Comparisons of Radiata Pine Cuttings of Hedge and Tree-Form Origin after Seven Growing Seasons

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Summary

This experiment was designed to test the hypothesis that cuttings of radiata pine derived from hedge-form plants consistently grow different from cuttings from tree-form plants

Clonal pairs of plants originating as cuttings from these two types of cutting donor were compared seven years after planting. On average, hedge-origin and tree-origin cuttings grew to similar height, but hedge-origin cuttings had larger volumes, larger, more, and longer branches which took more time to prune, produced fewer cones, had more taper, and poorer form than tree-origin cuttings.

Furthermore, the data suggest that frequent hedging maintained a juvenile condition in the hedge-form donor plants, while the tree-form donors matured. Differences associated with maturation state were evident between the rooted cuttings derived from these two kinds of donors for at least eight years after the cuttings became independent of the donors.

Differences in heights and bole volumes among cuttings from the three mainland populations of radiata pine were as expected, based on a provenance study employing seedlings in a nearby plantation of similar age.

Key words: Bole size, Clones, Height, Juvenility, Maturation, *Pinus radiata*, Provenance, Pruning time, Stem form, Strobilus production.

Zusammenfassung

Der vorliegende Versuch wurde durchgeführt, um die Hypothese zu testen, daß Stecklinge von *Pinus radiata* von heckenförmigen Mutterpflanzen ein durchweg anderes Wachstum aufweisen, als Stecklinge von baumförmigen Mutterpflanzen.

Die Stecklings-Klone stammten von Mutterpflanzen dieser beiden Typen und wurden sieben Jahre nach dem Auspflanzen verglichen. Im Mittel waren die Stecklinge der hecken- und baumförmigen Mutterpflanzen zu gleicher Höhe herangewachsen, aber die Stecklinge der heckenförmigen Mutterpflanzen hatten ein größeres Volumen; mehr, breitere und längere Äste; benötigten länger zur natürlichen Astreinigung; produzierten weniger Zapfen; verjüngten sich stärker und hatten eine schlechtere Form als Stecklinge von baumförmigen Mutterpflanzen.

Weiterhin machten die Daten deutlich, daß ein ständiges Beschneiden die heckenförmige Pflanze in einem jugendlichen Zustand erhält, während die baumförmige altert.

Unterschiede, die mit dem Reifegrad in Verbindung stehen, waren zwischen den Stecklingen für mindestens acht Jahre nach dem Werbetermin wirksam.

Unterschiede in den Höhen und den Stammvolumina der Stecklinge der drei Festlands-Populationen von *Pinus radiata* basierten, wie erwartet, auf einem Provenienzversuch, in dem Pflanzen gleichen Alters auf einer nahe gelegenen Pflanzung verwendet wurden.

Introduction

Libby, Brown and Fielding (1972) reported that annual hedging of radiata pine (*Pinus radiata* D. Don) at heights of one or two meters (pruning branches and main stems to hedge height) affected the rooting and early growth of cuttings from such hedges. Hedged donors provided cuttings that rooted faster and in higher percentages, survived better on a difficult site, and grew faster during the year following rooting, than did cuttings from tree-form donors. They suggested that these and other such characters that vary with state of maturation might be reliably reproduced by members of clones maintained in a juvenile condition, they further suggested that a juvenile state might be conserved within selected clones by hedging the cutting donors.

It was not clear in 1972, however, whether observed differences associated with hedge or tree-form origin are due to epigenetic changes in the cutting meristems, or to environmentally induced changes in the physiological state of the cuttings. For example, the environment might alter such things as the cutting's nutritional or hormonal status. On the other hand, the developmental genetic state (specifically, the maturation state) of the donor plant might be transmitted to its vegetative offspring. If these early differences were strictly environmentally induced, or if the epigenetic change was labile, the effects would be expected to disappear over time. If so, in a fair experiment, members of a clone, whether of hedge or tree-form origin, would be expected on average to exhibit similar growth and form after a few years.

This paper presents a comparison of clonal pairs of cuttings taken from hedge and tree-form donors belonging to 32 radiata pine clones. Contrary to the above expectation of increasingly similar growth and form, many differences between cuttings from hedge and tree-form donors either remained or increased during the seven growing seasons that these cuttings grew in a paired test.

Background

Research during the past two decades in Australia, New Zealand, and California allows the generalizations in the following five paragraphs concerning the effect of ortet age (or cutting maturation state) on growth and form of radiata pine rooted cuttings (Thulin and Faulds, 1968; Fielding, 1970; Libby, Brown and Fielding, 1972; Tufuor and Libby, 1973; Brown, 1974; Nicholls, Brown and Pederick, 1974; Shelbourne and Thulin, 1974; Sweet and Wells, 1974; Brown and Miller, 1975, Libby and Hood, 1976; Nicholls, Pederick and Brown, 1977; Hood and Libby, 1978; Eldridge, 1981).

Compared to plants grown from seed, plants started as rooted cuttings or grafts from adolescent or mature ortets develop fewer, shorter, and smaller-diameter primary branches on the lower bole. These primary branches occur at a more perpendicular angle (i.e., 90°) from the bole, and have fewer secondary and tertiary branches. This combination of branch characteristics generally results in faster pruning times, as well as less knot-related defects.

Early height-growth of seedlings is greater than that of rooted cuttings or grafts from ortets more than a few years old. However, after the first 1—3 growing seasons, the height growth of cuttings or grafts from ortets in the age range 5—15 (or perhaps more) years then seems to equal that of seedlings, and may even exceed it.

By contrast, diameter growth during at least the first 8—10 growing seasons is strongly and negatively related to the maturation state of the propagule, with seedlings having the greatest diameter growth and cuttings or grafts from mature ortets the least. Part of this effect is due to the thicker bark of seedlings and juvenile propagules, while most of the difference is due to the more-juvenile propagules having more needles, resulting in a greater production of total dry-matter.

The lower boles of seedlings have more taper, and a greater tendency to sweep, crook and fork than do those of grafts or rooted cuttings. Propagules from more mature ortets have generally better bole form than do those from juvenile ortets. However, stem cones, which cause a timber defect, occur lower on the boles of mature-ortet propagules than on propagules from juvenile ortets or on seedlings.

The onset of male and female strobilus production is earliest on propagules from mature ortets, and latest on seedlings. However, several years after the onset of strobilus production, seedlings may produce more strobili per year than grafts or rooted cuttings, due to differences in the number of branches.

A more detailed review of these and other characteristics, as expressed by seedlings and by grafts or cuttings, is available in Tufuor, Libby and Arganbright (in press). The following two paragraphs review earlier observations on replications of the experiment reported in this paper.

Rooted cuttings from hedge and tree-form donors of the same clones were outplanted in three locations. Protocols are described in Materials and Methods, below. Libby and Hood (1976) reported the first three years' performance of these plants, as follows. At one plantation, hares preferentially browsed the cuttings from tree-form donors. At a second plantation, which suffered high general mortality, cuttings from hedge donors survived substantially better than did those from tree-form donors. (The data presented in this paper are from the third plantation in this experiment, which suffered from neither of these problems.) Cuttings from hedge donors consistently and significantly exceeded those from tree-form donors in: total needle length; number and average length of primary branches; number of secondary branches; and third-year bole volume; but the hedge-origin cuttings had fewer male and female strobili. Based on these and other observations, they concluded that the cuttings from tree-form donors were more mature than the cuttings from hedge donors of the same clones (which were, of necessity, of the same chronological age). Cuttings from the two kinds of donors were not consistently different in height or in bole taper after three growing seasons in the field.

Part way through the 5th growing season, the first replication was measured, cut, divided into needles, twigs, branches, and boles, and analyzed for differences in growth and in allocation of above-ground dry-matter (Hood and Libby, 1978). In this first replication, the hedge-origin plants had significantly more branch, twig and needle dry-weight than tree-origin plants. Bole weights and volumes of the hedge-origin plants were also greater, but not significantly so. However, the tree-origin plants were significantly taller than the hedge-origin plants, and they were also less tapered, although not significantly so. Stem-form was similar. The few male strobili observed were all on tree-origin plants, and tree-origin plants had significantly more cones and conelets than did hedge-origin plants. The hedge-origin plants allocated relatively more above-ground dry-matter to branches and needles, and the tree-origin plants allocated relatively more to new growth and bole wood. These differences in allocation were statistically highly significant. They concluded that effects of hedging were still detectable and important five years after the cuttings were removed from their hedge or tree-form donors.

Materials and Methods

Fifty-one clonal pairs, rooted during the California experiment reported in Libby, Brown and Fielding (1972), were outplanted in December 1971 on a level uniform site at Russell Reservation (near Lafayette, California: 37° 55'N; 122° 08'W; 245 m elev.). The cutting donors were themselves rooted cuttings. They had been collected from native- population seedlings in late 1962 and had been planted near each other in early 1963. Beginning in 1965, half were hedged annually at one-meter height, and the other half continued to develop as trees. Cuttings were taken and set during winter 1970—71. At the time of planting in December 1971, each clonal pair consisted of 2 rooted cuttings of similar size and health, one from a hedge-form donor and the other from a tree-form donor of the same clone. Not all clonal pairs were of the same size, differences at the time of planting occurring both between different pairs of the same clone and between clones. But all comparisons of hedge- and tree-origin effects reported below have been made within pairs, not between them.

The two plants comprising a clonal pair were planted next to each other, randomized so that site differences were not consistently associated with one of the donor types. Members of a pair being adjacent minimized site-related differences within pairs. We selected well-rooted cuttings of similar size for each clonal pair to avoid the problems of later growth analysis that are associated with planting cuttings of different sizes (Sweet and Wells, 1974). This may have resulted, however, in some of the slower-growing cuttings of hedge origin being paired with faster-growing cuttings of tree origin, as the hedge-origin cuttings generally had rooted earlier.

Of the 47 clonal pairs surviving in 1979, 16 were originally from the Monterey, 13 from the Cambria and 18 from the Año Nuevo populations, with 32 different clones being included (i.e., some clones contributed more than one pair). Clonal pairs from the three different populations were systematically planted in alternate locations across the planting site, so that site differences were not associated with population of origin.

Ten attributes were assessed during a three-week period in late January and early February 1979, at which time the cuttings had completed 7 growing seasons on site *(Figure 1).*

Height was measured with a clinometer, from ground level to the tip of the main stem. Forking was uncommon, and did not seriously complicate height and diameter measurements. Stem diameters were measured at 0.3 (approximate stump height) and 2.75 meters above the ground, with calipers. These measurement points were moved short distances up or down to avoid stem swelling at nodes, as

Figure 1. — General view of the plantation, showing size and condition of the trees. The photograph was taken 10 months after the data and pruning were completed, near the end of the eighth growing season following planting, nine years after the cuttings were independent of the donors.

appropriate. A representative branch length was determined for each tree, by measuring the horizontal projection of the branch visually assessed to represent the average crown projection. Stem form components were integrated into a visually determined rating (1 = badly malformed, 5 = excellent), assessing the overall bole form. The rating number of each tree was determined by consensus of four crew members. Similarly, the abundance of male strobili was rated on a scale of zero (absent) to five (abundant) by two crew members. The basal diameters of the three largest branches were measured. The times required to prune the main bole of the plants to 2.6 meters were determined as in TUFUOR and LIBBY (1973), the pruner using a pair of long-handled secateurs for most of the branches, and a short-handled pruning saw for the larger branches.

The numbers of developing female stroboli (1979 pollination) and developing yearling conelets (1978 pollination) were determined for each plant with the aid of binoculars. Two calculated volumes, V1 and V2, were added to approximate the bole volume. V1 is the volume of a right-circular frustum 2.45 meters in height, with the bottom and top diameters equal to the stem diameters measured at 0.3 and 2.75 meters, respectively. V2 is the volume of a right-circular cone having a bottom diameter equal to the stem diameter at 2.75 meters and a height equal to the measured plant height minus 2.75 meters. Taper of the bottom (2.45 m) log was calculated as a ratio: diameter at 2.75 m divided by diameter at 0.3 m.

For each quantified attribute, the difference between the hedge- and tree-origin cutting in each pair was determined, and a paired-difference test performed (paired t-test or Whitney test). The bole-form and male-strobili ratings were assessed using a non-parametric sign test. Finally, for each attribute, the difference within pairs was divided by the standard deviation of the difference, and the resulting standardized within-pair differences were then regressed against chronological ortet age, against pairs of cut-

Table 1. — **Average values, significance of differences, and ratio of differences between cuttings of hedge and tree-form origin for 10 traits, after 7 growing seasons.**

Trait	Cutting origin: Tree-form donor ($\bar{T}$)	Hedge donor ($\bar{H}$)	Statistical probability of $\bar{H}=\bar{T}$ a/	$\frac{\bar{H}-\bar{T}}{\bar{H}}$
Total height (m)	8.24	7.78	≈.20	-.06
Bole volume (cm3)	31,231	36,870	<.01	+.15
No. of branches below 2.6 m height	26.21	31.51	<.01	+.17
Crown projection (cm)	139.77	165.65	<.01	+.16
Average diam of 3 largest branches (cm)	2.29	2.88	<.02	+.20
Pruning time (min)	1.19	1.50	<.01	+.21
Taper of bottom log	0.685	0.644	<.05	-.06
Stem form b/	4.12	3.47	<.01	-.19
Number of conelets & female strobili c/	9.43	5.15	<.01	-.83
Male strobili class (per branch) d/	2.89	1.70	<.05	-.70

a) Paired t-test used for all traits except female strobili, male strobili, and stem form, the former analyzed with a Whitney test, the latter two with a non-parametric sign test.
b) 1 = badly malformed, 5 = excellent.
c) Yearling conelets (1978 pollination) and female strobili were summed for each tree in February 1979.
d) 0 = absent, 5 = abundant, 1979 pollen crop.

Table 2. — Average heights and stem volumes of cuttings of hedge and tree-form origin, by population.

Donor	Population			Statistical probabilities a/		
	Año Nuevo (A)	Monterey (M)	Cambria (C)	A=M	A=C	M=C
Clonal Pairs	18	16	13			
	- - - Height (m) - - -					
Tree-form	9.2	7.8	7.6	<.2>.1	<.2>.1	>.50
Hedged	8.5	7.5	7.1	<.3>.2	<.2>.1	>.50
	- - - Bole Volume (cm^3) - - -					
Tree-form	35,660	28,293	28,705	<.2>.1	<.3>.2	>.50
Hedged	42,041	33,650	33,684	<.2>.1	<.2>.1	>.50

a) Statistical probabilities based on t-tests.

tings rooted per clone (5 pairs set, each clone), and against height of original ortet.

Results and Specific Discussions

A summary of comparisons of cuttings from hedge vs tree-form donors is presented in *Table 1*.

Tree-origin plants were 6% taller on the average than hedge-origin plants ($p \approx 0.2$). Measurements of the same plants taken in 1974 (Libby and Hood, 1976) revealed a non-significant 3% difference in height, hedge-origin plants being taller at that time. At another replication of this experiment, Hood and Libby (1978) noted that tree-origin plants had become (significantly) taller at 4.5 years in the field, and suggested that the more mature (tree-origin) cuttings allocate relatively more above-ground dry-weight to new extension growth than do the more juvenile (hedge-origin) cuttings. The change in direction and amount of height difference on these Russell Reservation plants from 1974 to 1979 supports this hypothesis.

Tree-origin plants exhibited 15% less bole volume, a difference that is statistically highly significant. Data taken in 1973 and 1974 for the same plants (Libby and Hood, 1976) indicated smaller (4—5%) and non-significant bole-volume differences between tree- and hedge-origin plants. Thus, in spite of greater height growth by tree-origin cuttings, the hedge-origin cuttings produced a great deal more stem volume during the four growing seasons from late 1974 until early 1979.

Lower-crown primary branches on tree-origin plants were fewer, shorter, had smaller diameters, and took less time to prune than such branches on hedge-origin plants. These differences are all statistically significant, and are consistent with an earlier study of branch number and size, and of pruning times, for late-adolescent rooted cuttings and their seedling offspring (Tufuor and Libby, 1973).

Tree-origin plants showed significantly less taper than hedge-origin plants, a difference not statistically significant as measured for the same plants in 1973 and 1974 (Libby and Hood, 1976). General stem form was significantly better among tree-origin plants.

Tufuor, Libby and Arganbright (in press) found a non-significant difference in the number of cones on trees grown from seedlings, when compared to trees grown from (more mature) rooted cuttings after 14 growing seasons. They noted that the seedlings had more branches, and thus more places to produce cones once cone production began. At the earlier stage of growth in this study, the tree-origin plants had significantly more female strobili and yearling conelets.

All of the plants, of both hedge- and tree-origin, exhibited male strobili in 1979. The tree-origin plants had significantly more male strobili per branch. Given the rating system employed, it is not possible to state whether one or the other origin produced more total male strobili per plant.

We were interested in whether the magnitude of within-pair differences in the characteristics analysed could be related to the chronological age of the original ortet, which varied from 3 years to 11 years in 1962 when these ortets were first sampled in the native populations (Libby and Conkle, 1966). We also wondered whether the percentage of cuttings rooting in 1971 would be an indication of the clone's maturation state, or whether cuttings taken from shorter original ortets would produce clones that were more juvenile than those from taller trees. When the standardized within-pair differences for each attribute were regressed against the chronological ages of the clones, against the numbers of rooted pairs obtained per clone, or against the original ortet heights, only small and non-significant regression slopes were obtained. Thus, such early and possibly confounding causes of differences in ortet maturation states had little apparent effect in this experiment. The major cause of the differences between hedge- and tree-origin cuttings appears to be whether the donor plants were hedged repeatedly or allowed to grow in tree form during the 6 growing seasons from 1965 through 1970.

We included clones from all three mainland populations of radiata pine to achieve some generality. While the experiment is not large enough for an accurate analysis of population differences, the layout of the 32 clones allowed some between-population comparisons. Cuttings of the Año Nuevo population from both hedge- and tree-form donors were taller and produced more stem volume than the cuttings of the Cambria and Monterey populations, which were generally very similar to each other *(Table 2)*. Burdon and Bannister (1973) reported and reviewed studies in New Zealand and Australia, employing seedlings from these three provenances. In all these studies, trees of the Cambria provenance were consistently smaller than those from Año Nuevo. In Australia and New Zealand studies, trees of the Monterey provenance have generally been similar to or in some locations larger than those from Año Nuevo. However, nine-year height and diameter data from a nearby seedling provenance study at the Russell Reservation indicate similar average heights of the Cambria and Monterey provenance samples, the Monterey sample having the smallest average diameter, and the Año Nuevo sample having the largest average height and diameter (unpublished 1977 data of J. Crowley and C. Busby). While the results are hardly conclusive, it appears that clones of rooted cuttings have similar relative height and diameter growth as seedlings from these three populations. In our study, hedge-origin Cambria plants had significantly ($p < .01$) smaller branches than hedge-origin plants from either Monterey or Año Nuevo. All other between-population comparisons were not statistically significant.

General Discussion and Conclusions

The magnitude and significance of the differences in this and other experiments with rooted cuttings suggest several things. First, if rooted cuttings used in clonal selection programs come from ortets of differing maturation states, this may bias or reduce the effectiveness of selection.

Similarly, if rooted cuttings are used in extensive reforestation, and clones of different or undesirable maturation states are employed, then undesirable or unnecessarily variable growth rates or other characteristics may result.

Forest-tree breeders may be able to affect the utility of a clone by manipulation of the cutting donor's maturation state. For example, cuttings from more mature radiata pines typically produce trees with less volume, but they develop better stem form, have fewer and smaller knots, and take less time to prune, compared to juvenile cuttings or seedlings. If the objective is high-quality lumber production, then management may be willing to sacrifice some per-tree volume growth for these better bole characteristics, perhaps reducing initial spacing to recover some unit-area volume production. If the objective is high per-tree stem volume, or biomass for energy production, then a juvenile maturation state seems most desirable. Experiments are now in progress to determine whether different maturation states can effectively be set and maintained, depending on the height of the hedge. These same experiments are investigating whether low and frequent hedging maintains a very juvenile maturation state, similar to that of young seedlings.

The study reported in this paper, in concurrence with several others, indicates that hedging at least slows and perhaps arrests the maturation rate of cutting donors. Furthermore, the effects of hedging on growth and form of rooted cuttings are detectable (in fact, are increasingly detectable) during the first 7 growing seasons after planting cuttings from hedge and tree-form donors of the same clone.

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Differentation of Larix occidentalis Populations from the Northern Rocky Mountains

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Summary

Differentiation of populations of *Larix occidentalis* was studied in 2-year-old seedlings representing 82 populations from the Northern Rocky Mountains. Nursery studies of growth and phenology in three contrasting environments and laboratory tests of cold hardiness were used to assess differentiation. In accord with exogenous control of shoot growth, effects of nursery environments on growth and phenology were strong. Analyses of variance detected population differentiation for growth potential, phenology, and hardiness of buds when tissues were near maximum hardiness.

Multiple regression analyses related population differentiation to geographic, ecologic, and physiographic variables. Elevation of the seed source most strongly influenced regression analyses which accounted for 21, 39, 47, and 53 percent of the variance among populations in hardiness of buds,, bud burst, bud set, and height, respectively. Regression models suggested that seed transfer can be relatively broad geographically, but limited to ± 225 m altitudinally.

Key words: population differentiation, seed transfer, *Larix occidentalis.*

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Zusammenfassung

Unterschiede zwischen Populationen von *Larix occidentalis* wurden anhand zweijähriger Sämlinge von 82 Herkünften der nördlichen Rocky Mountains untersucht. Baumschuluntersuchungen für Höhe und Phänologie an drei kontrastierenden Standorten und Labortests der Frosthärte wurden verwendet, um die Unterschiede zu schätzen. Der Baumschulstandort hatte auf Triebwachstum und Phänologie einen signifikanten Einfluß. Varianzanalysen erga-