GROWTH AND MORPHOLOGY OF SEEDLINGS AND JUVENILE CUTTINGS IN SIX POPULATIONS OF PINUS RADIATA

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ABSTRACT

In a **Pinus radiata** D. Don provenance-progeny trial on two contrasting pumiceland sites, the development of seedlings and juvenile cuttings was compared through to 9 years from planting. The populations represented were Ano Nuevo, Monterey, Cambria, Guadalupe, Kaingaroa, and Nelson. At planting the seedlings were 1 year and the cuttings 4 years from seed, the cuttings having been taken the previous year from 50–60 cm above the original root collars.

The cuttings showed appreciable maturation, with an earlier shift to producing sealed buds, and they outgrew the seedlings. These differences were evident even after covariance adjustments were made to allow for the carry-over of an initial size difference between seedlings and cuttings. Bark thickness was less in the cuttings, but only after adjusting for covariance on stem diameter. The cuttings generally gave slightly better ratings for butt sweep, stem crookedness, branch angle, general branch habit, and Dothistroma resistance, although the differences for stem straightness and branch habit tended to be reduced when adjustments were made for covariance on stem diameter. However, height in relation to diameter and adjusted branch frequency scores did not differ materially between seedlings and cuttings. At one site the cuttings had less butt sweep but more forking

With a few exceptions all populations showed similar seedling-cutting differences.

Keywords: Pinus radiata; vegetative propagation; cuttings; maturation; growth; morphology; cyclophysis.

INTRODUCTION

Mass vegetative propagation by stem cuttings is a potential means of improvement of *Pinus radiata*. It could capitalise on non-additive gene effects as well as additive ones, while avoiding unwanted genetic variability from genetic segregation. It also offers improved tree form through maturation effects (Fielding 1970; Thulin & Faulds 1968; Tufuor & Libby 1973).

Maturation in *P. radiata* is progressive. A young, first-year seedling shows mainly primary foliage, with prominent green apical tufts of primary leaves, and the secondary needles are relatively thin. As the seedling gets older and larger, green primary needles

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are no longer formed, the apical tufts being superseded over a period of time by brown, sealed buds. The secondary needles become thicker and a deeper green. The branching pattern becomes more regular and eventually the frequency of branch clusters on the main stem increases. Apical dominance, after a phase of being comparatively weak, becomes stronger, and the stems become less sinuous. Pollen production generally begins at around age 5 years, and seed cone formation from around this age depending very much on the individual genotype (Bannister 1965). While the onset of flowering may be a qualitative phenomenon, it is probably a threshold effect in a steady and asymptotic advance towards some ultimate maturation state (cf. Burdon 1982). On this basis the classification into juvenile and adult maturation states is somewhat arbitrary, but we would regard trees under 3 to 4 years old as being normally juvenile and those over about 12 years as essentially adult. However, the rate of maturation can differ markedly amongst populations (Burdon & Bannister 1973) and even among individuals within populations (Burdon & co-workers, unpubl.). The order in which the various manifestations of maturation are expressed can also vary among individuals.

Present understanding of the maturation phenomenon in *P. radiata* (Libby *et al.* 1972; Hood & Libby 1978; Bolstad & Libby 1982) is that it does not reflect the age of the tree *per se*, but rather the length along the stem axis from the seedling root collar.

The maturation state of *P. radiata* ortet material is fully expressed in the ramets, and it has to date defied all attempts to achieve rejuvenation. Adult stem cuttings have the advantages of straighter and less tapered stems, lighter branching, and less malformation. They also show persistently thin, smooth, unfissured bark down to ground level, unlike seedlings. However, mass-propagation of adult cuttings has serious problems. The preparation, collection, and rooting of mature material is far more difficult and costly. Although older ortets can provide many cuttings each, the material needs careful culling and this, plus the time lags, means that multiplication rates can be very slow despite good multiplication factors per propagation cycle. Further difficulties and costs arise in producing even lines of stock with well-balanced root systems. The growth of adult to semi-adult cuttings in the field is often disappointing (Sweet & Wells 1974; M. D. Wilcox & J. T. Miller, unpubl.), at least in the early stages, and this unreliability is a major disadvantage.

Interest now centres on vegetative multiplication of more juvenile material. One potential application is rapid multiplication of scarce but intensively improved genetic material. Another, and not mutually exclusive, application is the use of cuttings from trees 2 to 5 years old, in the hopes that they will combine easy rooting and reliable growth with advantages in stem form. The testing of such material to date has been limited and, except for studies by Libby and co-workers (Tufuor *et al.* in press; Bolstad & Libby 1982), has involved a narrow range of genetic material.

In a combined provenance-progeny trial of *P. radiata* it was possible to study juvenile cuttings through to 9 years after planting. This report covers cutting-seedling comparisons for all but one of the natural populations of the species plus two New Zealand control populations. Incidentally, it is believed to be the first published report of the performance of cuttings of the Guadalupe population.

MATERIALS AND METHODS

The Experiment

The experiment has been described elsewhere (Burdon & Bannister 1973). It involved wind-pollinated progenies sampled from the five natural populations (Ano Nuevo, Monterey, and Cambria on the Californian mainland, and Guadalupe and Cedros Islands) and two New Zealand populations (Kaingaroa and Nelson). It was replicated on contrasting sites in Kaingaroa Forest: one (Site A), in the Northern Boundary region, was appreciably warmer than the other (Site B) which was a typical "plateau" site. Planting was spread over 3 years (1964, 1965, and 1967) on both sites.

This study concerns only the 1967 plantings, which contained both seedlings and clones (cuttings). The seedlings comprised 8 individuals × 50 wind-pollinated progenies per population per site. The cuttings comprised 4 ramets × 2 clones × 30 of the above progenies per population per site. Clones were replicated only within sites. The Cedros population was not represented as cuttings.

The seedlings were planted as 1-year tubed stock, randomised when pricked out from the sowing boxes.

The cuttings came from the 1963 seed sowing. Ortets were lined out in the nursery during the first summer, and in 1965 these seedlings were hand-wrenched. Four vigorous seedlings from each of 40 progenies per population were then lined out at 0.5 × 0.5 m spacing in the nursery during winter. During the next growing season they were hedged to less than 50 cm height to encourage the production of suitable shoots for cuttings. Early in May 1966 cuttings about 15–20 cm long were taken, six from each seedling, all with intact terminal buds or apical tufts. The bases of almost all the cuttings were about 50–60 cm above the root collars. The cuttings were set in polythene tubes, unrandomised. A pilot run in the previous year had confirmed that almost 100% rooting success was obtainable with such material in all six populations.

In 1967 the families were culled to 30 per population, initially on numbers of plantable cuttings and then at random. The first four good plantable cuttings per clone were chosen, the rest being lined out as blanking stock. All seedlings and cuttings were planted in essentially random tree-by-tree mixture, in a single 4-ha block at each site.

About 5% blanking was required in 1968 for the seedlings and 3% for the cuttings at Site A, but only about one-tenth as much at Site B.

At planting, the cuttings were larger and sturdier than the seedlings. In the second and third seasons after planting there was heavy mortality from frosting in some small shallow gullies at Site B, which affected the larger cuttings less. A few cuttings at Site A were nipped back by hares and rabbits in the first year after planting, without actually being killed.

Assessments

From the first year after planting several assessments were made, until 8 years at Site A and 9 years at Site B. Particulars of the times, traits assessed, and units of measurement are shown in Table 1. Trees that had died or become suppressed before the final assessment were disregarded.

TABLE 1—Particulars of relevant assessments. All scores were subjective ratings or categorisations

Variable	Score range	Measurement units	Year(s) from planting	
			Site A	Site B
Height (Ht)		cm/dm	1,2,3,8	1,2,3,5,9
Retarded leader, current	0–1		1,2,3	1,2,3
Branch clusters on main stem		count	1,3	1,3
Onset of sealed buds, leader	[0–4]			
Inset of sealed buds, laterals	[0–4]			
Onset of sealed buds, total (Buds)	0–8		2	2
*Dothistroma infection (Dothi)	0–4		–	8
Stem diameter b.h.o.b. (Diam)		mm	8	9
Bark thickness (Bark)		mm	8	9
†Forking occurrence (Forks)	0–1		8	9
Butt straightness (Butt)	1–4		8	9
Stem straightness (Str)	1–9		8	9
‡Branch habit quality (Br qu)	1–9		8	9
Branch angle (Angle)	0–5		8	9
Branch cluster frequency (Br fr)	1–5		8	9
§Leader dieback occurrence (Dbk)	0–1		8	–
‖Crown density (Crown)	1–4		8	–

* Part of block only, scoring in relation to neighbours on basis of vertical progression of disease from ground.

† Ignoring forks below breast height (1.4 m).

‡ Regularity of branching and size and angle of branches in relation to branch cluster frequency.

§ Putatively reflecting infection by **Diplodia pinea** (Desm.) Kickx.

‖ Primarily reflecting resistance to needle cast that is associated with **Cyclaneusma minus** (Butin)DiCosmo et al. (syn. **Naemacyclus minor**).

Statistical Treatment

Seedlings and cuttings were compared trait by trait and population by population. The initial size difference between the two categories obviously influenced later growth. That in turn appeared to influence the expression of various morphological traits. It was therefore appropriate, in order to achieve more realistic comparisons between cuttings and seedlings, to make covariance adjustments, correcting the later growth measurements for the between-class difference in a measure of starting size, and correcting morphological traits for the difference in current size. Covariance adjustments were indicated when there were appreciable within-subclass associations and, usually, only when there were plausible cause-and-effect relationships. In a situation with two or more prospective covariate traits that were equally plausible, the covariate that showed the closer association with the trait under comparison was used for the adjustment.

The covariance adjustments were made population by population. They were on the basis of the pooled within-clone regressions for the population, adjusting the cuttings mean for the Y variable to the value corresponding to the seedlings mean for the covariate (X). This procedure was adopted because of a tendency for the cuttings to show different within-subclass regressions from the seedlings, which argued against the usual analysis of covariance procedure of pooling all subclass regressions and adjusting the Y values to the over-all means for the covariates. The within-clone regressions have the advantage of being strictly non-genetic in nature. A cross-check, however, was provided by adjusting the Y values for the seedlings to the covariate means for the cuttings, using pooled within-seedling-family regressions. Further cross-checks were afforded by using over-all within-population regressions for the cuttings and the seedlings instead of the within-clone and within-family regressions respectively.

Comparisons between cuttings and seedlings were finally expressed as relative performances of cuttings, seedling means equalling 100 for each particular population. For growth variables, and for subjectively scored traits with values clustering around mid-scale, a simple percentage ratio was used. For the occurrence of dieback and forking, and subjectively scored traits with values clustering towards ends of the scales, the following expression was used:

$$\text{Relative performance} = 100 \sqrt{\frac{(\overline{Y}_c - Y_{min})(Y_{max} - \overline{Y}_s)}{(\overline{Y}_s - Y_{min})(Y_{max} - \overline{Y}_c)}} \qquad (1)$$

where $\overline{Y}_c$ and $\overline{Y}_s$ are the mean values for cuttings and seedlings respectively,

and Y_{max} and Y_{min} are respectively the upper and lower bounds of the scale.

This measure of relative performance is independent of convention. For example, it accommodates the fact that $1\% : 3\%$ of forking represents the same situation as $99\% : 97\%$ of unforked trees. At the same time it gives a comparative measure that is reasonably stable with respect to wide variations in the average expression of the trait.

Relative performances are based, where applicable, on scales that assign maximum values to the most desirable expressions of the respective traits. Exceptions are branch cluster frequency (Br fr) and degree of sealed bud formation (Buds), in which maximum expression is not necessarily preferable.

Standard errors of individual differences were not pursued; their expected values were complex, concern was with cumulative evidence, and seedling-cutting comparisons in other trials (Tufuor et al. in press; M. D. Wilcox & J. T. Miller unpubl.) have seemed far less repeatable than indicated by standard errors within experiments. For the same reasons, explicit tests of population × propagule class interactions were not pursued.

RESULTS

The cuttings maintained a size advantage over the seedlings at both sites (Table 2), especially Site B. They showed generally higher percentages of live, unsuppressed trees at final assessment: at Site B c. 70% v. 55% in Guadalupe, and c. 95% v. 85% over the other populations; at Site A, c. 90% v. 65% in Guadalupe, and c. 95% v. 97% over the other populations. Year-1 height showed marked within-clone associations with

TABLE 2—Over-all comparisons for growth variables between cuttings and seedlings, as means of population means

Site	Category	Height (cm)					D.b.h.o.b. (mm)
		— — — — — — Year after planting — — — — —					
		1	2	3	5	8/9	8/9
A	Cuttings	52.6	122	234	–	1234	188
	Seedlings	40.8	100	203	–	1162	168
	Difference	11.8	22	31	–	72	20
B	Cuttings	50.0	102	189	573	1110	184
	Seedlings	37.8	78	155	498	1021	150
	Difference	12.2	24	34	75	89	34

final diameter over bark (R = c. 0.5) and final height (R = c. 0.3, p < 0.001). Early heights showed similar associations with sealed bud scores, while straightness, branch habit quality, and branching frequency scores generally showed weaker but still statistically significant (p < 0.05) associations with stem diameter.

Table 3 shows relative performance of cuttings for each variable, without covariance adjustments, by populations, on the respective sites. For final height and diameter the seedling-cutting differences were consistent among the populations. Bark thicknesses were actually greater in the cuttings, particularly at Site B where the cuttings had a greater stem diameter advantage. The cuttings were much more advanced in sealed bud formation, although relative performance figures did vary widely. For freedom from butt sweep, stem straightness, and branching variables the cuttings were generally better than the seedlings, although this advantage was not clearly evident for butt sweep at Site B. Crown density (Site A) scored marginally better in the cuttings, and Dothistroma resistance (Site B) appreciably better. Leader dieback (Site A) showed no consistent pattern among populations. Surprisingly, forking was more prevalent in the cuttings at Site A.

Branch cluster counts (Fig. 1) were initially greater, relative to height, in cuttings but by Year 3 this comparison was sometimes reversed, which parallels results for branching frequency scores. Retarded leader was initially much more prevalent in cuttings (Fig. 2), but this difference was very transient except in Cambria and Monterey.

Among potential covariates Year-1 height was used as a measure of starting size. For obtaining more realistic comparisons of morphological variables final diameter (over bark) was favoured as a covariate, because it tended to show stronger within-clone associations with other variables than did height, although using height often gave essentially the same results. Sometimes no covariance adjustment was indicated. With forking, although there was a favourable within-clone association with diameter, no covariance adjustment was attempted in view of the binomial (0 or 1) nature of the data.

TABLE 3—Relative performance of cuttings (seedlings = 100 for the particular population) without covariance adjustments, for different variables at each site. Figures in brackets are calculated using Equation 1, other figures being simple ratios of mean measurements or scores. Variables are as defined in Table 1 and relate to Years 8 or 9 except for Buds (Year 2)

Population	Buds	Ht	Diam	Bark*	Butt	Str	Br qu	Br fr	Angle	Crown	Dbk	Forks	Dothi
Site A													
Ano Nuevo	233 (266)	111	117	111	110 (118)	115	117	110	106	101	(99)	(91)*	–
Monterey	295 (227)	103	110	107	109 (118)	105	99*	99*	102	100	(106)	(73)*	–
Cambria	713 (313)	105	110	110	107 (111)	96*	95*	95*	100	100	(97)	(79)*	–
Kaingaroa	198 (253)	107	113	110	106 (111)	117	109	108	110	101	(122)	(94)*	–
Nelson	238 (235)	106	112	109	109 (116)	114	104	106	96*	100	(88)	(89)*	–
Guadalupe	116 (150)	106	108	103	112 (129)	108	110	110	104	107	(106)	(83)*	–
Site B													
Ano Nuevo	201 (216)	109	122	133	100 (104)	116	104	111	103	–	–	(107)	105
Monterey	186 (166)	109	123	126	97 (95)*	111	97*	103	98*	–	–	(102)	122
Cambria	159 (139)	111	123	128	97 (95)*	110	106	103	97*	–	–	(91)*	105
Kaingaroa	198 (243)	109	127	137	110 (119)	117	112	115	112	–	–	(115)	125
Nelson	201 (204)	109	121	121	98 (96)*	114	105	106	100	–	–	(109)	113
Guadalupe	128 (173)	106	116	118	104 (113)	106	108	98*	103	–	–	(99)*	118

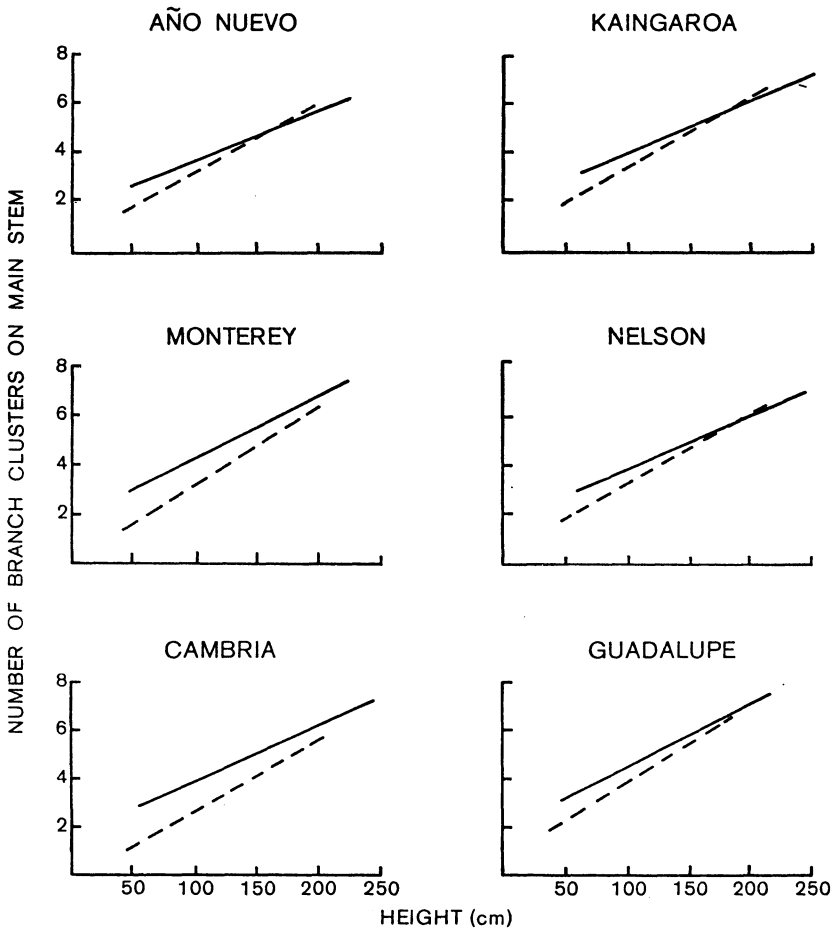* Difference in opposite direction from expected (see Introduction).

FIG. 1—Mean numbers of branch clusters on main stems v. mean heights,
         Site A, Years 1 and 3, by populations. Solid lines denote cuttings,
         dashed lines seedlings.

Comparisons, after any appropriate adjustment, are summarised in Table 4 for growth variables and several morphological traits. Adjustment generally reduced the differences, except with bark thickness where it almost always reversed them and a very few other comparisons where differences were slightly accentuated. Use of various alternative covariance adjustments generally had very little bearing on final comparisons.

After adjustment for Year-1 heights, final heights and diameters were generally greater in the cuttings, particularly at Site B. The most striking post-adjustment differences between categories were in Year-2 sealed bud scores, the seedlings of some populations having barely started to produce sealed buds. The smallest differences occurred for Guadalupe, in which both seedlings and cuttings were producing almost entirely sealed buds. After adjustment for stem diameter, bark thicknesses were almost all lower in the cuttings, the main exception being Guadalupe in which even seedlings
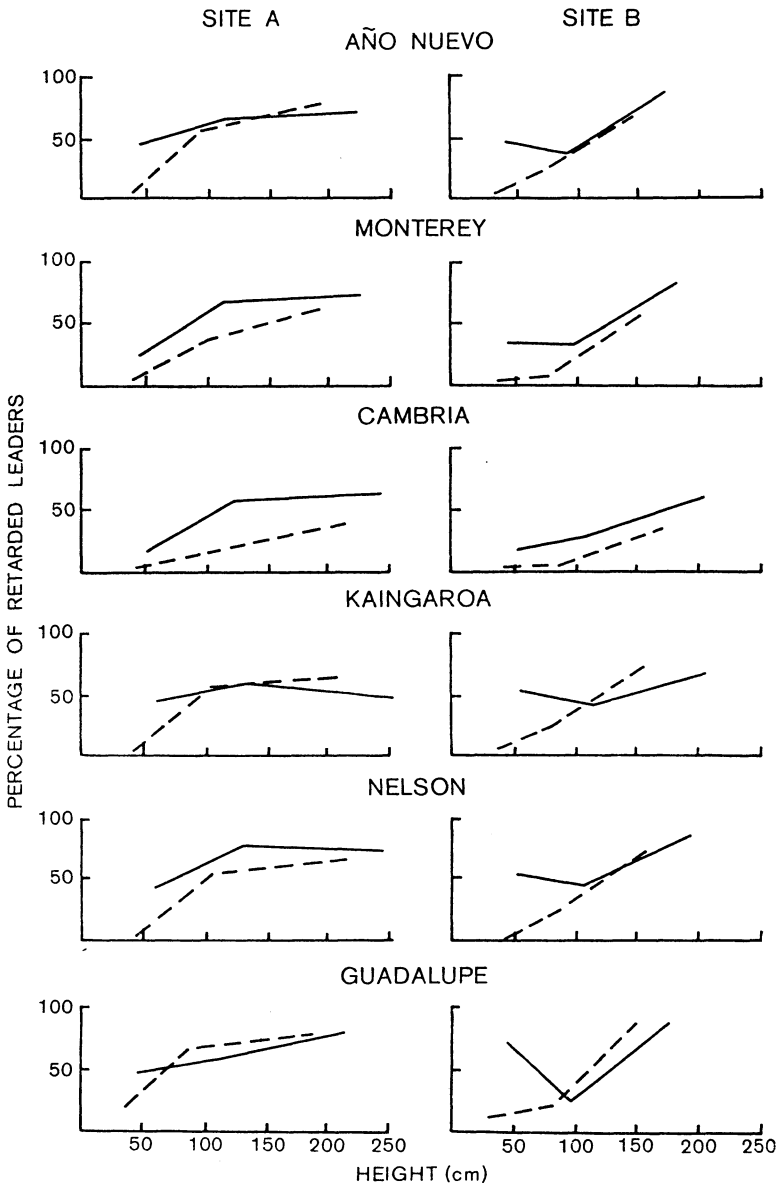
FIG. 2—Comparative incidence (%) of retarded leader, Years 1-3. Solid lines denote cuttings, dashed lines seedlings.

show adult-type bark down to the root collar. Stem and butt straightness scores were almost always better in the cuttings, and branching quality and branch angle scores were generally so. Branching frequency scores were not consistently higher in cuttings. Height in relation to stem diameter was marginally greater in cuttings.

TABLE 4—Relative performances of cuttings (seedlings = 100 for the particular population), after covariance adjustments, for different variables at each site. Figures in brackets are calculated using Equation 1, other figures being ratios of mean measurements or scores. All variables as defined in Table 1 and relate to Years 8 or 9 unless otherwise indicated

Population	Variable: Covariate:	Buds 2 Ht 2	Ht Diam	Ht	Diam - - Ht 1 - -	Bark — —	Str — — Diam	Br qu — —	Br fr — —
Site A									
Ano Nuevo		229 (326)	102	107	109	98	111	109	104
Monterey		281 (227)	98	100	105	97	102	95*	92*
Cambria		611 (256)	101	100	102	101*	92*	90*	89*
Kaingaroa		197 (358)	101	102	102	99	106	103	102
Nelson		235 (260)	100	101	102	96	110	101	100
Guadalupe		109 (152)	103	104	101	99	106	109	107
Site B									
Ano Nuevo		187 (228)	104	107	115	99	118	107	100
Monterey		177 (165)	101	105	111	93	109	100	95*
Cambria		142 (127)	102	106	110	97	104	105	94*
Kaingaroa		193 (293)	102	106	112	98	106	101	101
Nelson		181 (190)	101	106	102	91	108	104	102
Guadalupe		126 (258)	101	101	99	107 *	105	107	99*

* Difference in opposite direction from expected (see Introduction).

Morphological differences between seedlings and cuttings in the opposite way from that expected were more frequent in the Cambria and Monterey populations, which are the most persisently juvenile (Burdon & Bannister 1973).

DISCUSSION

The most appropriate covariance adjustments may be arguable, but the choice of covariance procedure clearly had little bearing on results. Irrespective of adjustments used, however, there were several factors that may have led to under-correction. Errors in measuring either a dependent or an independent variable will tend to bias regression slopes downwards. The subjective scores undoubetdly contained substantial error. Height at the end of the first year was adopted as implicitly the best available measure of starting size, since it embodies the large contribution of the sturdiness of planting stock to post-planting growth (cf. Chavasse 1980) and the short-term effects of planting shock. However, it must have been an imperfect measure. Moreover, the regressions related to environmental effects arising over the whole 4 ha of a block and not necessarily to the effects that influence trees' competitive positions with respect to

neighbours. There was no reason to believe that the use of multiple covariates would have given materially better adjustments.

Threshold traits present statistical difficulties. No explicit adjustment of the incidence of forking was attempted, although at Site A, where forking was more prevalent in the cuttings, forking was positively associated with stem diameter. The relationship between forking and stem diameter is ambivalent – the leader damage that often leads to forking can lead to loss of dominance, and yet competition which reduces stem diameter growth may help suppress competing laterals.

The relatively poor growth of the seedlings at Site B merits comment. For stem diameter, very slight bias could have arisen through preferential survival of the cuttings in the gullies where the survivors would have suffered less competition. The initial size advantage of the cuttings may have been more important on the generally harder site, and such a factor could be accounted for only if the covariance adjustment was fully efficient. Heavier Dothistroma attack at Site B could have affected the comparison. The cuttings appeared to have been less defoliated by Dothistroma than the seedlings, even using a scoring system designed to allow for the tendency for the upwards progression of Dothistroma infection to cause lower percentages of defoliation on taller material. This accords with the results of Power & Dodd (1984).

On both sites the superior growth of the cuttings could reflect some selection for ortet vigour in obtaining suitable plants for the vegetative propagation. This element of selection was not duplicated in choosing the seedlings.

Minor differences between populations in the seedling-cutting comparisons could have arisen from various, potentially complex, sources of error. Allowing for this, trends emerge clearly. Even so, it is worth commenting on several specific discrepancies. The thin bark of the Guadalupe seedlings is a distinctive feature of this population. The onset of sealed bud formation was too far advanced in this population for strong differences to emerge between seedlings and cuttings, unless relative performance was calculated by using Equation 1. And it is tempting to relate the absence of some expected seedling-cutting differences in Monterey and Cambria to the persistence of juvenile characteristics in those populations (Burdon & Bannister 1973).

Of note were the slightly lower, adjusted, branch cluster frequency scores for the cuttings in the majority of the provenances. Superficially, this is at variance with the well-known high branching frequency (as distinct from total numbers of branches) of adult propagules. However, there is no conflict of evidence if the frequency passes through a minimum after the early juvenile state.

The seedling-cutting comparisons must be interpreted in relation to the quantitative differences in maturation state. Chronologically the cuttings were 3 years older from seed than the seedlings, but the effective difference is viewed as more like 2 years. As explained in the Introduction, the maturation state of the cuttings seems to be defined best by the 50–60 cm from the ortet root collar to the base of a cutting.

This study involved cuttings that were more juvenile than in most others. The good vigour shown by the cuttings therefore augurs well for vegetative multiplication of seedlings. Some slight concern, however, must attach to the difference between sites in the growth of cuttings relative to the seedlings.

CONCLUSIONS

Despite having been taken only 50–60 cm above the root collars, the cuttings showed appreciably greater maturation than the seedlings, which is best reflected in sealed bud scores. There was no evidence that this degree of maturation entailed any loss in growth potential; by all available measures the cuttings actually grew slightly better. The cuttings on the whole had slightly thinner bark, straighter stems, and more desirable branching. However, no clear effect of maturation was evident for either height in relation to stem diameter or branch cluster frequency.

ACKNOWLEDGMENTS

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