$$\int_{-\infty}^{\infty} P(x) \left[\prod_{j}^{NS} r_j(x) \right]_{i^*} dx$$

Therefore (1) becomes,

$$\psi_{i^*} = \frac{\int_{-\infty}^{\infty} P(x) \left[\prod_{j}^{NS} r_j(x) \right]_{i^*} dx}{\sum_{i^*} \int_{-\infty}^{\infty} P(x) \left[\prod_{j}^{NS} r_j(x) \right]_{i^*} dx}$$

The numerical integration is made by using Simpson's rule between 4 standard deviations with 64 subdivisions.

Literatures Cited

CARR, R. N. and NASSAR, R. F.: Effects of selection and drift on the dynamics of finite populations. 1: Ultimate probability of fixation of a favourable allele. Biometrics 26: 41—49 (1970a). — CARR, R. N. and NASSAR, R. F.: Effects of selection and drift on the dynamics of finile populations. 2: Expected time to fixation or loss of favourable allele. Biometrics 26: 221—228 (1970b). — FALCONER, D. S.: Introduction to quantitative genetics. Ronald Press, New York, 365 pp. (1960). — KANG, H. and NAMKOONG, G.: Limits of artificial selection under balanced mating systems. Silvae Genetica 28: 53—60 (1979). — KANG, H. and NAMKOONG, G.: Limits of artificial selection under unbalanced mating systems. Theor. Appl. Genet. 58: 181—191 (1980). — NAMKOONG, G. and ROBERDS, J.: Choosing mating designs to efficiently estimate genetic variance components for trees. Silvae Genetica 23: 43—53 (1974). — ROBERTSON, A.: A theory of limits in artificial selection. Roy. Soc. B. Proc. 153: 234—249 (1960).

Clonal Differences in Dry Matter Distribution, Wood Specific Gravity and Foliage „Efficiency" in Picea sitchensis and Pinus contorta

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Summary

Seven clones of both *Picea sitchensis* and *Pinus contorta* growing at a lowland site in Scotland were felled at age 8, and measurements were taken at each annual height level, of stem, branch and needle dry weights, foliage areas, and the specific gravities and volumes of each annual ring of stemwood.

On average, *P. sitchensis* clones had similar stem dry weights to *P. contorta* clones, but only 56 % as much branch wood and 61 % as much needle dry weight. The branch wood on *P. sitchensis* was "spread" over a long total branch length, and the needles were "spread" over a large projected needles area. At ages 6—8 *P. sitchensis* produced 44 % more stemwood per unit needle area than *P. contorta*.

Within both species, sparsely branched clones were the most efficient stemwood producers, allocating a high proportion of their dry matter to stems, and, at ages 6—8, producing 1.5 to 2.0 times as much stemwood per unit of needles as heavily branched clones. These sparsely-branched clones varied in height and total weight, indicating that large genetic gains in stemwood production per tree could be made by selecting simultaneously for rapid growth and a high harvest index. Tallness, sparse branching and, in *P. contorta*, the absence of large basal branches, were the most important characters associated with large, efficient stemwood production.

Stemwood specific gravities differed by 20—30 % between clones and between the innermost and outermost annual ring cylinders. For all clones the specific gravity of the annual cylinders of stemwood decreased linearly with $\log_e$ cylinder volumes, and both the initial specific gravities (the intercepts) and their rates of decrease (the slopes) differed between clones (especially in *P. sitchensis*). That is, the value of juvenile stemwood specific gravities, and clonal rankings, were dependent upon volume growth rates.

Key words: *Picea sitchensis, Pinus contorta,* clones, harvest index, dry matter distribution, needle area, wood specific gravity, branching.

Zusammenfassung

Es wurden je 7 Klone von *Picea sitchensis* und *Pinus contorta* einer Versuchsfläche auf einem Tieflandstandort in Schottland im Alter 8 gefällt und in jedem Jahrestrieb das jeweilige Trockengewicht des Stammes, der Zweige und der Nadeln, der Umfang der Benadelung und die spezifischen Gewichte und Volumina in jedem Jahrring des Stammes gemessen.

Im Durchschnitt hatten die *Picea sitchensis*-Klone ähnliche Stammtrockengewichte wie die *Pinus contorta*-Klone, aber nur 56 % soviel Astholz und 61 % des Nadeltrockengewichtes. Bei *Picea sitchensis* waren die Astlängen in der Summe größer als bei *Pinus contorta* und die Nadeln über eine größere Zone verbreitet. Im Alter 6—8 produzierte *Picea sitchensis* 44 % mehr Stammholz pro Nadeleinheit als *Pinus contorta*. Innerhalb beider Arten produzierten Klone mit weniger Ästen effektiv mehr Stammholz, da ein hoher Anteil an Trockenmasse den Stämmen zugute kam, was im Alter 6—8 1,5 bis 2,0 mal soviel Stammholz als bei stark beasteten Klonen ausmachte. Diese wenig beasteten Klone variierten in der Höhe und im Gesamt-Trockengewicht, woran zu erkennen ist, daß darin eine Möglichkeit zur Selektion von starkwüchsigen Individuen mit einem genetischen Gewinn besteht. Die wichtigsten Kriterien für eine effiziente Stammholzproduktion waren Stammstärke, spärliche Beastung und bei *Pinus contorta* das Nichtvorhandensein einer breiten basalen Verzweigung. Das spezifische Gewicht differierte zwischen 20 % und 30 % zwischen den Klonen und zwischen den am weitesten innen und außen liegenden Jahrringzylindern des Stammholzes. Bei allen Klonen verringerte sich die Holzdichte der Jahrringzylinder des Stammholzes mit dem $\log_e$ Zylinder-Volumen, wobei sich die Ini-

tial-Holzdichte und der Grad der Verringerung zwischen den Klonen, besonders bei *Picea sitchensis* unterschied. Das heißt, der Wert der Holzdichte in juvenilem Stammholz und dessen klonale Einordnung waren vom Volumenwachstum abhängig.

Introduction

CAHALAN (1981) described large differences in the heights, diameters, branching characteristics and phenology at age 5 among 20 clones of both *Picea sitchensis* (BONG.) CARR. and *Pinus contorta* DOUGL. growing at both a lowland and an upland site near Edinburgh, Scotland. This paper reports the results of destructive analyses of 7 clones of each species that were harvested at the lowland site at age 8, before there was appreciable inter-tree competition. Clones with different heights and contrasting branching habits were chosen (including 3 *P. sitchensis* clones not included in CAHALAN's analysis) to determine the magnitude of differences in (a) the distribution of dry matter between stems, branches and needles, (b) the values and age trends in stemwood specific gravities, and (c) the weights of stemwood produced per unit weight and area of needles.

Although genotypes with narrow crowns and thin branches are favoured by many conifer breeders (notably in Finland; ANON, 1980) and despite speculation about the advantages and disadvantages of a high investment in stemwood i.e. a high harvest index (LEDIG, 1975; CANNELL, 1979) there are few instances in which contrasting genotypes have been destructively analysed to quantify apparent differences in the efficiency of stemwood dry matter production per unit of foliage. None of the 600 or so forest stand biomass and primary production studies reviewed by CANNELL (1982) compared genotypes.

Only three studies on dry matter distribution in conifer genotypes are known to the authors. MATTHEWS *et al.* (1975) felled 20 half-sib families of *Pinus virginiana* MILL. at age 8, before crown closure, and found significant differences in the percentages of stem to total dry weight (32 to 43 %) and branch to total dry weight (48 to 61 %) which were highly heritable ($h^2 = 1.2$) and were not significantly correlated with tree height or total weight; that is, the tallest and heaviest progenies did not necessarily have the lowest percentages of stem. VAN BUIJTENEN (1978) felled 15 half-sib families of *Pinus taeda* L. at age 14, after crown closure, and rogued 9 clones of *Pinus elliottii* ENGELM. from a seed orchard at ages 7 to 11. He found no significant differences in the percentages of stem to total dry weight among the *P. taeda* families (58 to 66 %), but he found significant and heritable ($h^2 = 0.5$) differences among the *P. elliottii* clones (30 to 47 %) and, again, they were not significantly correlated with tree size. THOMPSON (1974) compared the distribution of dry matter in *P. contorta* trees of Long Beach (coastal Washington) and Fort Frazer (inland British Columbia) origins and found that the proportion of total shoot dry matter allocated to stem was least in trees that produced only one whorl of first-order branches per year.

Table 1. — Clones of *Picea sitchensis* and *Pinus contorta* destructively analysed at age 8. Clones labelled A, B, C or D were measured at age 5 by CAHALAN (1981). * Candidate elite trees of Queen Charlotte Islands provenance.

Picea sitchensis	Pinus contorta
'Plus' tree 8013*	North Bend C (43°N)
'Plus' tree 8010*	North Bend A (43°N)
Queen Charlotte Islands (54°N)	Anahim Lake A (52°N)
San Juan C (49°N)	Anahim Lake B (52°N)
Skidegate A (53°N)	Queen Charlotte Islands A (54°N)
Sitka D (57°N)	Skagway C (59°N)
Cordova D (61°N)	Skagway D (59°N)

Materials and Methods

Seven contrasting clones of both *Picea sitchensis* and *Pinus contorta* were analysed (*Table 1*). The clonal parents were randomly chosen trees within provenance experiments in Britain, except for three of the *P. sitchensis* clones which were propagated from plantation trees of Queens Charlotte Islands provenance. The clone trials were planted in April 1973 on agricultural loam near Edinburgh, Scotland (55° 50' N, 184 m. alt.), and the destructive analyses described here were done in August 1981, at age 8. Each trial consisted of 3 replicate blocks, each with 5 provenances (main plots), representing the latitudinal range of natural variation within the species, with 4 clones per provenance (sub-plots), each represented by three ramets at 1 m spacing in rows 1.5 m apart. The central or average-sized ramet was felled for analysis; that is, one tree was taken of each of seven clones from each of the three blocks.

The stems (= trunks or boles) of each of the 42 trees (2 species, 7 clones, 3 blocks) were divided into annual height increments above each set of first-order whorl branches. Sample discs were cut from each stem section and sample branches were taken from each section (i.e. at each height level). Each sample and corresponding non-sample was weighed fresh soon after the trees were felled. The samples represented at least 20 % of the total fresh weight. The sample branches at each level were cut into individual shoot lengths which were sorted into age groups, and the fresh weights, numbers and lengths of the shoots in each age group were recorded. Only one replicate tree per clone of *P. sitchensis* was measured in length. All samples were oven-dried at 90° C for 3 days, after which needles were separated from wood and the samples were re-weighed .

The dry weights of the unsampled portions of the stems were estimated from the fresh/dry weight ratios of the sampled portions. The dry weights and lengths of the shoots on the unsampled branches at each level were estimated assuming that, (a) the percentage fresh weight of age 1, 2 . . . . . 7 shoots, (b) the fresh/dry weight ratios, and (c) the length/dry weight ratios, were the same as on the corresponding sampled branches.

The weights of needles present on the trees in 1979 and 1980 were estimated assuming that the dry weight of needles per unit shoot length, in each age class, was the same as found in 1981. This gave estimates of fallen needle dry weights, and enabled estimates to be made of annual stemwood production (see below) per unit of needle weight and area in 1979 and 1980, as well as in 1981.

Discs taken from the non-sample sections of the stems at each height level were used to determine the volumes and specific gravities of stemwood in each annual ring. Volumes were estimated from the lengths of each stem section and the means of 4 radii per annual ring measured on the disks, assuming the rings to be concentric circles. Blocks of wood, about 120 mm³, were cut from each annual ring, except for many of the small innermost rings and a few of the incomplete outermost rings, remembering that the trees were felled in August. The blocks were ovend-ried and weighed, $Wood_{(dry)}$, and then saturated for 48 hours in ethyl alcohol and re-weighed, $Wood_{(alc)}$. Their volumes were then estimated, in a thermostatically controlled room, at 20° C, from the difference in weight of a volumetric flask, filled first with alcohol alone, $Flask_{(alc)}$, and then with alcohol plus the block of wood, $Flask_{(alc\ +\ wood)}$. The flask was filled to a critical level using a syringe and overflow tube inserted through a rubber bung. Taking the specific gravity of ethyl alcohol as 0.791 g/cm³ then: Wood volume ($Wood_{(vol)}$) = ($Flask_{(alc)} - Flask_{(alc\ +\ wood)} + Wood_{(alc)}$)/0.791, and Wood specific gravity = Wood/$Wood_{(vol)}$.

The annual stemwood dry weight increments were estimated by multiplying the annual ring volumes by their specific gravities, where necessary substituting missing specific gravity values on innermost and outermost rings with values for the following or preceding years. The total stem increments in each year, including bark and pith, were estimated by dividing the total stem dry weight into annual increments in the same proportion as the stemwood.

Fresh green needles were collected from unfelled trees of each clone in September 1981. One branch was cut from each annual whorl down the trees and divided, as before, into age classes. Needles were taken from along the lengths of each branch and projected areas of samples of 100 needles of *P. contorta* and 200 needles of *P. sitchensis,* in each age class at each level, were measured using an LI-31000 Area Meter (Lambda Instrument Corp.). The needles were then oven-dried and weighed to give estimates of specific needle area (cm²/g). Needles on the main stems were assumed to have the same specific needle areas as needles of the same age on branches at the same level.

Analyses of variance (7 clones, 3 replicates) were done on each variate and percentage values were analysed with and without transformation to arcsin.

Results

Heights, dry weights, branch lengths and foliage characteristics

The *P. sitchensis* clones were, on average, 19 % taller in 1981 than the *P. contorta* clones (4.6 and 3.6 m, respectively). They had similar stem dry weights (2.87 and 2.76 kg/tree, respectively), but the *P. sitchensis* clones had, on average, only 56% as much branch wood dry weight (2.30 and 4.11 kg/tree), and only 61% as much needle dry weight (2.59 and 4.23 kg/tree). However, the branch wood on *P. sitchensis* clones was "spread" over a long total branch length, averaging 552 m/tree, over twice the branch length on *P. contorta* (211 m/tree). And the needle weight of *P. sitchensis* was "spread" over a relatively large projected needle area, averaging 41.9 cm²/g compared with 34.9 cm²/g on *P. contorta,* so that the average projected needle area per tree was only 26 % less on *P. sitchensis* than on *P. contorta* (10.9 and 14.8 m²/tree respectively).

The clones of both species differed significantly in height (in 1981) and stem dry weight *(Figure 1),* and in the weights, lengths, and needle areas of many of the component parts of the trees *(Figures 2* and *3).*

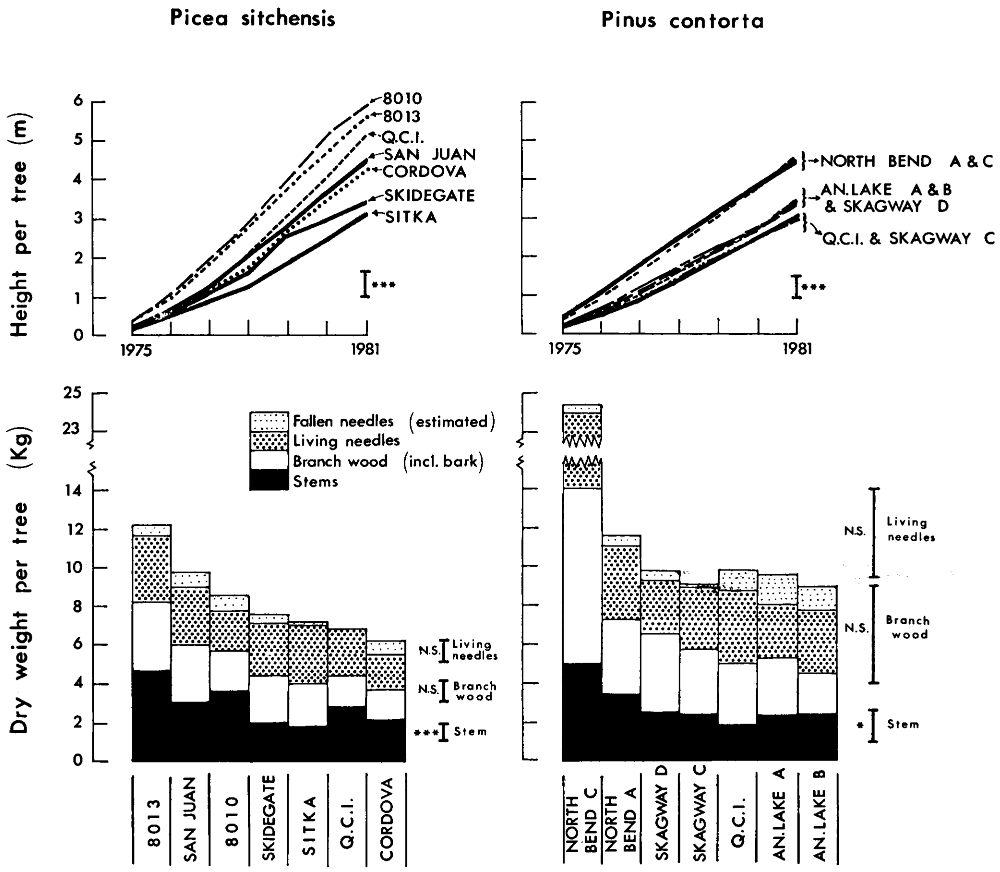

Figure 1. — Heights and dry weights of 7 clones of *P. sitchensis* and *P. contorta* at age 8 (in 1981). The vertical bars are L.S.D. values at P = 0.05 for tree heights in 1981 and tree weights. The asterisks indicate the significance of the F-ratio in the analyses of variance, * P = 0.05, ** P = 0.01, *** P = 0.001. Clonal differences in total needle and branch weights were not significant at P < 0.05.

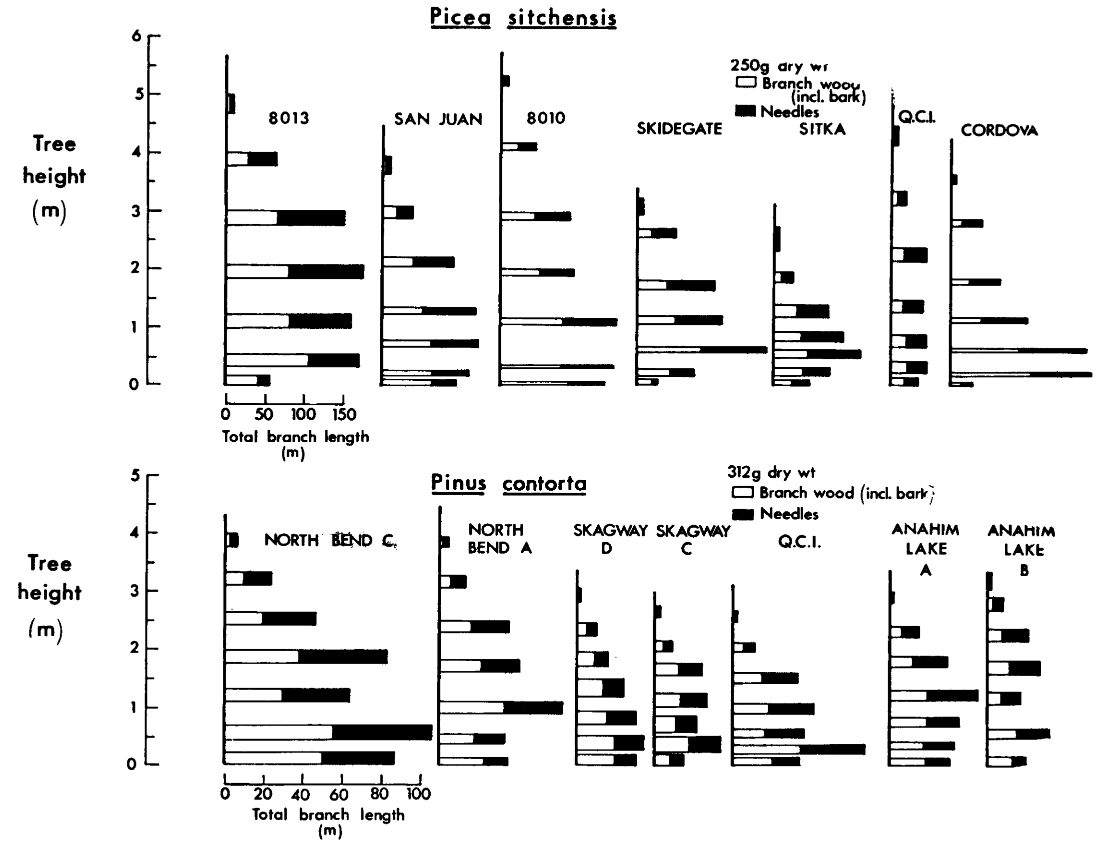

Figure 2. — The dry weights and lengths of branches at each height level on 7 clones of *P. sitchensis* and *P. contorta* at age 8. The branch lengths are the total accumulative lengths of all shoots on all branches at each level. The thickness of the branch bars are proportional to the average dry weights of wood plus needles per unit length of branch. Note that the scales are different for the two species.

Within *P. sitchensis* the clone ranking in total tree dry weight was different from the ranking in height, because some of the relatively tall clones were sparsely branched, and vice versa. In particular, clones 8010, Cordova and Q. C. I. had small branch weights for their heights: 8010 and Cordova had relatively long lengths of branches but they were light per unit length, whereas Q. C. I. had a short length of heavy branches *(Figure 2)*. Clones 8013, 8010 and Cordova had relatively small individual needles, while Q. C. I. had relatively large needles *(Table 2)*.

Clonal comparisons within *P. contorta* were dominated by North Bend C, which was over twice as heavy as any of the other clones, largely because it bore a great length of heavy branches, particularly basal branches *(Figures 1* and *2)*. North Bend A was equally as tall, but had fewer, shorter branches, especially at the base. Q. C. I., like North Bend C, had long basal branches, whereas the two Skagway and two Anahim Lake clones had relatively short heavy branches, more uniformly distributed down the trees *(Figure 2)*. North Bend C and Anahim Lake B had the largest individual needles *(Table 2)*.

In both species the specific needle areas (cm^2/g) tended to decrease with age of needles. *(Table 3)*. That is, on these open-grown trees, the old needles were the heaviest per unit area. However, within each age group the needles towards the base of the trees tended to be the lightest (having the greatest specific needle areas, *Table 3)*.

Distribution of dry matter

The mean dry matter percentage of stem: branches: needles on *P. sitchensis* at the time of harvest was 37:29:34, and on *P. contorta* was 27:35:38. That is, *P. sitchensis* had a higher percentage of stem dry weight, and a smaller percentage of branches (6 % less) and needles (4 % less).

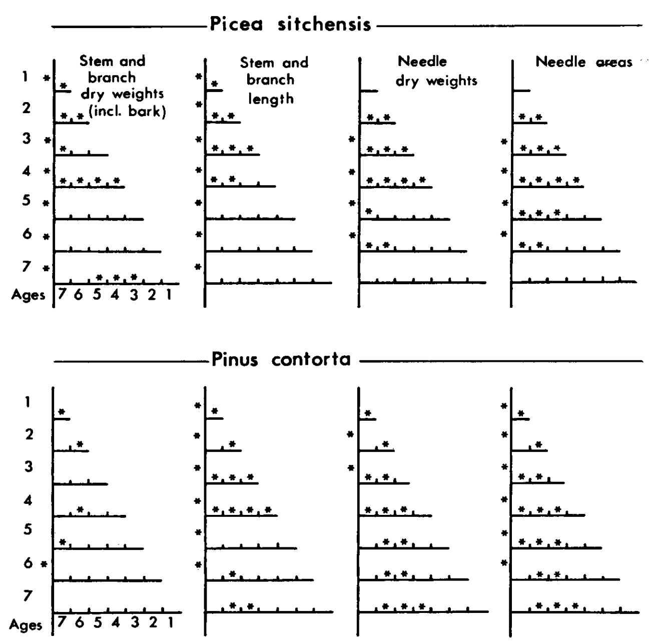

Figure 3. — The presence of significant differences among 7 clones of *P. sitchensis* and *P. contorta* in wood dry weights, stem lengths, needle dry weights and needle areas, on the component parts of the trees. The stems are divided into annual height increments, and the shoots on branches at each level are divided into up to 7 age groups. * denotes significant differences among clones at $P < 0.05$.

Table 2. — Mean foliage characteristics of 7 clones of *Picea sitchensis* and *Pinus contorta* (Listed in order of decreasing total tree weight as in *Figure 1*).

	Clone name	Needle area m^2/tree††	Needle number† 1000's/tree	Mean needle size† d.wt. (mg)	Mean needle size† cm^2††	Mean specific needle area (cm^2/g)
Picea sitchensis	8013	16.2	1062	3.3	0.15	46
	San Juan	13.1	666	4.4	0.20	45
	8010	9.4	573	3.5	0.16	47
	Skidegate	11.6	502	5.4	0.23	42
	Sitka	10.7	538	5.5	0.20	36
	Q.C.I.	8.4	337	6.7	0.25	37
	Cordova	7.0	472	3.7	0.15	40
	L.S.D. P=0.05	5.77	-	-	-	-
Pinus contorta	North Bend C	34.4	529	18.4	0.65	35
	North Bend A	14.0	294	12.7	0.48	38
	Skagway C	11.9	256	12.2	0.46	38
	Skagway D	10.1	208	16.3	0.49	30
	Q.C.I.	12.0	249	14.5	0.48	33
	An. Lake A	10.3	182	17.0	0.57	33
	An. Lake B	10.9	155	19.0	0.70	37
	L.S.D. P=0.05	16.93	-	-	-	-

†Half-fascicles of *P. contorta* ††Projected areas

Within *P. sitchensis,* ramets within clones which differed greatly in absolute weights were more similar in their percentage distribution of dry matter; consequently clonal differences in the percentage distribution of dry matter were significant at $P < 0.05$ (with and without arcsin transformation) whereas differences in absolute needle and branch weights were not (*Figures 1* and *4*). The clones with the greatest percentage of stem dry weight were 8013, and the three relatively sparsely branched clones, 8010, Cordova and Q. C. I. Among these clones 8010 and Q. C. I. retained significantly more of their old needles (over 2 years old) than did the other clones (*Figure 4*).

Within *P. contorta,* the smallest percentage of stem dry weight occurred on the two clones with long, heavy basal branches, namely, North Bend C (the very heavy clone) and Q. C. I. (*Figures 2* and *4*). Significant clonal differences in needle retention were not related to stem weight percentages, but rather to total tree dry weights; the heaviest clones tended to be those that retained most old needles, while the lightest clones shed them, especially the two Anahim Lake clones and Q. C. I. (*Figures 1* and *4*).

Stemwood specific gravity

The mean specific gravities of the accumulated stemwood (excluding the bark and pith) of *P. sitchensis* and *P. contorta* at age 8 (1981) were very similar (0.33 and 0.34 g/cm^3, respectively) but there were large differences between the annual rings. The mean values at ages 3, 4 . . . . . 8, were, for *P. sitchensis* 0.48, 0.47, 0.40, 0.36, 0.33 and 0.31 g/cm^3, and for *P. contorta* 0.41, 0.38, 0.36, 0.34, 0.34, and 0.32 g/cm^3. That is, there was a marked decrease in stemwood specific gravity with age, especially in *P. sitchensis,* which occurred in all clones (*Figure 5*). However, it should be noted that the 1981 annual ring was measured in August (the month of harvest) before the latewood was fully formed.

Within both species there was a tendency for clones that produced large stem dry weights to produce stemwood with a low specific gravity (*P. sitchensis,* $r = 0.55$, *P. contorta,* $r = 0.46$). However, within *P. sitchensis,* clone Q. C. I. (the clone with short heavy branches, large needles, good needle retention and a high percentage of stem weight) had a very low stemwood specific gravity, and within *P. contorta,* clones Anahim Lake B and Skagway D produced stemwood with relatively low and high specific gravities, respectively.

Stemwood production per unit of needles ("stemwood production efficiency")

The dry weights of stemwood produced at ages 6, 7 and 8 (1979, 1980 and 1981) were divided by the estimated dry weights and projected areas of needles on the trees in August of those years (the month of harvest in 1981), on the assumption that the proportions of age 1, 2 . . . . . 7 year-old needles, and the weights and areas of needles per unit length of shoot of ages 1, 2 . . . . . 7, were the same in 1979 and 1980 as in 1981. Clonal differences were similar in all three years, but, because the 1981 ring was incomplete stemwood production efficiency appeared to be lower in 1981 than in the previous two years (*P. sitchensis* 0.62, 0.61 and 0.45 g/g and *P. contorta* 0.34, 0.34 and 0.26 g/g in 1979, 1980 and 1981, respectively). Consequently mean efficiencies are presented here for the 3 year period.

Over the years 1979—1981, *P. sitchensis* produced an average of 0.53 g of stemwood dry weight per gramme of needle dry weight, whereas *P. contorta* produced only 0.31 g. Equivalent values per m^2 of needle projected area were 128 g for *P. sitchensis* and 89 g for *P. contorta* (*Table 4*).

Table 3. — Specific needle areas (cm^2/g) within 8-year-old trees of *Picea sitchensis* and *Pinus contorta.* Each value is the mean of samples taken from one tree of each of 7 clones.

Picea sitchensis

Top of tree	38.2						
↑	32.5	42.3					
	33.5	37.5	44.2				
	37.7	37.0	40.9	47.8			
	32.1	37.5	36.9	39.5	49.7		
	-	36.9	37.4	40.9	43.0	56.7	
Base	-	-	-	37.4	39.6	39.3	47.5
Ages:			5	4	3	2	1
Means:			34.5	37.5	37.6	38.8	46.6

Pinus contorta

Top of tree	33.2						
↑	29.8	35.6					
	29.6	31.6	38.6				
	28.5	30.2	32.9	38.6			
	28.8	33.0	31.5	33.4	38.4		
	-	30.2	26.4	32.7	34.5	42.0	
Base	-	-	-	32.7	33.0	34.1	43.0
Ages:			5	4	3	2	1
Means:			29.5	30.2	31.4	32.7	38.5

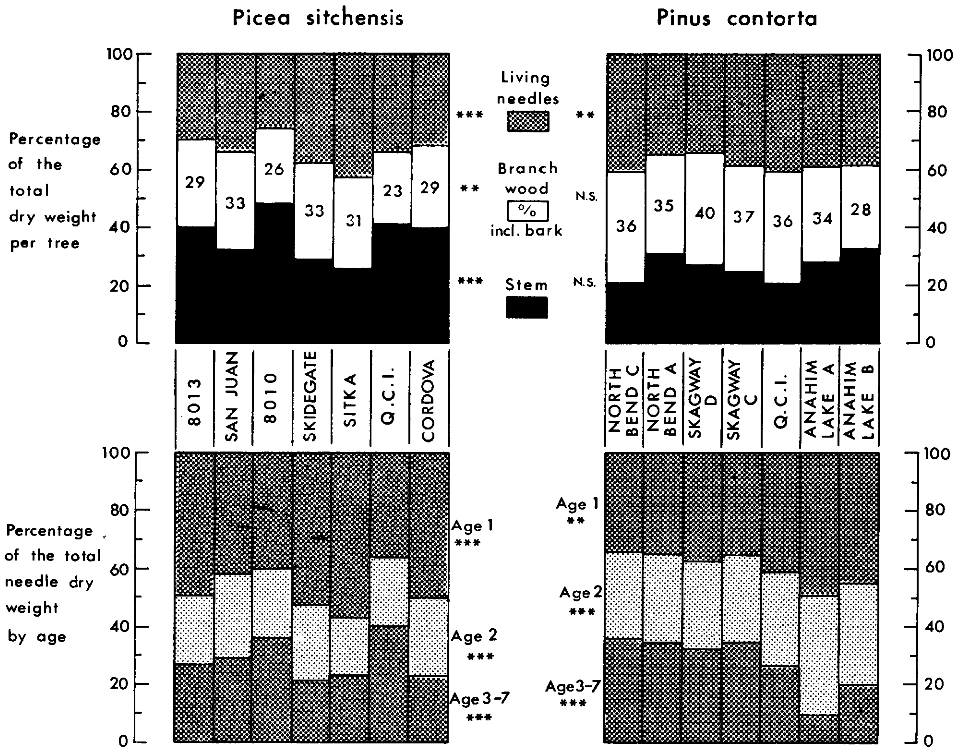

Figure 4. — The percentage distribution of dry matter in 7 clones of *P. sitchensis* and *P. contorta*. Upper: percentage of living needles, branches (wood and bark) and stems; the percentage values are given for branches. Lower: percentage of living needles aged, 1, 2, and 3—7. The asterisks indicate the level of significance of the F-ratios, which were the same with or without transformation to arcsin; * P = 0.05, ** P = 0.01, *** P = 0.001.

Within *P. sitchensis* there were approximately twofold clonal differences in stemwood production efficiency *(Table 4).* The least efficient clones — Sitka, Skidegate and San Juan — were little more efficient than the *P. contorta* average, both on the basis of needle dry weight and needle area. Reference to the characters described above and the correlation coefficients in *Table 5,* revealed that large stemwood production efficiencies in *P. sitchensis* were associated with the following inter-related characters: — (a) tree height (the tallest clones were 8013, 8010, Q. C. I.; *Figures 1* and *2),* (b) sparse branching (8010, Cordova, Q. C. I.; *Figure 2),* (c) the allocation of a high proportion of the total dry matter into stems rather than branches or needles (8010, 8013, Q. C. I., Cordova; *Figure 4),* (d) low stemwood specific gravity (Q. C. I., 8013, 8010; *Figure 5),* and (e) a tendency to retain old needles (Q. C. I. and 8010; *Figure 4).* There was no relationship with individual needle size or total tree dry-weight.

Within *P. contorta* the two clones with heavy basal branches, Q. C. I. and North Bend C, were the least efficient stemwood producers — the latter especially so in units of needle projected area *(Table 4).* These two clones had the lowest percentage stem dry weight, and the highest percentage needle dry weight, and consequently both of these characters were correlated with stemwood production efficiency among the 7 *P. contorta* clones *(Table 5).* Unlike *P. sitchensis,* clonal differences in stemwood production efficiency in *P. contorta* were not correlated with tree heights, stemwood specific gravities or needle retention.

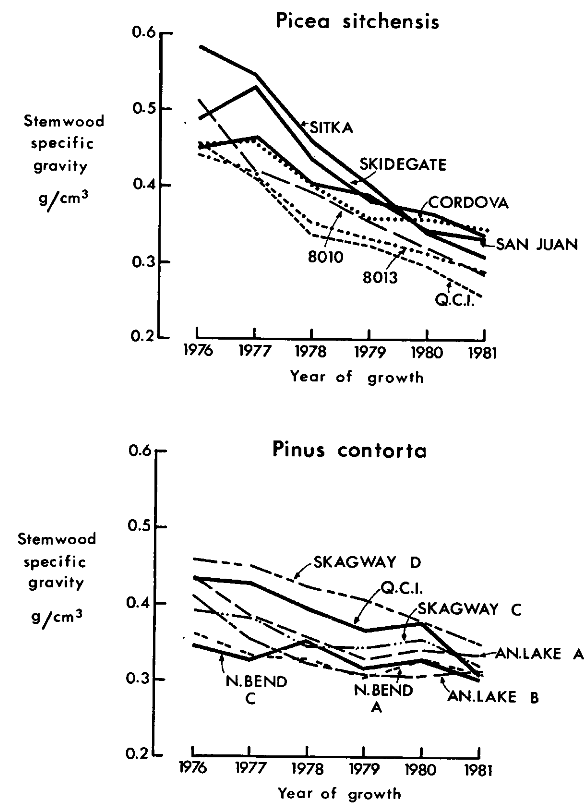

Figure 5. — Mean stemwood specific gravities at ages 3 to 8 (1976 to 1981) in 7 clones of *P. sitchensis* and *P. contorta.* The values are means for the total cylinder of wood produced each year, and are derived from measurements of the volumes, dry weights and specific gravities of the wood in each ring at each annual height level up the stem. The F-values of analyses of variance of *P. sitchensis* in 1976, 1977 . . . . 1981 were 2.2, 3.8, 13.1***, 4.0, 6.6* and 17.8*** and of *P. contorta* were 1.9, 11.9**, 5.3*, 21.2***, 12.7** and 3.6, respectively. * P = 0.05, ** P = 0.01, *** P = 0.001.

Discussion

There were three salient findings of this study on 8-year-old open-grown trees of contrasting clones.

1. At ages 6—8 (1979—1981) *Picea sitchensis* produced

44 % more stemwood per unit of foliage projected area than *Pinus contorta* (128 and 89 g/m^2, *Table 4)*, and 71 % more stemwood per gramme dry weight of foliage. This high stemwood production efficiency by *P. sitchensis* was attributed to (a) the allocation of a high proportion of the total dry matter to stems (37 %, compared with 27 % in *P. contorta)* and (b) the efficient structure of the *P. sitchensis* canopies, which had long lengths of relatively thin branches bearing needles with large projected areas per unit weight.

2. The proportion of the total dry matter allocated to stems ranged from 26 % to 48 % among clones of *P. sitchensis* and 21 % to 31 % among clones of *P. contorta (Figure 4)*. The clones that allocated most to stems were those that were sparsely branched (in different ways) and at ages 6—8, they produced 1.5 to 2.0 times as much stemwood per unit of foliage as heavily branched clones *(Table 4)*.

3. The mean stemwood specific gravity (green volume/oven dry weight) at age 8 differed by 25 % among *P. sitchensis* clones (0.29 to 0.36 g/cm^3), and by 21 % among *P. contorta* clones (0.31 to 0.38 g/cm^2), but equally importantly there was a 35 % drop in specific gravity between the innermost and outermost annual rings in *P. sitchensis* (0.48 to 0.31 g/cm^2) and a 22 % drop in *P. contorta* (0.41 to 0.32 g/cm^3).

Stemwood production

The results of this study are consistent with the notion that large genetic gains in stemwood production per tree, before canopy closure, can be achieved by selecting simultaneously for both rapid total dry matter production per tree, and a high harvest index (the proportion of the total dry matter allocated to stems). These two traits were not necessarily inversely related: rapidly growing genotypes did not necessarily allocate a large proportion of their dry matter to photosynthetic capital at the expense of the stems. Consequently, there were large clonal differences in stemwood production per unit of needles. Within *P. sitchensis* and *P. contorta* the clones with the greatest total dry matter tended to be the tallest, and those with the greatest harvest index and stemwood production per unit of needles at ages 6—8 were those with fewest or smallest branches or lacking large basal branches. In short, selection for tallness and any kind of sparse branching seemed to be an effective way of selecting for efficient stemwood production. This finding agrees with the results of Matthews *et al.* (1975) and Van Buijtenen (1978), mentioned in the introduction, and supports the selection strategy adopted by many tree breeders. Indeed clone 8013 of *P. sitchensis*, which was propagated from a candidate "plus" tree, had both rapid growth and a relatively large stemwood production efficiency.

Table 4. — Mean stemwood dry matter increment per unit weight (g/g) and per unit projected area (g/m^2) of needles on 7 clones of *Picea sitchensis* and *Pinus contorta.*

Picea sitchensis				Pinus contorta			
Clone#	g/g	g/m^2	Branching characteristics	Clone#	g/g	g/m^2	Branching characteristics
8013	0.64	134	moderately sparse	N. Bend C	0.23	66	large basal
San Juan	0.43	91	-	N. Bend A	0.40	105	-
8010	0.75	165	sparse	Skagway D	0.34	106	-
Skidegate	0.39	93	-	Skagway C	0.31	88	-
Sitka	0.33	88	-	Q.C.I.	0.22	65	large basal
Q.C.I.	0.59	156	sparse	An. Lake A	0.30	88	-
Cordova	0.56	169	sparse	An. Lake B	0.40	108	-
Means	0.53	128	-	-	0.31	89	-
L.S.D. P=0.05	0.180	52.0	-	-	0.146	43.7	-

Listed in order of decreasing total dry weight, as in *Figures 1* and *4*.

Table 5. — Correlation coefficients (r) between the efficiency of stemwood production averaged over ages 6—8 (1979—1981) and other tree characteristics, for 7 clones of *Picea sitchensis* and *Pinus contorta*.

		Picea sitchensis		Pinus contorta	
		A	B	A	B
Tree size	Tree height	0.96***	0.81	0.33	-0.15
	Total dry wt/tree	0.36	0.06	-0.35	-0.60
Dry weight distribution at age 8 (1981)	Percentage stem	0.96***	0.88**	0.69	0.62
	Percentage branches	-0.76*	-0.93**	-0.01	0.07
	Percentage needles	-0.89***	-0.66	-0.86*	-0.95***
Needle characteristics	Dry wt. per needle	-0.44	-0.09	-0.43	-0.24
	Specific needle area (cm^2/g)	0.50	0.09	0.39	-0.05
	Percentage of needles over 3 years old (d.wt.)	0.64	0.70	0.11	-0.06
Wood specific gravity	Mean stemwood specific gravity	-0.66	-0.78*	-0.21	0.24
	Sp. gr. of stemwood produced 1979-81	-0.77*	-0.85**	-0.17	0.29

A = Stemwood dry weight increment per unit of needle dry weight.
B = Stemwood dry weight increment per unit of needle projected area.
* ** *** denote significance at P = 0.05, 0.01 and 0.001, respectively.

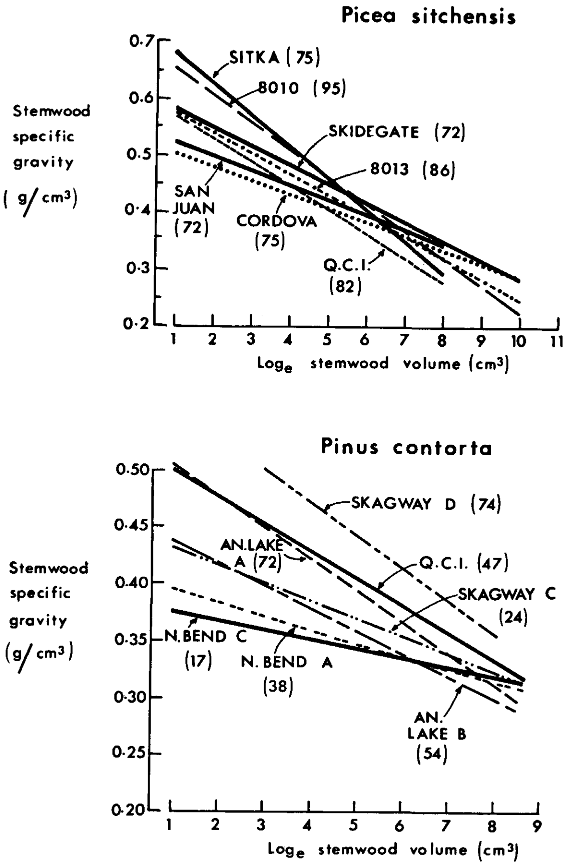

Figure 6. — Relationships between the specific gravity and the volume of stemwood in annual ring cylinders produced at ages 3 to 8 (1976 to 1981) by 7 clones of *P. sitchensis* and *P. contorta*. Each regression was calculated using 18 values (6 years × 3 replicate trees). The percentage of the total variance accounted for is given in brackets after each clone name. F-values for clonal differences were, for *P. sitchensis:* slope 6.7***, intercept 6.8***, and for *P. contorta:* slope 2.1 n.s., and intercept 13.8***, *** P = 0.001.

The magnitude of the genetic gains available can only be guessed at from this intensive study of a few contrasting clones. But if the high harvest index and stemwood production efficiency of *P. sitchensis* clone 8010 could be found in a clone with the total dry matter production of 8013, such a clone would produce about 5.6 kg of stem by age 8, compared with 4.7 kg produced by 8013, which was already 64 % above the 7-clone average. A similar calculation for *P. contorta* suggested that the stemwood production of clone North Bend C, which produced 71 % more than the 7-clone average (4.8 *cf.* 2.8 kg/tree) could be increased by at least a further 50 %. CAHALAN's (1981) results, and the small within-clone variation in percentage dry matter distribution found in this study, suggest that clone selection for branching characteristics, and associated stemwood production efficiency, would be effective, especially in *P. sitchensis.*

Insofar as the clonal differences in stemwood production per unit of foliage were associated with branchiness (owing to differences in apical control, branch ageing and branch retention) rather than with differences in foliage amount and mutual shading, it is possible that the major differences will persist after crown closure. However, the absolute value of stemwood production efficiencies often increase after crown closure anyway, because the ratio of stem cambial surface area to foliage amount increases (see MITCHELL, 1975 his p. 9 and *Figure 7)* and it is noteworthy that the stemwood production efficiency of a 17-year-old *P. sitchensis* stand measured by FORD (1982) was 0.62 g/g, compared with the 7-clone average of 0.53 g/g in this study. However, both of these values were much smaller than the stemwood production efficiencies of 19—32-year-old *Tsuga heterophylla* in Oregon (0.97 g/g, FUJIMORI, 1971) and 6-year-old *Pinus radiata* in New South Wales (1.56 g/g, FORREST and OVINGTON, 1970).

Stemwood specific gravity

The differences in stemwood specific gravity between clones and annual rings *(Figure 5)* are related in *Figure 6* to the different volumes of wood in the annual rings. For all clones, stemwood specific gravity decreased as a linear function of $\log_e$ annual stemwood volume production. Within *P. sitchensis* both the initial specific gravity (the intercepts) and its rate of decrease (the slopes) differed significantly between clones ($P < 0.01$), whereas within *P. contorta* only the initial values differed significantly. Furthermore, in both species the values of the intercepts and slopes were negatively correlated ($r^2 > 0.95$) indicating that those clones with the greatest initial stemwood specific gravities suffered the greatest decrease in specific gravity as volume production increased.

These findings have disturbing implications for breeders attempting to select for high stemwood specific gravity on the basis of juvenile wood, because both the values obtained and the clonal rankings in stemwood specific gravity (especially in *P. sitchensis)* will differ with age and between sites because of differences in annual volume production.

References

ANON.: The Foundation for Forest Tree Breeding in Finland. Annual Report (1980). — BUIJTENEN, J. P. VAN: Genetic differences in dry matter distribution between stems, branches and foliage in loblolly and slash pine. *In:* Proceedings of the Fifth North American Forest Biology Workshop. ed. C. A. HOLLIS and A. E. SQUILLACE. p. 235—241. School of Forest Resources, University of Florida, Gainsville, Fl., U.S.A. (1979). — CAHALAN, C. M.: Provenance and clonal variation in growth, branching and phenology in *Picea sitchensis* and *Pinus contorta.* Silvae Genetica 30: 40—46 (1981). — CANNELL, M. G. R.: Improving per hectare forest productivity. *In:* Proceedings of the Fifth North American Forest Biology Workshop. ed. C. A. HOLLIS and A. E. SQUILLACE. p. 120—148. School of Forest Resources, University of Florida, Gainsville, Fl., U.S.A. (1979). — CANNELL, M. G. R.: World Forest Biomass and Primary Production Data. 391 pp. Academic Press, London and New York. (1982). — FORD, E. D.: High Productivity in a polestage Sitka spruce stand and its relation to canopy structure. Forestry 55: 1—17 (1982). — FUJIMORI, T.: Primary productivity of a young *Tsuga heterophylla* stand and some speculations about biomass of forest communities on the Oregon coast. U.S.D.A. Forest Service, Research Paper PNW - 123 11 pp. (1971). — FORREST, W. G. and OVINGTON, J. D.: Organic matter changes in an age series of *Pinus radiata* plantations. J. appl. Ecol. 7: 177—186 (1970). — LEDIG, F. T.: Increasing the productivity of forest trees. *In:* Forest Tree Improvement — The Third Decade. ed. B. A. THIELGES. p. 189—206. Louisiana State University, Baton Rouge, La., U.S.A. (1975). — MATTHEWS, J. A., FERET, P. P., MADGEWICK, H. A. I. and BRAMLETT, D. L.: Genetic control of dry matter distribution in twenty half-sib families of Virginia pine. *In:* Thirteenth Southern Forest Tree Improvement Conference. p. 234—241 (1975). — MITCHELL, K. J.: Dynamics and simulated yield of Douglas-fir. Supplement to Forest Science 21. Monograph 17 (1975). — THOMPSON, S.: Shoot growth and dry matter production in two contrasting provenances of *Pinus contorta* DOUGL. Ph. D. thesis, University of Aberdeen, Scotland (1974).