5254	5411	3552	3223	3230	3248	3733	4719	5468	3697	3163	3074	2135	3507
		xy	x	ab	bc	bc	bc		y	x	a	c	c	d	
Number of first-order branches	Assessed data 1971	36.2	42.3	49.9	50.0	52.3	45.8	48.1	32.9	39.2	40.0	35.5	28.7	24.5	33.6
	1971 data adjusted on 1971 tree height	38.7	37.1	42.9	45.0	47.7	39.6	42.5	35.6	37.4	40.4	40.1	36.6	36.0	38.1
		cd	d	bc	ab	a	cd		d	d	cd	cd	d	d	
First-order branch length (cm)	Assessed data 1971	2531	3780	2657	2009	1985	1830	2452	2207	3114	1734	1167	852	518	1477
	1971 data adjusted on 1971 tree height	2799	3236	1923	1483	1496	1187	1865	2495	2925	1774	1645	1674	1722	1948
		b	a	d	f	f	f		c	b	de	ef	def	def	
Second- (and higher-) order branch length (cm)	Assessed data 1971	3076	5450	1769	800	878	785	1936	2830	4153	920	421	159	77	1146
	1971 data adjusted* on 1971 tree height	3663	4483	1232	411	515	312	1591	3455	3865	935	749	732	923	1441
		x	x	a	cd	cd	d		x	x	ab	bc	bc	ab	
Total branch length (cm)	Assessed data 1971	5607	9253	4404	2809	2885	2612	4574	5237	7267	2650	1603	1011	595	3078
	1971 data adjusted* on 1971 tree height	6494	7792	3213	1948	2081	1565	3320	6182	6832	2682	2327	2280	2468	3318
		y	x	a	de	cd	e		y	xy	b	bcd	bcd	bc	

Stem volume per unit of branch length	Assessed data 1971	0.82	1.08	2.06	2.30	2.16	2.83	2.08	0.80	0.96	1.56	1.54	1.62	1.51	1.44
	1971 data adjusted* on 1971 tree height	0.93 x	0.91 x	1.83 bcd	2.13 b	2.01 bc	2.63 a	1.90	0.91 x	0.89 x	1.57 d	1.68 cd	1.87 bcd	1.87 bcd	1.58
Incidence of retarded leader	Assessed data 1970 (arbitrary scale) ‡	54 ab	45 b	8 c	4 c	2 c	2 c	12	62 a	55 ab	11 c	2 c	3 c	5 c	15
Incidence of scarious winter buds	Assessed data 1969 (arbitrary scale) ‡	10 b	90 a	90 a	90 a	90 a	90 a	90	11 b	90 a	90 a	90 a	90 a	89 a	90
Number of trees (out of 45) with one-year-old female strobili	Assessed data 1969	0 e	0 e	31 b	30 b	35 a	33 b	26	0 e	0 e	5 d	10 c	1 e	1 e	3
Number of trees (out of 45) with pollen catkins	Assessed data 1969	0 c	0 c	2 c	1 c	1 c	1 c	1	0 c	0 c	2 c	13 b	19 a	21 a	11
Number of trees (out of 45) with one-year female strobili	Assessed data 1970	0 d	11 cd	23 ab	40 a	41 a	39 a	31	0 d	0 d	15 bc	19 abc	21 ab	12 bc	13
Number of trees (out of 45) with pollen catkins	Assessed data 1970	0 d	7 bcd	13 abcd	24 abc	18 abc	23 ab	17	0 d	4 cd	10 abcd	28 a	29 a	15 abc	17

* = Adjustment on the basis of separate regressions (i) for Groups S2, G6 and C6; and (ii) for the remaining groups.

† = Adjustment on the basis of separate regressions (i) for Groups S2, G6 and C6; and (ii) for the remaining groups, using naturally logged data.

‡ High value = high incidence of character assessed.

For any assessment parameter, values which do not share a common letter, differ significantly at the 1% level by Duncan's (1955) test.

t_2 and t_1 respectively. The mean values were calculated for yearly intervals from 1968-71.

3. Stem diameter (mm) at the base of the tree, and at half-height. Measured with calipers, 1971.
4. Stem form factor — calculated by $\frac{\text{diameter half-height}}{\text{basal diameter}}$, 1971.
5. Stem volume (cc) — calculated by $V_1 + V_2$, where V_1 is the volume of a cylinder equivalent in height and mean cross-sectional area to the bottom half of the tree, and V_2 the volume of a cone equivalent in height and basal area to the top half of the tree, 1971.
6. The number of first-order branches per tree (= branches attached to the main stem) — recorded by counting, 1971.
7. The cumulative length (cm) of first-order branches per tree — measured directly, 1971.
8. The cumulative length (cm) of second- and higher-order branches per tree (= branches attached to other branches) — measured directly, 1971.
9. Total branch length per tree (cm) — obtained by adding (8) and (9), 1971.
10. Stem volume per unit of branch length (cc/cm). Calculated, 1971.
11. Retarded growth of the leading shoot — recorded on the following 3-point scale and totalled (1969, 1970):
    0 — not retarded
    1 — retarded less than 5 cm
    2 — retarded 5 cm or more.
12. The presence of scarious winter buds — recorded on a 3-point scale and totalled (1969, 1970):
    0 — no scarious buds
    1 — scarious buds on apical shoots only
    2 — scarious buds on lateral and apical shoots.
13* The incidence of trees with first-year female strobili (1969, 1970).
14* The incidence of trees with pollen catkins (1969, 1970).

Statistical Analysis of Data

Analysis of the heights for 1969 and 1970 showed a high degree of site uniformity, with little advantage gained by analysing the data as a balanced incomplete block. As to do so with existing computer facilities would have delayed computation of the 1971 assessment, and as preliminary examination of the data did not show large interactions, the decision was made to analyse the trial on a hierarchical basis.

Because it was important to have seedling/graft, seedling/cutting comparisons, seedlings were introduced to the design as a sixth "Group" in each trial. This was done by selecting at random 45 seedlings for assessment in each of the cutting and the graft trials and dividing them (again randomly) into five series each of nine trees.

Two main types of statistical analyses were carried out: (i) a fixed model hierarchical analysis of variance with equal numbers of trees within clones (of a total of 540 trees

* No account was taken of the number of conelets or catkins per tree.

required for assessment in 1971 only nine were unassessable). The format of this is illustrated in Table 3; (ii) regression analyses based on individual tree values (*see* Table 4 for format). In two of the parameters assessed in 1969 and 1970 the distribution of the data was far removed from normality, and in these cases arcsin transformations were carried out prior to the analysis of variance (*see* Table 3).

TABLE 2—Relative height growth rate data (cm/cm/week)

Period	Graft Experiment							Cutting Experiment						
	S2	G6	G15	G25	G43	G66	$G\bar{x}$	S2	C6	C10	C19	C23	C43	$C\bar{x}$
1968–69	.0158	.0079	.0115	.0102	.0101	.0106	.0101	.0170	.0058	.0081	.0086	.0078	.0079	.0077
	a	bc	b	b	b	b		a	c	bc	bc	bc	bc	
1969–70	.0175	.0162	.0151	.0166	.0172	.0170	.0164	.0176	.0162	.0154	.0155	.0143	.0139	.0151
	a	abc	abc	abc	ab	ab		a	abc	abc	abc	bc	c	
1970–71	.0130	.0100	.0102	.0111	.0110	.0116	.0108	.0135	.0118	.0142	.0149	.0142	.0142	.0139
	abcd	d	d	cd	cd	bcd		abc	bcd	ab	a	ab	ab	
1968–71	.0153	.0116	.0121	.0125	.0127	.0130	.0124	.0164	.0114	.0126	.0130	.0122	.0119	.0122
	a	cd	bcd	bc	b	b		a	d	bc	b	bcd	bcd	

RESULTS

These are presented in four tables and two figures. Fig. 2 illustrates the appearance in 1971 of typical members of each of the groups in the graft experiment. Tables 1 and 2 present the assessed data by individual parameters for each group of plants, and Fig. 3 shows the mean within-group regressions of a number of these parameters on 1971 tree height. The regressions show that height accounts for much of the difference between group means. Tree height is not the independent variable expressing tree size which accounts for the maximum percentage of variation in *all* parameters, but because it always accounts for a high percentage, and because its measurement is not subject to assumption or marked inaccuracy, it has been selected as the covariate of tree size on which to examine and (where necessary) adjust other parameters. Where the assessed means have been adjusted by covariance analysis (using the average within-group regression on 1971 height as the basis for adjustment), they are presented in their adjusted form in Table 1 along with the assessed data.

Fig. 3 also shows that for several of the parameters assessed the regression slope of the seedlings and juvenile grafts and cuttings differs from that of the general "population" being examined. Where this is particularly marked adjustments have been made to the assessed data on the basis of separate covariance analyses (i) for Groups S, G6 and C6, and (ii) for the remaining groups; and these form the adjusted data presented in Table 1. The decision as to whether or not to do this has been somewhat arbitrary: in general it has been done only where adjustment on the basis of the average within-group regression for all groups combined would lead to a faulty interpretation of the data. As a procedure it has the disadvantages (1) that it does not allow direct comparison of the significance of difference of means adjusted by different analyses, and (2) that there are insufficient data on which to regard S2, G6 and C6 as belonging to the same

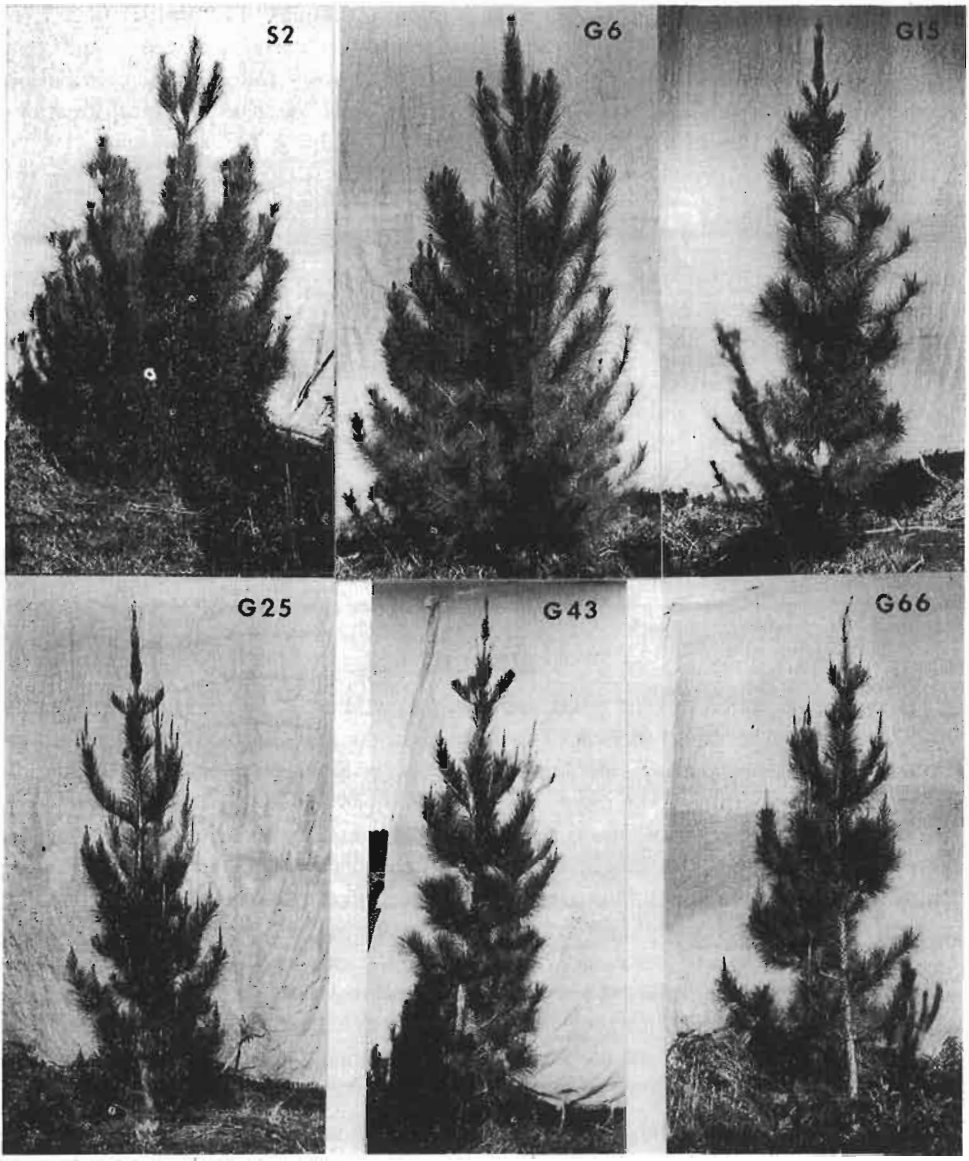

FIG. 2—A representative tree from each of the groups in the graft experiment. Photographed July 1971.

"population" for regression purposes. Where this procedure has been used, the fact is shown in Table 1.

Table 3 presents variance ratios from analyses of variance on the assessed data to indicate the relative importance of the various steps in the hierarchical structure of the experiment, and Table 4 presents variance ratios from regression analyses which are helpful to interpretation of the adjusted data in Table 1. Table 4 shows highly significant differences between individual group regressions for a number of parameters, and this

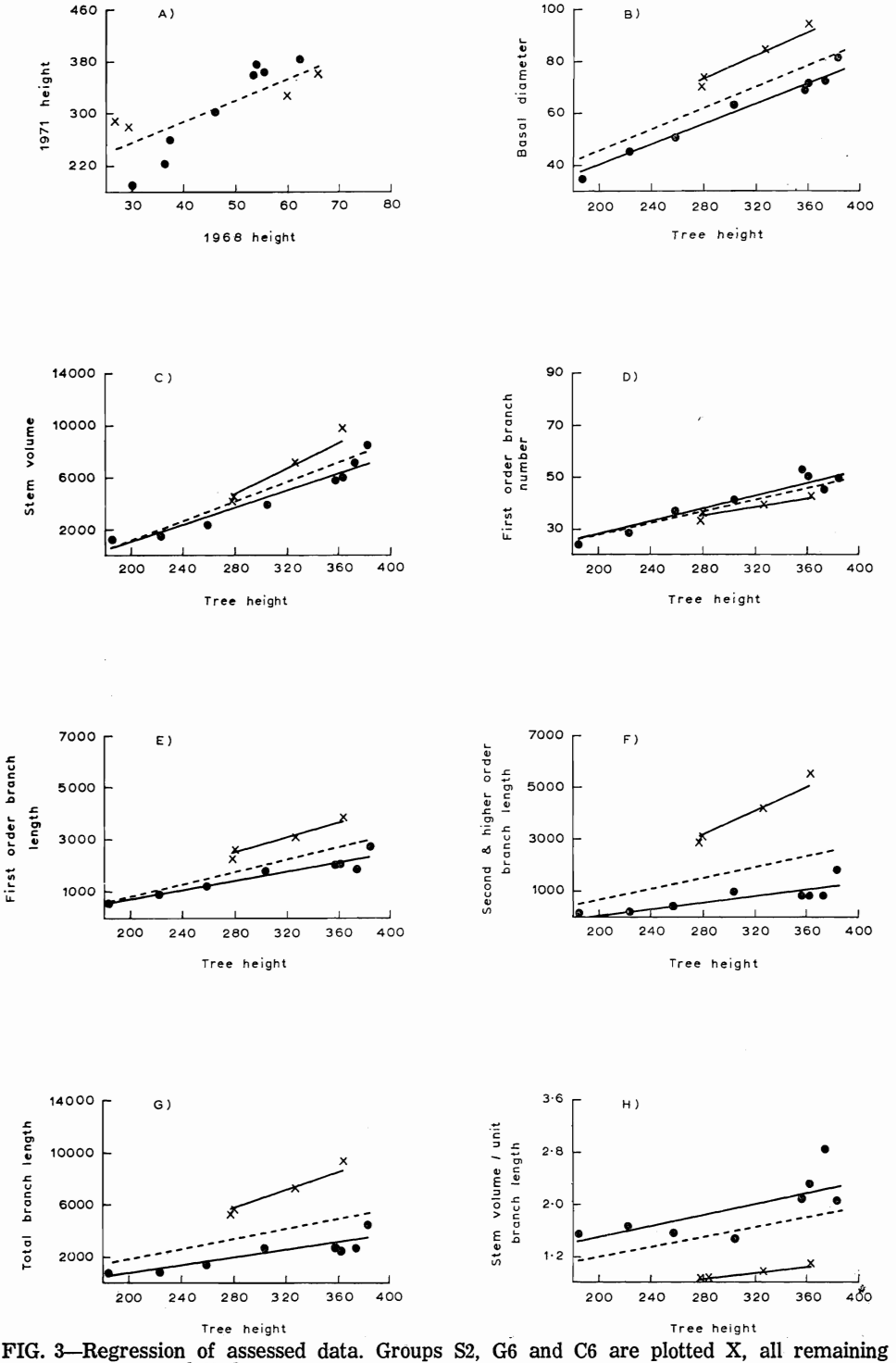

FIG. 3—Regression of assessed data. Groups S2, G6 and C6 are plotted X, all remaining groups are plotted ●.
- - - - = mean within group regression calculated on all 12 groups
——— = mean within group regression calculated on either 4 (X) or 8 (●) groups

TABLE 3—Analyses of variance

	d.f.	Symbol	F-Test Ratio	Minimum F-Value for Significance			F-Values												
				5%	1%	0.1%	Tree Height	RHGR	Basal Stem Diameter	Form Factor	Stem Volume	First-Order Branch Number	First-Order Branch Length	Second-Order Branch Length	Total Branch Length	Stem Volume per Unit of Branch Length	Retarded* Leader	Scarious* Winter Buds	Trees† With One-year Female Strobili	Trees† With One-Year Pollen Catkins
							1971	1968-1971	1971	1971	1971	1971	1971	1971	1971	1971	1970	1970	1969	1969
Between experiments	1	a	$\frac{a}{b}$	5.0	10.0	21.0	11.9	-†	5.3	-†	8.8	13.0	3.0	-†	-†	2.5	-†	-†	7.1	4.4
Between groups within experiments	10	b	$\frac{b}{c}$	2.0	2.6	12.4	9.8	23.2	18.3	17.9	3.7	11.2	21.6	8.3	9.3	15.0	30.4	105.0	10.6	3.8
Between clones within groups and experiments	48	c	$\frac{c}{d}$	1.4	1.8	2.0	4.7	1.8	4.6	1.9	13.2	2.3	4.3	11.2	11.9	5.4				
Between trees within clones, groups and experiments	471	d																		
Total	530																			

* These analyses were carried out on mean clonal values. The error term thus had 48 d.f and the total d.f were 59. † F-values less than one. ‡ Arcsin transformation made.

TABLE 4—Regression analyses

Source of Variation	d.f.	Symbol	F-Test Ratio	Minimum F-Value for Significance			F-Values									
				5%	1%	0.1%	1971 Tree Height on 1968 Tree Height	Basal Diameter on 1968 Tree Height	Form Factor on 1971 Tree Height	Stem Volume on 1971 Tree Height	1st Order Branch Number on 1971 Tree Height	1st Order Branch Length on 1971 Tree Height	2nd Order Branch Length on 1971 Tree Height	Total Branch Length on 1971 Tree Height	Stem Volume per Unit of Branch Length on 1971 Tree Height
Grand total	530															
Due to average regression	1	a	$\frac{a}{b}$	3.9	6.7	11.1	114.3	735.1	9.2	954.2	225.4	661.0	130.6	257.0	45.7	
Deviations from average regression	518	b														
Between individual group regressions	11	c	$\frac{c}{d}$	1.8	2.3	2.9	3.7	2.1	1.0	16.1	1.1	6.2	4.8	5.9	4.0	
Deviations from individual regressions	507	d														
Between group constants	11	e	$\frac{e}{b}$	1.8	2.3	2.9	33.8	64.4	29.9	29.9	10.6	97.3	86.1	106.4	53.6	
Percentage variation accounted for by the average within-group regression							18.2	58.7	1.7	64.8	33.0	56.1	20.1	33.2	8.1	

fact will have affected the accuracy of the adjustments made to means on the basis of the average within-group regression. In addition, because the mean height of the tallest group in 1971 was more than 100% greater than that of the smallest, the size of the adjustments resulting from covariance were in some cases very large. For both these reasons, the precision of the adjustments made, particularly to groups with heights at either end of the range, is poor, and the results should always be interpreted with these factors in mind.

Tree Height

Mean heights for each group for the four yr of assessment are presented in Table 1. In broad terms the mean graft was markedly taller in 1971 than the mean cutting: within the grafts there was little height difference between groups, but within the cuttings there were large and significant differences.

The overall regression of 1971 height on 1968 height accounted for 47.2% of the variation present, and the differences between groups in 1971 were very similar proportionately to those present at planting in 1968. For example, the height of the mean cutting was 72% that of the mean graft in 1968, and in 1971 the value was 70%: the mean height of Group C43 was 56% that of G43 in 1968 and 51% in 1971. These data suggest the possibility of a dependent relationship between the 1968 and 1971 values, and thus the possibility of adjusting the 1971 heights by covariance analysis. However, there were problems in finding a suitable relationship to fit the data. The mean within-group linear regression of 1971 height on 1968 height (Fig. 3A) accounted for only 18% of the total variation, and there were significant differences (0.1% level) between the individual group regressions (Table 4). Other types of regression tested did not fit the data appreciably better, and it was clear that adjustment of the 1971 heights on the basis of simple regression analysis had only limited precision.

The technique of growth analysis allows an alternative method to examine the effect of planting size on subsequent growth, and the calculation of relative height growth rate (RHGR) for the groups makes no assumptions as to the way in which the growth changes with time (Williams, 1946). The calculated RHGR data are presented in Table 2, and the analysis of variance for the 1968-71 data in Table 3.

Over the period 1968-71 there was no difference in RHGR between the graft and cutting experiments: the major difference present was between the seedlings and the vegetative propagules. The seedlings, with a RHGR nearly 30% higher than that of the mean vegetative propagule, appeared to constitute a different "population" in terms of height growth. Within the vegetative propagules, Groups G6 and C6 had the lowest RHGR values, and though there were differences between the mean values of the other groups, these were not statistically significant. A breakdown of the period 1968-71 into yearly intervals (Table 2) shows that the maximum difference in RHGR between seedlings and vegetative propagules was in the year immediately after planting, and that the difference diminished rapidly after that time. The analysis of variance of the RHGR data (Table 3) gives no indication that, per unit of height at planting, there was any difference between the rates of height growth of grafts and cuttings. Thus the differences present in 1971 height between grafts and cuttings must essentially reflect the differences present in planting height.

Basal Stem Diameter

The assessed data showed diameter differences paralleling those assessed for height: broadly the mean graft had a greater stem diameter than the mean cutting, and between the groups of cuttings there were large differences. The regression of stem diameter on 1971 height (Fig. 3B) shows that Groups S2, G6 and C6 have a markedly higher basal diameter per unit of tree height than do the remaining groups, and would appear to constitute a separate population in this respect. Table 4 shows that this is due essentially to differences in the regression constant rather than the regression slope.

After covariance adjustment (on the basis of 1971 tree height) the difference in diameter between the mean cutting and the mean graft was small (Table 1). The differences which remained important were those between the juvenile groups (regardless of whether seedling, graft or cutting) and the mature groups. The juvenile plants had a significantly greater diameter (after adjusting for height) than the more mature ones with Groups G15 and C10 being intermediate in this respect. The increased diameter of the more juvenile plants was quite considerable, with e.g. G6 having a 25% greater diameter than that of the mean graft in the experiment.

Stem Form Factor

While the average regression of stem form factor on tree height was significant at the 1% level, the relationship accounted for only 1.7% of the overall variation in form factor (Table 4). Thus adjustment of the means has changed the assessed data very little (Table 1). The analysis of variance (Table 3) showed no significant difference in this parameter between the graft and cutting experiment, but did show significant differences between groups within experiments. Essentially the juvenile trees, regardless of which experiment they came from, had a significantly lower form factor (i.e., a significantly greater stem taper) than did the more mature trees. The juvenile effect was essentially restricted to Groups S2, C6 and G6 (see Table 1).

Stem Volume

The pattern of the assessed data essentially paralleled that shown for height and diameter, and to make useful group comparisons it was necessary to carry out covariance adjustments. Figure 3C indicates (i) that Groups S2, G6 and C6 had larger stem volumes per unit of height than the remaining groups, perhaps constituting a separate population and (ii) that the regression of stem volume on tree height is probably curvilinear. Table 4 shows that significant differences exist between groups both in the regression constant and the regression slope. After covariance adjustment of stem volumes, most of the differences between grafts and cuttings disappear (Table 1). The major significant differences present are between the juvenile and the more mature plants, with G6 for example having a stem volume 45% greater than that of the mean graft. Groups G15 and C10 appeared to be intermediate between the juvenile and mature plants, but there was little difference between any of the other mature groups apart from C43 which was significantly lower than the others. Though significant, this difference may not be real, but rather may be an artefact of the adjustment and/or transformation procedure, as C43 had the lowest height of all the groups.

Number of First-Order Branches

The regression of number of first-order branches on tree height (Fig. 3D) accounted for 33% of the variation in this parameter and there was no significant difference between groups in the regression slopes (Table 4). Adjustment on the basis of tree height removed the major differences between groups (Table 1). There were then no significant differences between any of the cuttings or the seedlings, but three of the mature groups of grafts did have a higher number of first-order branches than the remaining groups. The fact that G43 had 49% more branches per unit of height than C43 when the groups had three of their five clones in common may be meaningful, but more probably it simply indicates that the adjustment was not totally successful as a basis for the comparison of two groups of very different height, when the regression accounted for a fairly low percentage only of the total variation.

First-Order Branch Length

These measurements were strongly correlated with height as shown in Table 4. Fig. 3E shows that, per unit of height, Groups S2, G6 and C6 had a higher first-order branch length than the remaining groups, and apparently constituted a separate "population" in this respect. The first-order branch length data adjusted by covariance in Table 1 show little in the way of significant differences between mature grafts and cuttings. Juvenile plants, however, had a significantly higher first-order branch length than mature plants, with Group G6, for example, having more than twice the branch length of Group G43. G15 was intermediate between the juvenile and mature groups.

Second- and Higher-Order Branch Length

The correlation between this parameter and tree height is considerably lower than that for first-order branch length (Table 4). Fig 3F shows, however, that once again Groups S2, G6 and C6 appear to constitute a different population from the remaining groups. The adjusted data in Table 1 show no significant difference between the seedlings and juvenile grafts or cuttings, but these groups as a whole, have appreciably higher branch lengths than the mature propagules: in the case of the G6 : G25 comparison the difference is ten-fold. G15 is intermediate in value between the juvenile and mature groups. In the more mature propagules some groups of cuttings have significantly greater second- and higher-order branch lengths than some grafts. It is possible that this is not a real effect but rather is an artefact of the adjustment procedure.

Total Branch Length

The correlation of total branch length with height was mid-way between that for first-order and higher-order branch length (Table 4), and Fig. 3G again shows Groups S2, G6 and C6 to have a higher branch length per unit of height than the remaining groups. The major difference shown by the adjusted data in Table 1 is that between the juvenile and the mature plants: the mean value for S2, G6 and C6, for example, equals 6825 cm compared with a mean of all other values of 2320 cm. Again G15 constitutes an intermediate between the juvenile and mature values. There was no difference between the branch length of the mean cutting and the mean graft.

The Ratio of Stem Volume to Total Branch Length

The photographs in Fig. 2 suggest that differences in foliage amount between juvenile and mature trees may be much greater than differences in tree height, and it seems likely that, per unit of foliage, stem volume production is much higher in the mature plants. As destructive harvesting was not acceptable in the trial the relationship was examined by using total branch length as an indicator of foliage quantity. Thus the ratio stem volume per unit of branch length was calculated for each tree. Fig. 3 shows that Groups S2, G6 and C6 have a markedly lower ratio per unit of height than do the other groups, although the variation accounted for by the regression is not high (Table 4). The adjusted data in Table 1 show that stem volume per unit of branch length is very similar in Groups S2, G6 and C6, but the value for the mature propagules is nearly twice as high in the juvenile ones. Within the mature plants the differences between groups were mostly non-significant.

Incidence of Retarded Leader

Retarded leader is characteristic of the adolescent stage of the ontogeny of radiata pine (Jacobs, 1937). The results of the 1969 and 1970 assessments were comparable,

and only the 1970 data are presented in Table 1. The correlation between retarded leader and height was not significant ($r = 0.01$) so the data are unadjusted. Groups S2, G6 and C6, show a markedly higher incidence of retarded leader than the remaining groups, with G15 and C11 forming a (statistically non-significant) intermediate group. There was little overall difference between grafts and cuttings, but the seedlings may have a slightly higher incidence of retarded leader than the vegetative propagules G6 and C6.

Incidence of Scarious Winter Buds

The absence of scarious winter buds characterises the more juvenile phase of radiata pine's development. Table 1 shows that in 1969 the seedlings differed clearly from all vegetative propagules in this respect, but there were no differences between any of the vegetative propagules. By 1970 (data not presented) there was no significant difference between any of the groups.

Reproductive Behaviour

In 1969 significantly more trees in Groups G15, G25, G43, and G66 had first-year female strobili than in the remaining groups. With pollen, however, the situation was reversed: more trees in Groups C19, C23 and C43 had pollen catkins than in the remaining groups (Table 1). Both these situations tended to even out by 1970, when sizeable numbers of cuttings from older ortets bore female strobili, and more grafts bore pollen catkins (Table 1).

DISCUSSION

The results of the experiments will be discussed essentially under two headings: (1) the information they provide on the processes of maturation and phase change in radiata pine, and (2) the implications of this for a plantation establishment and genetic improvement programme with cuttings in this species.

(1) The trial provides answers to some of the questions posed by Sweet (1964) on the way in which phase change (the change from the juvenile to the mature organism—Brink, 1962) occurs in radiata pine.

It is accepted that in woody plants generally phase change may occur gradually or abruptly, and that the timing of its occurrence is under both genetic and environmental control (Brink, 1962; Sax, 1962). The literature has shown that it is unsafe to use a single criterion (such as the initiation of flowering) as an indicator that phase change has occurred in plants, and generally workers in the field of maturation have tended to categorise as many indicators of juvenility or maturity as possible. This was one reason for assessing a range of characteristics in the trial reported here.

In broad terms, the trial showed differences in a number of parameters between the juvenile group of plants (S2, G6 and C6) and the mature groups (C19, C23, C43, G25, G43, and G66), with Groups C10 and G15 being intermediate. It was possible to separate Group S2 statistically from Groups G6 and C6 on the basis of several different parameters, but (after adjustment of the data using height as a covariate) it was not possible to separate clearly the mature groups of clones from one another statistically.

On this basis one could suggest that phase change in radiata pine is a process commencing early in the ontogeny and proceeding gradually for some years. With the ortets and conditions used in this trial it appeared that phase change in the cuttings was nearly complete by ortet age 10, but grafts from ortets aged 15 years at the start of

the trial still had a number of properties intermediate between the juvenile and adult condition. It may be that this merely represents differences in the age of phase change of the particular clones comprising Groups C10 and G15, but the horticultural literature does offer evidence to suggest that the rate of phase change in woody plants may be accelerated by the presence of a mature (as distinct from a juvenile) root system (Tydeman, 1937; Kemmer, 1953). Thus there is a possibility that if vegetative propagation in radiata pine is carried out close to the time of phase change, then completion of the change will be delayed somewhat in grafts as compared with cuttings.

The trial contributes information which is important to two particular aspects of phase change in radiata pine. (a) It suggests that growth rate (as measured by height, stem diameter or stem volume) is one of the factors which alters in the change from the juvenile to the mature plant—a point which had previously been obscure (Sweet, 1964), and (b) it supports the belief that phase change may be a finite rather than a continuing process. This latter point has been discussed at some length in the literature but soundly-based evidence has been somewhat limited. Obviously it is important if one wishes to propagate and use a clone vegetatively for 20 to 50 yr, to know whether or not the maturation process is continuing during this time, and if so, what effect it is having on parameters of growth and form. The virtual lack of significant difference shown between the mature groups in any of the parameters assessed in this experiment supports the suggestion that phase change is not a continuing process, but rather is finite.

It has been suggested by Fielding (1969) and Pawsey (1970) that repeated repropagation of radiata pine either temporarily halts or reduces the rate of maturation. The concept is an important one (*see* later), and it is pertinent to query whether the trial gives any information on the subject. Unfortunately it does not. Clearly if maturation is a finite process then to halt or reduce its rate by propagation it is necessary to propagate *prior* to phase change. The only clones which had been propagated repeatedly prior to use in this experiment (those in Groups G43 and C43) were first propagated vegetatively at about ortet age 25, an age which, from the results of this experiment, is well past the time of phase change. And certainly comparison of Groups C43 and G43 with other groups of higher and lower ortet age does not indicate any effect of the repeated repropagations on the parameters assessed.

(2) Implications for a Plantation Establishment-cum-Genetic Improvement Programme with Cuttings.

As stated in the Introduction, one of the major reasons for contemplating the use of rooted cuttings of radiata pine in production plantations lies in a reduction of the defects associated with the juvenile habit, and this, of course, implies the usage of non-juvenile ortets. The forester planning a production plantation/genetic improvement programme with cuttings has to face (inter alia) the following questions:

(a) What ages of stand are possible for efficient genetic selection, and what age is optimal?

(b) What is the practical effect of ortet age on the rooting ability of cuttings and how does this change with further maturation? Is this affected by repeated repropagation and/or treatments such as hedging (Libby *et al.*, 1972)?

(c) Reconciling (a) with (b) what is the optimal age of ortet for selection for production plantation-cum-genetic improvement, bearing in mind that it will be necessary to maintain selected clones in use for a number of years? How

will the growth rate and form of cuttings from such ortets compare with that of seedlings? How will these relationships change with time and with further maturation of the ortets?

This trial, by providing a comparison of the early growth rates of cuttings and seedlings, and giving information on changes in the growth rate of cuttings with ortet age offers preliminary answers to some of these questions.

By using RHGR calculations to adjust for differences in height at planting it is seen that while there were no significant differences in the rate of relative height growth between or within the mature grafts and the cuttings, the seedlings did have a faster rate of relative height growth than the vegetative propagules. The fact that the S2 Group differed so clearly from the G6 and C6 Groups suggests that the change in rate of height growth is something that occurred early in the gradual process of phase change. This is confirmed by examination of the RHGR data. The year of maximum difference in RHGR between the seedlings and the vegetative propagules was immediately after planting (1968-69). The effect was less strong during 1969-70 and was quite weak by 1970-71.

How important is this early difference in height growth between seedlings and vegetative propagules? Using the 1968-71 RHGR data one can calculate that had the trial been planted with plants of uniform height 40 cm high and had the RHGRs remained as assessed, then three growing seasons later the mean seedling would have been 424 cm high compared with a mean vegetative propagule height of 259 cm. That is, the potential height loss by using cuttings compared with seedlings three yr after planting would be some 40%. While this is quite a large height difference, the trial also indicates how readily such differences can develop by other means, such as differences in the size of planting stock. Using the RHGR data again, it can be calculated, for example, that had the mean vegetative propagule been planted at a height of 65.5 cm (compared with a seedling at 40 cm), they would both three yr later have been 424 cm high.

However, height is not the only parameter of growth, and the trial shows that after differences in height have been adjusted for, differences still exist both in basal diameter and stem volume. Juvenile trees (which for these parameters included trees in Groups S2, G6 and C6) had both a higher basal diameter and a higher stem volume per unit of height than mature trees. The basis for adjustment makes a direct comparison between juvenile and mature trees difficult, but the experiment suggests that after three yr in the field the diameter of the mature plant may be some 20% lower, and the stem volume some 40% lower than that of the juvenile plant of the same height.

Thus the forester contemplating a production plantation/genetic improvement programme with cuttings needs to balance the effect of a known loss in height, diameter and volume growth (at least in the very early stages of the rotation) against the improvement he obtains by eliminating the defects of form associated with the juvenile habit. It may be pertinent to examine whether any compromise is available, by propagating from ortets with sufficient maturity to improve on the juvenile stem form and branching characteristics, but without having lost all the juvenile advantages of stem diameter, and volume growth. The clones in Group C10 were selected seven yr after planting (eight yr after sowing) and ramets of these clones were established in the trial 10 yr after sowing of the original ortet. Trees in this group had most of the advantages

of the mature trees in stem form and branching, but still had a small part of the advantage in growth rate of the juvenile. It is possible to make adequate genetic selection in stands aged 7 to 8 yr (I. J. Thulin, pers. comm.) and rooting of cuttings from such trees poses few problems (Thulin and Faulds, 1968). Thus seven to eight years may seem a reasonable aged stand in which to initiate a production planting/genetic improvement programme with cuttings.

However, Thulin and Faulds (1968) have shown that it takes 15 yr from selection through testing to provide large numbers of cuttings of tested clones. If one selects at age seven to eight, the ortet age 15 yr later will be 22 or 23, a fully mature age. This time lag thus negates any advantages of selecting in trees as young as seven or eight yr, *unless* the processes of maturation can be halted or slowed down in some way during the period between selection of the clones and their establishment in the field. The suggestion that this may be possible by repeated repropagation, or by special means of propagation has been made by several workers (Fielding, 1969; Pawsey, 1970; Libby *et al.,* 1972). If it does prove possible, the major importance to the programme would be in maintaining ease of rooting of cuttings from clones which otherwise will be steadily maturing. However, this experiment suggests that there might also be advantages in terms of early growth rates in the field, provided that the level of maturation could be held static during the time between initial selection and field establishment. It is perhaps more likely that the processes will retard rather than halt maturation, and if so, foresters who wish to use rooted cuttings in plantations will need to accept the full reduction in growth rate that the use of mature clones involves in (at least) the early years of the plantation. In this context, however, it will clearly be of importance to follow these growth differences in the trial through to the completion of the rotation. It would be foolish to place too much emphasis on growth differences in the first three years of a rotation.

A final point requiring discussion concerns the influence of size of planting stock on subsequent height growth. Although the trial contained groups differing in mean height by a factor of more than two times, these differences were shown to have been present at the same order of magnitude at the time of planting. It is pertinent to consider how these initial height differences arose, as cuttings are normally set at a standard length. It is thought probable that they represent simply differences between groups in the rapidity of rooting and thus the quality of the early root system, rather than differences in early growth rate *per se.* Certainly the presence of initial size differences of this order has profoundly affected the subsequent nature of the trial, and this fact has important implications for the early assessment of all clonal trials. It may also raise issues of importance to the early assessment of seedling progeny trials as Sweet (1966) has shown that early size differences of a similar magnitude to these can arise in seedling progenies from initial differences in seed size.

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