Effects of long-term pruning, meristem origin, and branch order on the rooting of Douglas-fir stem cuttings

DONALD L. COPES

United States Department of Agriculture, Forest Service, Pacific Northwest Research Station, Corvallis, OR 97331, U.S.A.

Received December 30, 1991

Accepted May 4, 1992

COPES, D.L. 1992. Effects of long-term pruning, meristem origin, and branch order on the rooting of Douglas-fir stem cuttings. Can. J. For. Res. **22**: 1888–1894.

The rooting percentages of 14 Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) clones were examined annually from 1974 to 1988. The trees were 10 and 13 years old in 1974 and were pruned to 2.0 m in 1978 and 1979 and then recut annually to 0.5, 1.0, or 1.5 m, starting in 1983. The pruned trees showed no evidence of decreased rooting percentage even after 15 years: average rooting increased from 47% in 1974 to 74% in 1986. Rooting percentage was significantly influenced by tree height. Cuttings collected from 0.5 m tall ramets exhibited better rooting than cuttings from 1.0 or 2.0 m tall ramets, and cuttings from 1.0 m tall ramets rooted better than cuttings from 2.0 m tall ramets. Rooting of cuttings collected from 0.5 m high subinterval zones within trees showed a negative linear relation between rooting percentage and collection height. Cuttings collected from the 0–0.5 m zone rooted 25% better than cuttings from the 1.5–2.0 m zone of the 2 m tall trees. That difference was significant at $p < 0.05$. A test of rooting of larger, more orthotropic cuttings gathered from the upper flat surface of pruned ramets indicated that the cuttings from the top rooted significantly less than smaller, more plagiotropic cuttings from the contiguous side areas (24 versus 33%, respectively). Rooting comparisons of meristems of primary and secondary origin showed significantly greater rooting of secondary meristems. Comparison of rooting of second-order and first-order meristems of secondary origin indicated the second-order twigs averaged 26% better rooting than the first-order branch tips when the cuttings were collected in January and placed in the rooting beds in February.

COPES, D.L. 1992. Effects of long-term pruning, meristem origin, and branch order on the rooting of Douglas-fir stem cuttings. Can. J. For. Res. **22** : 1888–1894.

L'aptitude à l'enracinement de 14 clones de sapin de Douglas (*Pseudotsuga menziesii* (Mirb.) Franco) est étudiée annuellement de 1974 à 1988. Les arbres, âgés de 10 et 13 ans en 1974, sont taillés à 2,0 m en 1978 et 1979 puis rabattus annuellement, à partir de 1983, à 0,5, 1,0 ou 1,5 m de hauteur. Le taux d'enracinement ne montre aucune diminution chez les arbres taillés même après 15 ans; l'enracinement moyen augmente de 47% en 1974 à 74% en 1986. Le taux d'enracinement est influencé significativement par la hauteur de l'arbre. Des boutures récoltées sur des ramets maintenus à une hauteur de 0,5 m s'enracinent mieux que celles provenant de ramets de 1,0 ou 2,0 m de haut. De la même façon, des boutures récoltées sur les ramets de 1,0 m de haut s'enracinent mieux que celles provenant de ramets de 2,0 m. En divisant la cime en zones successives de 0,5 m, les résultats montrent que les taux d'enracinement suivent une relation linéaire inverse avec la hauteur de récolte des boutures. Chez des arbres de 2,0 m, les boutures récoltées dans la zone de 0 à 0,5 m s'enracinent à des taux supérieurs de 25% relativement à ceux de boutures prélevées dans la zone de 1,5 à 2,0 m (différence significative, $p < 0,05$). Dans un essai, des boutures de plus forte dimension et plus orthotropes, provenant de la partie supérieure des ramets taillés en plateau, s'enracinent à des taux significativement inférieurs à ceux des boutures plus petites et plagiotropes, récoltées sur les côtés (24 et 33%, respectivement). Des boutures issues de méristèmes d'origine secondaire s'enracinent à des taux significativement supérieurs à ceux des boutures d'origine primaire. Dans le cas des méristèmes d'origine secondaire, les boutures correspondant à des branches latérales de deuxième ordre ont un taux d'enracinement moyen supérieur de 26% par rapport aux branches latérales de premier ordre, pour des boutures récoltées en janvier et mises à raciner en février.

[Traduit par la rédaction]

Introduction

Rooting percentage of stem cuttings of conifers usually decreases as tree age increases (Copes 1983; Cornu 1973; Libby *et al.* 1972), so maintaining juvenile behavior or culturing older trees to maintain or increase rooting percentage is often a goal of vegetative propagation. Serial propagation (Dormling and Kellerstram 1981; Franclet 1985; St. Clair *et al.* 1985), annual hedging, and pruning or shearing of crowns (Black 1972; Copes 1983; Dormling and Kellerstram 1981; Libby *et al.* 1972; van den Driessche 1983) are used to reduce the effects of aging. Other factors such as stage of plant development at time of cutting collection (Black 1972; Miller *et al.* 1982; Roberts and Fuchigami 1973; van den Driessche 1983; Wise *et al.* 1985), position of cuttings on the tree from which cuttings are collected (Black 1972; Riding 1976; Roberts and Moeller 1979; van den Driessche 1983), and hormone treatment and rooting environment (Miller *et al.* 1982; Proebsting 1984; Roberts and Fuchigami 1973; Roberts and Moeller 1979; van den Driessche 1985) are factors that may interact and influence rooting success.

Hedging, pruning, and shearing treatments all remove a portion of the foliage from each tree and, for simplicity, will be collectively termed pruned in this paper. Pruning may stimulate rejuvenation or reinvigoration. Pruning treatment may also enhance development of meristems that remain stable and juvenile (Franclet 1985). Researchers do not know how long juvenile rooting percentage can be maintained by annual pruning, but good rooting may continue for many years if annual pruning is done. Radiata pine (*Pinus radiata* D. Don) cuttings show no decrease in rooting percentage after 6 years of annual pruning (Libby *et al.* 1972). Pruning of ortets and rooted ramets of 14 Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) clones results in an increase in rooting of 3% per year for 7 years (Copes 1983). Repeated cycles of serial propagation are also used to maintain high rooting success. Rooting trials with Norway spruce (*Picea abies*

Printed in Canada / Imprimé au Canada

Karst.) show stable rooting success through a 13-year period in which five 3-year serial propagation cycles were made (St. Clair *et al.* 1985).

Variable rooting occurs with cuttings of different branch orders. Pruning also influences the production of twigs of different branch orders. Investigation of the effect of branch order on rooting percentage is difficult because of complex interactions with date of cutting collection (Black 1972; Roberts and Fuchigami 1973), hormone treatment (Cornu 1973; Roberts and Fuchigami 1973), and tree age (Black 1972). As a result, some studies comparing rooting percentage among cuttings of different branch orders report no difference in rooting percentage (Brix 1974; Hinesley and Blazich 1984), whereas other studies (some done with the same species) report significant differences (Black 1972; Cornu 1973; Miller *et al.* 1982; Roberts and Fuchigami 1973).

In the following study, a number of separate rooting investigations were conducted. The primary rooting tests were made from 1982 to 1988 and investigated the annual rooting performance of ortets and ramets of the same 14 Douglas-fir clones that were pruned each January from 1978 to 1988. The ability of pruning to maintain or increase rooting was examined, as was the effect of tree height and position of cuttings on the trees (height above the ground). Other trials were conducted to test differences in rooting percentage between cuttings collected from the very top of the trees versus cuttings collected from the sides of the trees, between primary versus secondary meristems, and between first- and second-order secondary meristems. The study results will be useful to vegetative propagators, geneticists, and tree improvement workers who wish to maintain or increase rooting percentage of Douglas-fir and will provide additional insight into how pruning achieves that goal with Douglas-fir.

Methods

The primary test of continued-pruning effect on rooting percentage encompassed the period 1982–1988. Cuttings were gathered each year from rooted ramets of the same 14 Douglas-fir clones. Rooting procedures and percentages of the same ramets and ortets from 1974 to 1981 were previously reported (Copes 1983). The source trees were either 18 or 21 years old from seed in 1982. The 212 ramets of the 14 clones had been selected and rooted in 1972 and 1973 and field planted in 1975 and 1976, respectively (Copes 1981). Pruning trees to 2-m height was initiated in 1978 and 1979 when the ramets exceeded that height limit. In most cases, only shoots from the past growing season were cut, but some cutting back into older branch wood was needed during the first 3 years of pruning to smooth the irregular surface of the tree for future prunings. In 1983, equal numbers of the 2.0 m tall ramets of each clone were pruned to heights of 0.5, 1.0, and 2.0 m. The foliage from the top and side of each tree was pruned annually through 1988. In 1988, twigs were collected for rooting from 0.5 m wide subinterval zones. The subinterval zones were the areas between horizontal planes dividing the vertical dimension of each tree into 0.5 m wide areas starting at the ground. In 1990, a secondary test was made comparing the rooting percentage of cuttings collected from the top or sides (within 25 cm of the top surface) of each pruned ramet. Another secondary test of rooting percentage resulting from differences in meristem origin and branch order was made in 1987 with 5 trees that were 15 years old and 84 trees that were 7 years old. The trees had never been pruned previously and all 7-year-old trees selected had two terminal leaders.

Propagation procedures were identical with those used for the same clones from 1974 to 1981 (Copes 1983). In brief, the cuttings, consisting entirely of growth from the past year, were collected in January and stored in plastic bags at 1 to 2°C until early February; the basal 3 cm was soaked for 5 s in 5000 ppm indole-3-butyric acid; they were pricked into sphagnum peat moss and fine sand (2:1 v/v) in clonal rows of 13 or 14 cuttings in outdoor rooting houses, subjected to intermittent mist during daylight hours, and grown in a medium maintained by electric soil cables at about 21°C and sprayed weekly with 20:20:20 (N–P_2O_5–K_2O) fertilizer and fungicide. The 1987 secondary rooting trial of meristem origin and branch order in 9-year-old trees was done as just described, except that the cuttings were grown in planting flats (56 × 30 × 9 cm) in a fog chamber in a conventional greenhouse. Cuttings grown in the fog chamber were also watered as needed. Cuttings were grown under a natural photoperiod in the misting beds and fog chamber until October or November. At that time, the cuttings were lifted and rooting success was recorded as the number of cuttings that had initiated roots in each clonal row of 13 or 14 cuttings.

Experimental designs of studies from 1982 through 1990 are listed in Table 1. Rooting trials were subjected to analysis of variance (ANOVA) using the SAS procedures for general linear models. The number of cuttings that rooted per clonal row of 13 or 14 cuttings was the experimental unit for all analyses, except in the first ANOVA analysis in Table 3. In that analysis the experimental unit was year × clone means. Percentage data were converted to angular values before ANOVA. Significance was achieved when $p < 0.05$. Clones were considered random effects because the trees had not been selected for rooting percentage. Additional details on design of individual tests can be determined from the ANOVA tables for each test.

Results

Clonal and yearly rooting percentages from 1974 to 1988 are shown in Table 2 for each of the 14 Douglas-fir clones. Rooting results from 1974 to 1981 were previously published for the same 14 clones (Copes 1983) and are included to facilitate the comparison of rooting over the entire 15 years. Data for 1978 and 1983 are omitted because extensive disease losses in the propagation beds prohibited gathering meaningful data on rooting percentage. In addition, the rooting percentage values for 1984 and 1987 are somewhat reduced because of moderate disease losses. Average yearly rooting from 1974 to 1988 increased from 45% in 1976 to 74% in 1986. Clones that rooted the poorest in 1974 generally experienced the greatest gains over the 15-year study. Plant age during that interval increased from 10 and 13 to 24 and 27 years old, respectively.

Both the year and clone effects were highly significant ($p < 0.05$) (Table 3). Average rooting percentage of each clone and individual year values for 1974 and 1988 are ranked clonally (Table 2) in order of highest to lowest rooting clones. In general, clones with the highest or lowest rooting percentage in 1974 remained the better or poorer rooting clones, respectively, 15 years later but exceptions did occur.

Rooting trials from 1984 to 1988 tested the rooting percentage of cuttings collected from ramets pruned to 0.5, 1.0, and 2.0 m. Cuttings gathered from the shorter trees exhibited greater rooting percentage than did cuttings collected from taller trees in 9 of the 10 height–year comparisons (Fig. 1). The one exception occurred in 1987, when cuttings collected from the 1.0 m tall trees rooted slightly better than the cuttings from the 0.5 m tall trees. Year, clone, and tree height main effects were all highly significant ($p < 0.05$) (Table 3). The main effect for tree height was predominantly a negative linear relation. Significant interactions were noted for year × clone and the quadratic component of clone × tree height (Table 3). The clone × tree height interaction had a significant nonlinear response primarily because of the rooting response

TABLE 1. Experimental designs of primary and secondary rooting tests

(A) Primary tests

	Year	No. of clones	Tree ht. (m)	No. of replications in rooting bed	No. of rows per replication	No. of cuttings per row
Aging and pruning	1982	14	2.0	7	6	14
	1984	14	0.5, 1.0, 2.0	4	1	14
	1985	14	0.5, 1.0, 2.0	1	2	14
	1986	14	0.5, 1.0, 2.0	3	1	14
	1987	14	0.5, 1.0, 2.0	3	1	14
	1988	14	0.5, 1.0, 2.0*	2	1	13

(B) Secondary tests

	Year	No. of clones	Tree height (m) or cutting type†	No. of replications in rooting bed	No. of rows per replication	No. of cuttings per row†		
Cuttings from top and side of tree‡	1990	14	0.5 1.0 2.0	3	1			13
						TS	FO	SO
Meristem origin and branch order	1987	84	TS, FO, SO	2	1	1	2	2
	1987	5	FO, SO	4	1		14	14

*Subinterval zone collections of cuttings from the 1.0 and 2.0 m tall trees were collected from areas 0–0.5, 0.5–1.0, 1.0–1.5, and 1.5–2.0 m above the ground.

†Meristem origin and branch order were noted by the following: terminal shoot, TS; first-order lateral, FO; second-order lateral, SO.

‡Cuttings from both the tops and sides of trees were collected from all three tree heights and kept separate by collection location on tree.

TABLE 2. Clonal and annual rooting percentage from 1974 to 1988, with 14 clones ranked from highest to lowest means

Clone*	Year 74	75	76	77	79	80	81	82	84	85	86	87	88	Mean†
a	83	88	77	74	76	71	82	65	62	88	91	75	81	78
b	78	49	58	49	58	52	62	62	76	92	89	74	96	69
c	80	59	38	62	76	65	81	84	32	67	84	67	68	66
d	41	61	38	36	71	68	74	78	55	82	73	63	87	64
e	51	73	49	74	61	64	73	68	47	56	69	72	63	63
f	66	58	32	66	62	56	77	82	48	70	80	55	73	63
g	40	49	72	67	64	68	67	75	55	67	70	47	68	62
h	23	37	74	62	66	65	82	70	33	64	87	53	69	60
i	17	45	—‡	42	68	—‡	65	83	70	67	63	52	71	58
j	41	18	37	66	55	58	70	76	56	61	81	70	46	57
k	36	27	27	66	67	62	63	57	39	37	65	44	54	50
l	57	60	15	25	65	65	56	62	10	38	54	37	52	46
m	33	32	49	41	37	32	36	49	54	80	66	40	45	46
n	16	16	23	31	59	46	34	71	37	58	68	55	38	42
Mean	47	48	45	54	63	59	66	70	48	66	74	57	65	59

*Clones in a previous study (Copes 1983) were coded as follows: a, 109; b, 23; c, 25; d, 197; e, 3; f, 102; g, 172; h, 241; i, 106; j, 4; k, 20; l, 14; m, 97; n, 223.

†Some values are dissimilar to those reported in Copes (1983) because a different weighting procedure was used when averaging clonal means.

‡Data missing because the clone was not collected for rooting.

of clones with intermediate rooting percentages (Fig. 2). The clones with the poorest and best rooting percentages were more consistent in rooting response.

Different rooting percentages were found among cuttings collected at different heights within trees. Cuttings collected from branches growing closest to the ground had the greatest rooting percentage (Table 4). A significant negative linear relation between rooting percentage and collection height was detected among cuttings gathered from the four 0.5 m wide subintervals of the 2.0 m tall trees, but not among the two 0.5 m wide subinterval zones of the 1.0 m tall trees (Table 5). Comparison of rooting percentage of cuttings from the 0–0.5

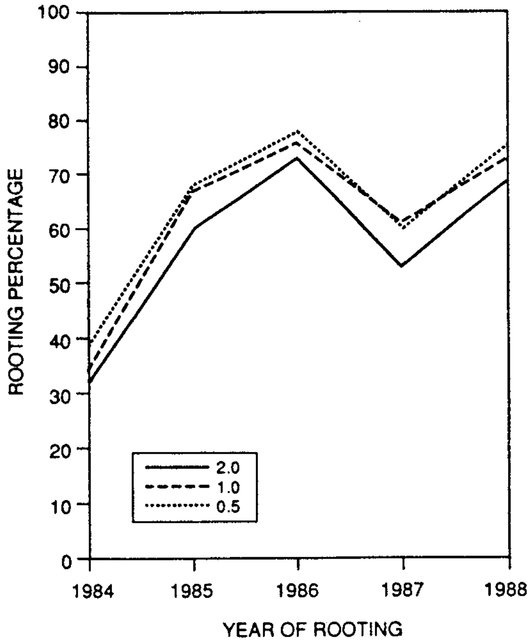

FIG. 1. The effect of tree height (0.5, 1.0, or 2.0 m) on rooting percentage from 1984 through 1988.

TABLE 3. ANOVA tables for rooting percentages of 14 clones for the period 1974–1978 for all tree heights and 1984–1988 for clones pruned to 0.5, 1.0, and 2.0 m heights

Source	df	SS	F	p >F
1974–1988 for all heights				
Year	12	1.756	7.63	0.000
Linear	1	0.713	37.22	0.000
Nonlinear	11	1.043	54.41	0.000
Clone	13	1.991	7.99	0.000
Year × clone (error)	154	2.952		
Total	179*	6.699		
1984–1988 for 0.5, 1.0, and 2.0 m tall trees				
Year	4	7.784	9.13	0.004
Linear	1	2.154	10.11	0.013
Nonlinear	3	5.629	8.81	0.006
Replications/year (error 1)	8	1.705		
Clone	13	13.651	7.06	0.000
Year × clone (error 2)	52	7.736	3.13	0.000
Tree ht.†	2	1.644	13.53	0.003
Linear	1	1.644	27.06	0.001
Quadratic	1	0.000	0.00	0.999
Year × tree ht.	8	0.318	0.70	0.690
Clone × tree ht.	26	2.021	1.37	0.134
Linear	13	0.531	0.72	0.739
Quadratic	13	1.490	2.02	0.026
Year × clone × tree ht. (error 3)	104	5.895	1.19	0.117
Experimental error	482	22.878		
Total	699	63.632		

*Clone i data are missing in 1976 and 1980.
†Satterthwaite approximation was used.

subinterval zones of the 0.5 and 1.0 m tall trees and the 0–0.5 and 0.5–1.0 subinterval zones of the 1.0 and 2.0 m tall trees indicated slightly less rooting percentage when the sub-

TABLE 4. Effect of tree height and subinterval collection zones on 1988 rooting percentage

Tree ht. (m)	No. of cuttings	Rooting % of subinterval zone 0–0.5	0.5–1.0	1.0–1.5	1.5–2.0	Mean
0.5	728	75				75
1.0	1456	77	69			73
2.0	2912	78	74	70	53	69
Mean		77	72	70	53	71

NOTE: Subinterval zones denote the 0.5 m wide sample-collection zones formed between horizontal planes cutting sample areas across the vertical dimension of the plant at the specified distances above ground.

TABLE 5. ANOVA table for 1988 rooting percentage of subinterval (0.5 m high) zones within the 1.0 and 2.0 m tall trees

Source	df	SS	F	p >F
Replication	1	0.388	14.29	0.0003
Clone	13	7.693	21.82	0.0001
Tree ht.	2	0.545	3.50	0.0450
Linear	1	0.495	6.35	0.0182
Quadratic	1	0.050	0.65	0.4283
Clone × tree ht. (error 1)	26	2.024	2.87	0.0000
S1*	3	2.594	11.63	0.0000
S1 × clone (error 2)	39	2.900	2.74	0.0000
S2†	1	0.184	2.72	0.1228
S2 × clone (error 3)	13	0.881	2.50	0.0054
Experimental error	97	2.631		
Total	195	19.842		

*Subintervals within 2 m tall trees.
†Subintervals within 1 m tall trees.

interval zones included a proportion of cuttings from the very top of each tree. Those differences were not significantly different at $p < 0.05$.

In 1990, cuttings were gathered solely from the very top of trees pruned at 0.5, 1.0, and 2.0 m or from the side areas immediately below the flat upper surface of each pruned tree. The overall average rooting success was 33 and 24% for cuttings from the side and top of the trees, respectively, among the three tree heights (Table 6). The difference in rooting percentage of cutting from the two areas was significantly different ($p < 0.05$) (Table 7). For all tree heights, cuttings gathered from the side of the trees rooted consistently better than cuttings collected from the top of the trees, even though relatively little difference in height differentiated sample zones. Significant interactions of clone × type of cutting, type of cutting × tree height, and clone × type of cutting × tree height were found ($p < 0.05$).

Cuttings collected that originated from primary meristems exhibited a different rooting percentage than did cuttings originating from secondary meristems (Table 8). The same was true of rooting percentage of cuttings from first-order and second-order branch tips of secondary meristems. Nine-year-old Douglas-fir trees increased rooting percentage in the following order: primary meristem (tree terminal), 21%; first-order secondary meristems (tips of main whorl branches), 49%; second-order secondary meristems (branches in whorl at the base of each first-order lateral meristem), 71%. The rooting percentage of first- and second-order lateral meristems of

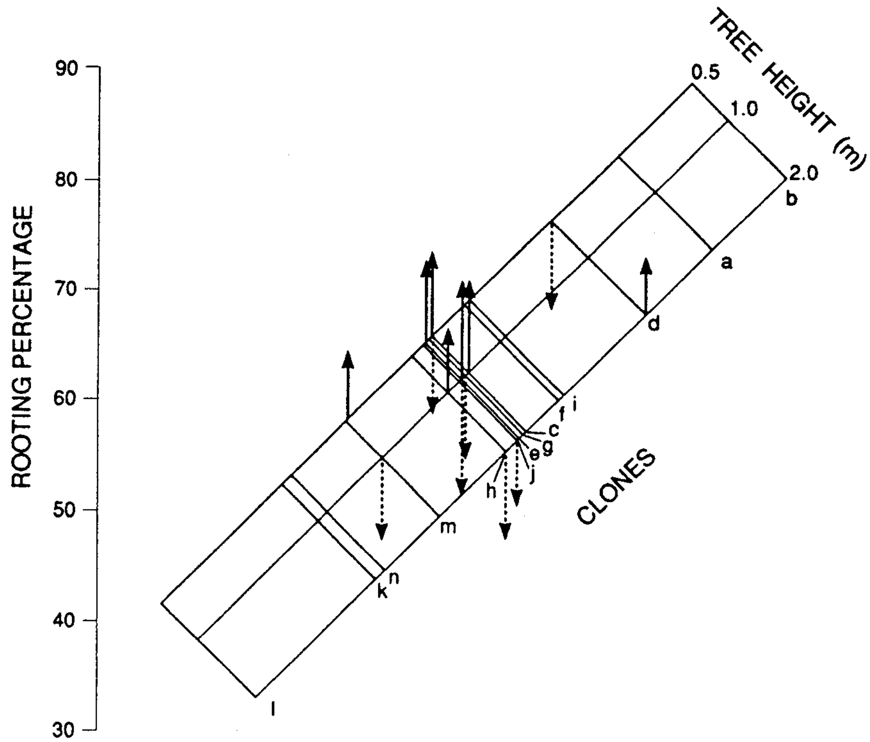

FIG. 2. A two-dimensional plot of clone-by-tree-height interactions. Clones are distributed on the long diagonal and tree heights on the short diagonal. Arrow lengths indicate the amount of positive or negative deviation from the expected values. Only interactions greater than 0.05 are shown.

TABLE 6. The 1990 rooting percentage of cuttings collected solely from the tops or sides of 0.5, 1.0, and 2.0 m tall trees

Tree ht. (m)	No. of cuttings	Rooting % by location of cuttings on tree		
		Top	Side	Mean
0.5	1092	30	36	33
1.0	1092	24	38	31
2.0	1092	17	25	21
Mean		24	33	28

15-year-old trees exhibited the same trend (Table 8). Rooting percentages for trees of both ages were significant for cutting type ($p < 0.05$) (Table 7).

Discussion

Results indicated that annual pruning techniques can be used to increase and maintain juvenile-like rooting potential for at least 15 years. Pruning was more successful with older trees than reported previously (Copes 1983). Rooting percentage increased by 27% during the 15 years in which tree age increased from 10 and 12 to 25 and 27 years, respectively. The average annual gain in rooting potential between ages 18 and 27 years was less than the 3% per year reported for the same clones between ages 10 and 20 years (Copes 1983). The long-term trend indicated that most gain in rooting percentage was obtained during the first 4 years of pruning. Continued annual pruning appeared to maintain the elevated rooting percentage, although unexpected disease losses in the rooting beds prior to root formation occasionally reduced rooting values below what would have occurred without the disease losses. Eliminating such environmental variation is virtually impossible when the tests span many growing seasons. Additional evidence of juvenility or invigoration of pruned ramets was their continued production of abundant lammas shoots each year. Lammas growth ceased on unpruned trees of the same clones when the trees were 10 to 12 years old (Copes 1983).

Most clones maintained approximate rank order during the 15-year study period, but large shifts by individual clones in rank order occurred some years. Roberts and Moeller (1979) observed similar unexpected changes in rank order among years. Clones that had low rooting percentage at the start of this study exhibited the greatest gains from pruning treatments.

Applied rooting programs will achieve higher rooting success with Douglas-fir if the pruned trees are kept at a low height or if the collection of cuttings is limited to lower crown areas of tall trees. Many conifers exhibit a lower rooting percentage when cuttings are rooted from branch tips that originated in the upper crown versus branches that originate in crown areas close to the ground (Riding 1976; Roberts and Moeller 1979; van den Driessche 1983). That same negative linear relationship between collection height and rooting percentage was detected in this study even though the pruned trees ranged in height from only 0.5 to 2.0 m. Rooting percentage of cuttings collected from the 2.0 m tall trees averaged 6% less than that of cuttings collected from the 0.5 m tall trees. Comparison of rooting percentage of subintervals collected at different heights within the pruned trees also demonstrated the same negative linear relation. Rooting

TABLE 7. ANOVA tables for secondary experiments comparing rooting percentage of the following: cuttings from top and sides of the 14 pruned clones, cuttings from primary and secondary meristems and first- and second-order branches of 9-year-old trees, and cuttings from first- and second-order branches of 15-year-old trees

Source	df	SS	F	p >F
Top versus side				
Replication	2	0.225	2.81	0.079
Clone	13	8.857	17.01	0.000
Replication × clone (error 1)	26	1.042		
Cutting type	1	0.815	23.88	0.000
Tree ht.	2	1.039	15.23	0.000
Clone × cutting	13	0.734	1.65	0.077
Clone × tree ht.	26	3.046	3.44	0.000
Cutting × tree ht.	2	0.124	1.81	0.167
Clone × cutting × tree ht.	26	2.072	2.34	0.001
Experimental error	140	4.775		
Total	251	22.729		
Meristem and branch order effects in 9-year-old trees				
Flat	13	3.153	2.95	0.000
Branch type	2	6.165	37.53	0.000
Flat × branch type	26	1.035	0.48	0.973
Experimental error	42	3.450		
Total	83	13.803		
Branch order effects in 15-year-old trees				
Replication	1	0.010	0.83	0.415
Clone	4	0.077	1.55	0.341
Replication × clone (error 1)	4	0.050		
Branch type	1	0.680	54.67	0.001
Clone × branch type	4	0.214	4.29	0.071
Experimental error	5	0.062		
Total	19	1.093		

percentage of the 0–0.5 m zone of 1.0 m tall trees was 8% greater than that of the 0.5–1.0 m zone of the same trees. Even greater differences were detected within the 2.0 m tall trees; a 25% difference in rooting percentage existed between the 0–0.5 and the 1.5–2.0 m zones.

One undesirable aspect of advocating collection of Douglas-fir cuttings from the lower crown of pruned trees is that those cuttings are usually smaller than cuttings of the same branch orders that grow higher or on the very top surface of pruned trees. The growth habit of Douglas-fir cuttings grown from second-order branch tips may be inferior to first-order branch tips of secondary meristem origin, as is true of Fraser fir (*Abies fraseri* (Pursh) Poir.) cuttings (Miller *et al.* 1982).

Propagators often favor collecting branch tips, for cuttings, that are large and have good potential for upright (orthotropic) growth habit rather than less vigorous, subordinate lateral branch tips. Collection of orthotropic shoots from the flat, upper surface of trees is preferred with radiata pine (Libby *et al.* 1972). In general, larger shoots are desired because the assumption is held that they grow into larger, higher quality plants (Miller *et al.* 1982). The flat upper surface that developed at the top of Douglas-fir trees that have been annually pruned for at least 3 years produced shoots that are often larger and more orthotropic. Comparison of rooting percentages in cuttings collected from the 0.5 m high subinterval

TABLE 8. Effect of meristem origin and branch order on 1987 rooting percentage

		Rooting % by		
			Secondary meristem by	
Age (years)	No. of cuttings	Primary meristem	1st branch order	2nd branch order
9	840	24	53	77
15	560	—*	9	39

*No multiple terminals were available for rooting from 15-year-old trees.

zones of 1.0 and 2.0 m tall trees indicated less rooting when cuttings were collected from crown areas that included the very top surface of the trees. Other tests of cuttings collected entirely from the top of trees versus cuttings collected entirely from the adjacent side of the trees indicate that cuttings collected from the side areas rooted an average of 9% better than cuttings from the top. Orthotropic cuttings from the tops of 14-year-old Fraser fire trees also rooted poorer than plagiotropic cuttings from secondary axes of intact plants (Wise *et al.* 1986).

Knowledge of the rooting properties of shoots from different meristem origins and branch orders facilitates understanding how pruning influences rooting percentage. Results of previous studies on branch-order influences on rooting percentage in Douglas-fir are quite contradictory. Black (1972) found that first-order cuttings rooted better than second-order cuttings if the cuttings were collected in the fall before the bud-dormancy chilling requirements were satisfied, but that second-order shoots root better than first-order branch tips if cuttings are collected during the winter. Roberts and Fuchigami (1973) also found better rooting of lateral branches that occurred with branch terminals when the cuttings were collected in February. They reported that first-order twigs from secondary meristems exhibit greater rooting percentage than do second-order twigs when collected from November to January. The present study generally supported those observations and indicated that considerable gains in rooting percentage can be made with January collections and February rooting of second-order lateral meristems. The rooting percentage of primary meristems of trees that had never been pruned was 28 and 50% less than first- or second-order lateral branches of the same trees. Second-order twigs of secondary meristem origin of 9- and 15-year-old trees rooted 22 and 30% better, respectively, than the larger, more dominant first-order lateral branch tips.

Studies in which large numbers of cuttings are collected annually from the same trees, in effect, subject the trees to yearly pruning. Such treatment changes the proportion of buds of different meristem orders that grow into twigs the following year and may be the reason Roberts and Moeller (1979) did not report a decline in rooting percentage when rooting the same Douglas-fir trees for 5 consecutive years. A study with Sitka spruce indicates that pruning changes the type of cuttings produced from first-order and second-order to predominantly third-order secondary meristems (van den Driessche 1985).

Annual pruning increased and then maintained the elevated rooting percentage of 10- and 13-year-old Douglas-fir over a 15-year period. Pruning Douglas-fir appears to be effective because it decreases the proportion of first-order twigs of secondary meristem origin and increases the proportion of secondary and higher order twigs of secondary origin. It requires at least 3 or 4 years of annual pruning to transform the crown areas to a condition that produces primarily higher branch order twigs.

Black, D.K. 1972. The influence of shoot origin on the rooting of Douglas-fir stem cuttings. Comb. Proc. Int. Plant Propag. Soc. **22**: 142–157.

Brix, H. 1974. Rooting cuttings from mature Douglas-fir. N.Z. J. For. Sci. **4**(2): 133–139.

Copes, D.L. 1981. Selection and propagation of highly graft-compatible Douglas-fir rootstock—a case history. USDA For. Serv. Res. Note PNW-376.

Copes, D.L. 1983. Effect of annual crown pruning and serial propagation on rooting of stem cuttings from Douglas-fir. Can. J. For. Res. **13**: 419–424.

Cornu, D. 1973. Essais préliminaieres sur la sélection de clones bouturables de Douglas (*Pseudotsuga menziesii* Franco). Ann. Sci. For. **30**(2): 157–173.

Dormling, I., and Kellerstram, H. 1981. Rooting and rejuvenation in propagating Norway spruce cuttings. *In* Symposium on Clonal Forestry, Swedish University of Agricultural Sciences, Uppsala. Res. Notes 32. pp. 65–72.

Franclet, A. 1985. Rejuvenation: theory and practical experiences in clonal silviculture. *In* Proceedings of the 19th Canadian Tree Improvement Association, 22–26 Aug. 1983, Toronto, Ont. *Edited by* L. Zsuffa, R.M. Rauter, and C.W. Yeatman. Canadian Forestry Service, Ottawa. pp. 96–134.

Hinesley, L.E., and Blazich, F.A. 1984. Rooting Fraser fir stem cuttings. J. Environ. Hortic. **2**(1): 23–26.

Libby, W.J., Brown, A.G., and Fielding, J.M. 1972. Effects of hedging radiata pine on production, rooting, and early growth of cuttings. N.Z. J. For. Sci. **2**(2): 263–283.

Miller, N.F., Hinesley, L.E., and Blazich, F.A. 1982. Propagation of Fraser fir by stem cuttings: effects of type of cutting, and genotype. HortScience, **17**(5): 827–829.

Proebsting, W.M. 1984. Rooting of Douglas-fir stem cuttings: relative activity of BA and NAA. HortScience, **19**(6): 854–856.

Riding, R. 1976. The shoot apex of trees of *Pinus mariana* of different rooting percentage. Can. J. Bot. **54**: 2672–2678.

Roberts, A.N., and Fuchigami, L.H. 1973. Seasonal changes in auxin effect on rooting of Douglas-fir stem cuttings as related to bud activity. Physiol. Plant. **28**: 215–221.

Roberts, A.N., and Moeller, F.W. 1979. Phasic development and physiological conditioning in the rooting of Douglas-fir shoots. Comb. Proc. Int. Plant Propag. Soc. **28**: 32–39.

St. Clair, J.B., Kleinschmit, J., and Svolba, J. 1985. Juvenility and serial vegetative propagation of Norway spruce clones (*Picea abies* Karst). Silvae Genet. **34**(1): 42–48.

van den Driessche, R. 1983. Rooting Sitka spruce cuttings from hedges, and after chilling. Plant Soil, **71**(1/3): 495–499.

van den Driessche, R. 1985. The influence of cutting treatments with indole-3-butyric acid and boron, stock plant moisture stress, and shading on rooting in Sitka spruce. Can. J. For. Res. **15**: 740–742.

Wise, F.C., Blazich, F.A., and Hinesley, L.E. 1985. Propagation of *Abies fraseri* by semidormant hardwood stem cuttings. HortScience, **20**(6): 1065–1067.

Wise, F.C., Blazich, F.A., and Hinesley, L.E. 1986. Propagation of *Abies fraseri* by cuttings: orthotropic shoot production from hedged stock plants. Can. J. For. Res. **16**: 226–231.