

from measurement of latex yield over two or three years. (TAN, 1978), and thus save the time and resources that are presently spent in testing clones for 15 to 25 years before recommendations are made.

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Provenance and Clonal Variation in Growth, Branching and Phenology in *Picea sitchensis* and *Pinus contorta*

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Summary

Four clones from each of five provenances of *Picea sitchensis* and *Pinus contorta* were grown from cuttings taken from 15 and 14 year-old trees, planted at a lowland and an upland site in Scotland and measured annually for five years. Fifth year data are presented here. Provenances, covering much of the species' natural ranges, accounted for 25—72% of the variation in fifth year heights and diameters, and clones within provenances for 9—31%. Significant and visually striking differences between clones within provenances occurred in branching characteristics in both species, and in dates of bud burst and bud set in *P. sitchensis*, the largest *P. sitchensis* clones being those with the longest seasonal periods of elongation. Significant ortet-ramet correlations were found in *P. contorta*, but clonal differences were not associated with differences in rooting speed in either species.

Repeatabilities of clone means for height and diameter were 0.84 and 0.76 for *P. sitchensis* at the lowland site, predicting genetic gains of 38% and 30% over the mean from selecting the best 5% of clones within provenances. Corresponding repeatabilities for *P. contorta* were 0.54

and 0.58, predicting gains of 10% and 14%. Genetic gains from selection at the upland site were expected to be somewhat lower.

Key words: *Picea sitchensis*, *Pinus contorta*, clones, provenances, variation.

Zusammenfassung

Vier Klone von je fünf Provenienzen von *Picea sitchensis* und *Pinus contorta*, die als Stecklinge von 14- und 15-jährigen Bäumen stammen, wurden im schottischen Hoch- und Tiefland an jeweils einem Standort ausgepflanzt und jährlich über den Zeitraum von fünf Jahren gemessen. Die Ergebnisse aus dem fünften Jahr werden in dieser Arbeit veröffentlicht.

Den Provenienzen, die nahezu das gesamte natürliche Verbreitungsgebiet der Art abdecken, war in bezug auf ihre Fünfjahreshöhen- und -durchmesser eine Variation von 25—72% zuzuordnen, den Klone innerhalb der Provenienzen eine von 9—31%. Signifikante und sichtbare Klonunterschiede innerhalb der Provenienzen traten bei den Zweigmerkmalen beider Arten, sowie im Zeitpunkt von Austriebsbeginn und Vegetationsabschluss bei *Picea sitchensis* zutage. Bei *Picea sitchensis* waren die Klone mit der längsten Vegetationsperiode am größten. Signifikante Mutterbaum-Stecklings-Korrelationen wurden bei *Pinus contorta* gefunden, aber die Klonunterschiede stan-

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den nicht mit der Wurzelwachstumsgeschwindigkeit in Verbindung.

Die Wiederholbarkeitskoeffizienten der Klonmittelwerte für Höhe und Durchmesser betragen 0,84 und 0,76 für *Picea sitchensis* bei der Pflanzung im Tiefland, was bei einer Selektion der 5% besten Klone innerhalb der Herkunft genetische Gewinne von 38 und 30% über dem Mittel verspricht. Die entsprechenden Wiederholbarkeitskoeffizienten für *Pinus contorta* waren 0,54 und 0,58, was genetische Gewinne von 10 und 14% verspricht. Die genetischen Selektionsgewinne bei der Pflanzung im Hochland waren entsprechend geringer.

Introduction

Widely-distributed forest tree species show genetic variation between geographic sources or provenances and between individuals of the same provenance. This genetic variance has additive and non-additive components, but only the former is exploited in breeding schemes designed to produce superior seed. Both additive and non-additive variation can be captured by vegetative reproduction, and expected gains from the selection and propagation of superior clones are generally higher than those from selection of seed parents, but there are problems in applying this on a commercial scale. Among the more serious of these are the need to select young trees whose mature traits are unknown in order to avoid the risk of growth rate reductions in cuttings taken from older trees, the difficulty of maintaining the juvenility of clones throughout a selection programme and the relatively high cost of producing clonal material.

Estimates of gains from clonal selection depend on a knowledge of clonal repeatabilities, which can be calculated from the data provided by replicated clonal tests. These are described here for *Picea sitchensis* (BONG) CARR. (Sitka spruce) and *Pinus contorta* DOUGL. (Lodgepole pine), the two most important commercial forest tree species in Britain.

Clones from provenances chosen to cover the natural ranges of *P. sitchensis* and *P. contorta* were grown at two contrasting sites in southern Scotland to assess the genetic variation between and within provenances and the relative performance of genotypes under different growing conditions. Morphological and phenological characters of silvicultural importance were measured after five years of growth.

Materials and Methods

Four clones from each of five provenances of both *P. sitchensis* and *P. contorta*, chosen to represent the latitudinal range of natural variation in each species, were grown at a lowland (Roslin) and an upland (Cloich) site in southern Scotland (Table 1). *P. sitchensis* clones came from a 15 year-old frost-damaged provenance trial at Wark, Northumberland; four randomly selected trees, one from each of four blocks, were used as mother trees (ortets) in each provenance. The clones of *P. contorta* came from a 14 year-old provenance trial at Selm Muir, Lanarkshire, where single trees of measured average height from each of four blocks were used as ortets in each provenance.

Eighty cuttings of each *P. sitchensis* mother tree and sixty of each *P. contorta* mother tree were taken in February 1972 and rooted on mist propagation benches. Cuttings were examined on three of five occasions between February and

Table 1. — Origins of provenances of *Picea sitchensis* and *Pinus contorta*. Four clones of each provenance were planted at the two sites in Scotland.

Location	Latitude (° N)	Altitude (m)
Planting sites (Scotland)		
Lowland (Roslin, Midlothian)	56	150
Upland (Cloich, Peebleshire)	56	310
<i>P. sitchensis</i> sites of origin		
Cordova (Alaska)	61	
Sitka (Alaska)	57	
Skidegate (Queen Charlotte Is.)	53	all < 150
San Juan (Vancouver I.)	49	
North Bend (Oregon)	43	
<i>P. contorta</i> sites of origin		
Skagway (Alaska, coastal)	59	< 150
Queen Charlotte Is. (coastal)	54	< 150
Anahim Lake (British Columbia, inland)	52	1220
Lady-smith (Vancouver I., coastal)	49	< 150
North Bend (Oregon, coastal)	43	< 150

July and the percentages of each clone rooted at each stage were used as measures of speed of rooting. At least 21 rooted cuttings per clone were potted and grown in an unheated glasshouse until November 1972, when they were taken outside to overwinter.

Clones were planted on agricultural land at the lowland site (Roslin, Table 1) in April 1973. A split-plot design with provenance main plots, clone sub-plots and three replications was used for each species. Each clone was represented by a row of three ramets at 1m spacing. In the winter of 1974 a similar split-plot trial was planted on peaty-gley soil on a north-facing upland site (Cloich, Table 1) using ramets which had been growing in buried containers at the lowland site since 1973. Each clone at the upland site was represented by four ramets per plot.

The annual height increment of each tree was recorded at the end of each growing season. Height, basal diameter 10 cm. above ground level and current year's growth were measured at both sites at the end of 1978, the fifth growing season. Branch number (the number of new first order branches produced during the fifth growing season), branch angle (the angle between a new first order branch and the main stem), the amount of free or lamma growth on trees of *P. sitchensis* and the number of whorls of branches produced on the main stem in the current year (i.e. the degree of cyclicity) on *P. contorta* were measured at the lowland site only. Plants at the upland site were too small for realistic measures of branching characters.

Clones of *P. sitchensis* at the lowland site were examined twice weekly during their fifth growing season to determine dates of flushing (bud burst) and of bud set (the first appearance of bud scales on the terminal bud of the leading shoot). Following a late spring frost at the start of the fourth growing season the number of frosted buds on each tree was counted.

For each character at each site, analyses of variance were carried out on plot means. A random effects model was

used, and the expectations of mean squares are shown in Table 2. After solving for $V_{c(p)}$, the variance due to clones

within provenances, the repeatability of clone means was calculated as:

$$h^2(c) \text{ (repeatability of clone means)} = \frac{V_{c(p)}}{(V_{c(p)} + V_{cb} + V_e/n)}$$

Table 2. — Analysis of variance.

Source	df	Expectation of MS
Provenances	p-1	$V_e + nV_{cb} + ncV_{pb} + ncbV_p$
Provs. x Blocks	(p-1)(b-1)	$V_e + nV_{cb} + ncV_{pb}$
Clones-within-provenances	p(c-1)	$V_e + nV_{cb} + nbV_{c(p)}$
Clones x Blocks	p(c-1)(b-1)	$V_e + nV_{cb}$
Residual		V_e
Total	bpc(n-1)	

b, c, n and p are numbers of blocks, clones within a provenance, trees within a clone subplot and provenances respectively.

An analysis of variance of the combined fifth year height data from both sites was carried out to detect genotype × site interactions.

Results

Heights and diameters (Figure 1, Tables 3 and 4).

Trees of both species, particularly those of *P. contorta*, were much larger at the lowland than the upland site, and southerly provenances grew bigger than northerly ones at both locations. Provenances accounted for 25–72% of the variation in height and diameter depending on species, site and character, but clonal variation within provenances was also significant in most cases, ranging from 9–31% of the total. Variation due to clones was higher in *P. sitchensis*, in which ortets had been chosen at random within provenances, and largest clone from Cordova (61° N) was taller than the smallest from North Bend (43° N). Clonal variation was less in *P. contorta* and was not significant at the upland site, perhaps because ortets within provenances had been of similar height.

Repeatabilities of clone means ranged from 0.57 to 0.84 for *P. sitchensis*, depending on site and character, and were higher than those for *P. contorta*, which were between 0.23

Table 3. — Variance components, repeatabilities of clone means and F values in *Picea sitchensis*.

Character	$V_{c(p)}$	V_{e2}	$h^2(c)$	F
Height (lowland)	2058	1200	0.84	16.4***
(upland)	434	990	0.57	6.3***
Diameter (lowland)	0.53	0.50	0.76	10.5***
(upland)	1707	5181	0.57	5.0***
Branch number	57.5	30.5	0.85	17.9***
Branch angle	29.5	35.3	0.72	8.5***
Lammas growth	16.4	19.2	0.72	8.7***
Bud burst	12.1	11.6	0.76	10.3***
Bud set	877.7	489.2	0.84	17.1***
Frost damage	34.4	32.6	0.76	10.5***

*** p = 0.001 $V_{e2} = V_e + nV_{cb}$ (see Table 2.)

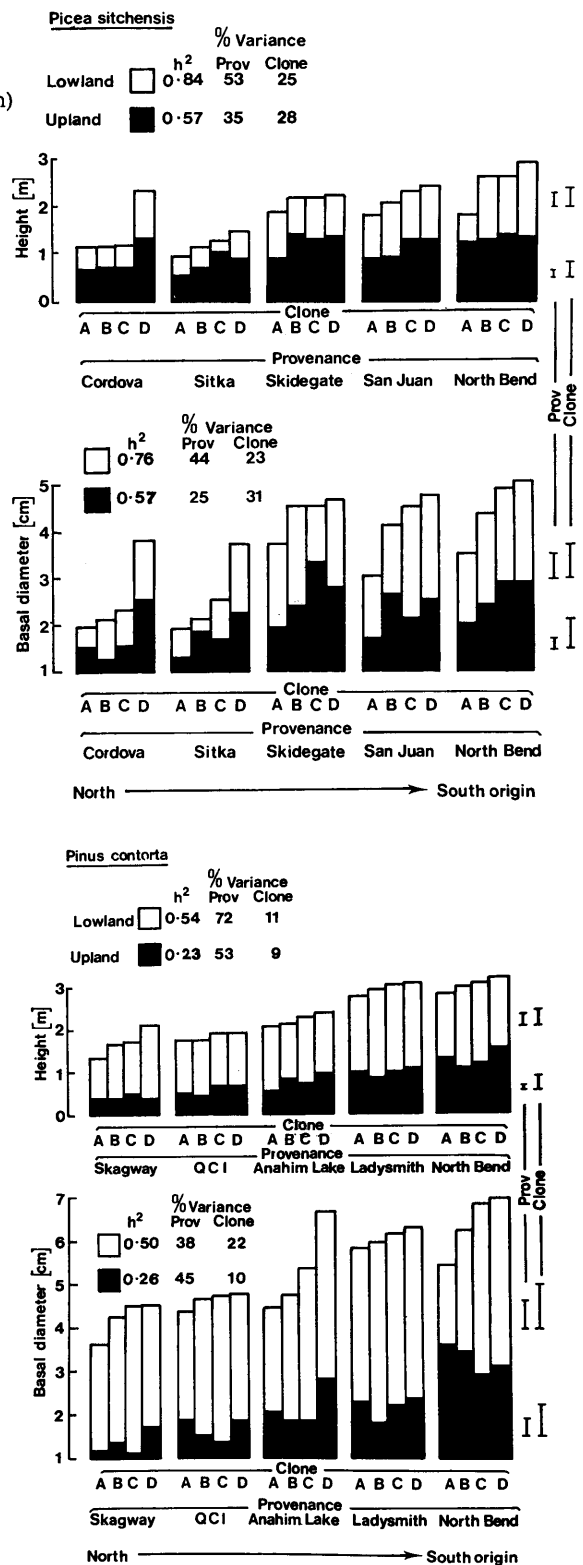


Figure 1. — Fifth year heights and basal stem diameters of provenances and clones of *Picea sitchensis* and *Pinus contorta* at an upland (shaded) and a lowland (unshaded) site in Scotland. Clones are labelled A-D in order of increasing height at the lowland site. Lines represent least significant differences (p = 0.05) between provenances and clones at the upland and lowland sites. Percentage contributions of clonal and provenance variation to total variance at each site are given. h^2 = repeatability of clone means, calculated separately for each site.

Table 4. — Variance components, repeatabilities of clone means and F values in *Pinus contorta*.

Character	V _{c(p)}	V _{e2}	h ² (c)	F
Height (lowland)	393	1002	0.54	4.5***
(upland)	76.2	1014	0.23	1.9
Diameter (lowland)	0.4	0.87	0.56	5.2***
(upland)	526	6037	0.26	2.0
Branch number	1.6	10.6	0.31	2.4*
Branch angle	46.3	159.8	0.47	3.6**
Whorl number	0.13	0.19	0.68	7.2***

* p = 0.05 ** p = 0.01 *** p = 0.001
V_{e2} = V_e + nV_{cb} (see Table 2.)

and 0.58. Repeatabilities were higher in both species at the lowland site.

Analysis of variance of the combined height data from both sites showed significant provenance × site and clone × site interactions in both species. In *P. sitchensis* there was a difference in ranking of provenances at the two sites, the mean for San Juan being greater than that for Skidegate at the lowland site but less at the upland one, and the relative heights of clones within four of the five provenances also changed with site. There was no provenance-site interaction affecting ranking of *P. contorta* provenances, but relative heights of clones within provenances did show differences between sites (Figure 1, Table 5).

Fifth year heights of clones were significantly correlated with their height increments in all earlier years of the trial (r = 0.63–0.99 for *P. sitchensis* and 0.67–0.98 for *P. contorta*) except for first year increments of *P. contorta* clones, which were unrelated to fifth year heights. Fifth year heights of *P. contorta* clones were significantly cor-

Table 5. — Analysis of variance of combined height data from two sites.

<i>Picea sitchensis</i>			
Source	df	MS	F
Provenances	4	37011	6.2
Sites	1	216470	115***
Provs. x Sites	4	6003	17.8***
Clones-within-provenances	15	5086	6.5***
Clones x Sites	15	784.7	2.4***
Provs. x Blocks	16	336.7	
Clones x Blocks	60	324.5	
<i>Pinus contorta</i>			
Source	df	MS	F
Provenances	4	47241	9.3*
Sites	1	715158	486***
Provs. x Sites	4	5097	4.3*
Clones-within-provenances	15	961	1.9
Clones x Sites	15	506	9.2***
Provs. x Blocks	16	1173	
Clones x Blocks	60	55.2	

* p ≤ 0.05 ** p ≤ 0.01 *** p ≤ 0.001

related with mother tree heights (r = 0.86), but repeated frost damage to mother trees meant that correlations could not be calculated for *P. sitchensis*. In neither species was the fifth year height of clones related to the speed at which cuttings had originally rooted (r = 0.17 and -0.16 for *P. sitchensis* and *P. contorta* respectively).

Branching characteristics and lammas growth (Figures 2 and 3, Tables 3 and 4).

There were significant differences between and within provenances in branch number and angle in both species, in the amount of lammas growth in *P. sitchensis* and in the

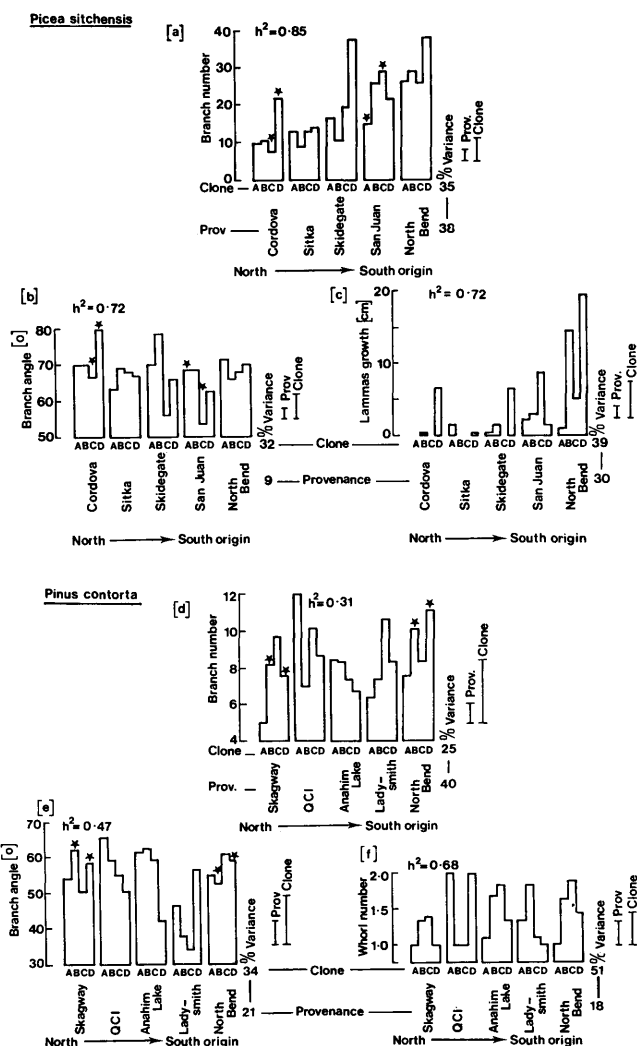


Figure 2. — Branching characters of provenances and clones of *P. sitchensis* and *P. contorta* and lammas growth of *P. sitchensis* at a lowland site. a,d — branch number; b,e — angle of first order branches from main stem; c = amount of lammas growth (*P. sitchensis*); f — number of branch whorls (one whorl = unicyclic) (*P. contorta*). Clones marked * are illustrated in Figure 3. See legend to Figure 1.

number of branch whorls (cyclic) in *P. contorta*. Southerly provenances of *P. sitchensis* generally produced more branches each year than northerly ones, but there were large differences between clones and some of the northerly types had many more branches than clones from further south (compare Skidegate D with North Bend A, B and C).

In both species clones within provenances accounted for less of the total variation in branch number than prove-

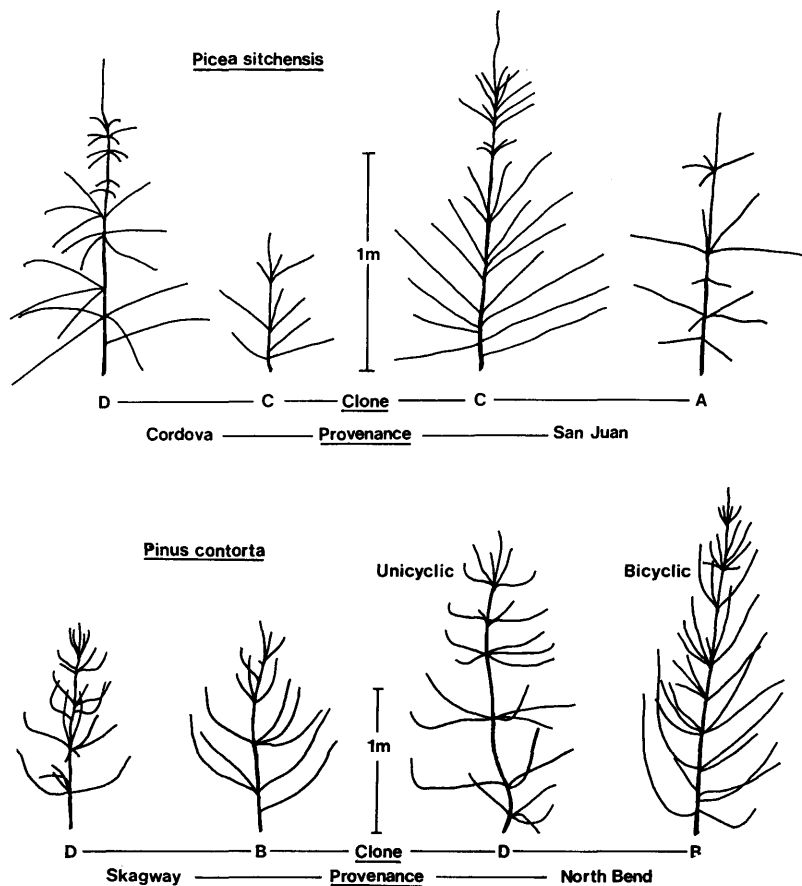


Figure 3. — Line drawings of four clones of *P. sitchensis* and four clones of *P. contorta* selected to illustrate the large differences between and within provenances in branching and form characteristics at a lowland site. Drawings were made by tracing photographs taken during the fifth growing season. See also Figure 2.

nances but more of the variation in branch angle, and clonal variation was also greater than that due to provenances in lammas growth of *P. sitchensis* and whorl number of *P. contorta*.

Repeatabilities of branching characteristics were lower and more variable in *P. contorta* than in *P. sitchensis*, but in both species clonal differences in branchiness and resulting crown form were visually striking, and examples are illustrated in Figure 3.

Branch number and angle were not correlated in either species, and neither character was associated with height or diameter in *P. contorta*. However, in *P. sitchensis* the clones which produced the most branches tended to be those which grew tallest ($r = 0.80$), had the largest diameter ($r = 0.74$) and produced most lammas growth ($r = 0.78$). There was also a significant negative correlation ($r = -0.60$) between branch number and flushing date.

Phenology of *Picea sitchensis* (Figure 4, Table 3).

50% of the variation in date of flushing was accounted for by clones within provenances, and was greater than the variation due to provenances, but variation in date of bud set, and hence in the period of elongation, was due almost equally to clone and provenance. Northerly provenances generally had shorter periods of shoot elongation than southerly ones, but there were exceptions. Clone D of the Cordova (Alaska) source, for example, had a particularly long extension period.

There was no significant correlation between dates of flushing and bud set; provenances and clones which flushed

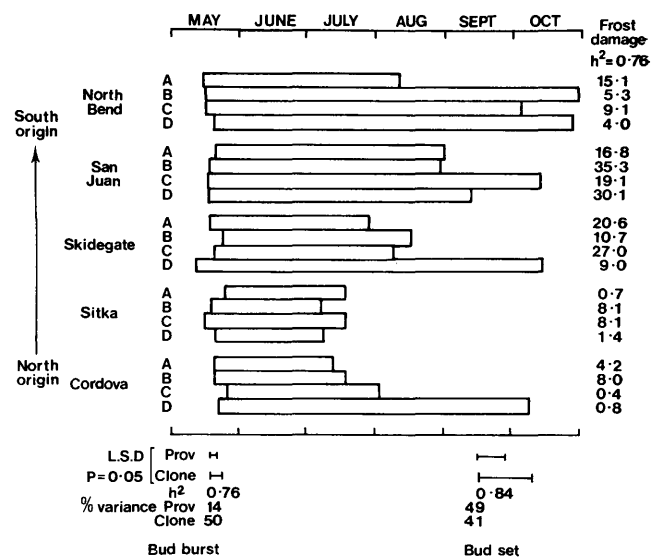


Figure 4. — Phenology of provenances and clones of *P. sitchensis* growing at a lowland site. Bars represent the period of leader elongation in the fifth growing season. Figures on the right of the diagram give the number of buds damaged in a late spring frost in the fourth growing season. See legend to Figure 1.

early did not necessarily stop growing early. However, clones with longer periods of shoot elongation tended to be taller ($r = 0.89$) and have greater diameters ($r = 0.78$),

and clone heights were closely correlated with dates of bud set ($r = 0.89$).

There were significant differences between and within provenances in the number of buds damaged by a late spring frost in their fourth growing season, but only a weak negative correlation between this and date of flushing ($r = -0.33$ n.s.).

Discussion

The variation between provenances described here reflects patterns of geographic variation already reported in *P. sitchensis* (ROCHE and FOWLER, 1975) and *P. contorta* (CRITCHFIELD, 1957; LINES, 1976). In both species southerly provenances were larger and had more branches than northerly ones, and the greater lammas growth of southerly origins of *P. sitchensis* has also been documented (CANNELL and JOHNSTONE, 1978). These differences are thought to be largely determined by phenological variation in the date of bud set and the length of the growing season (BURLEY, 1965; LINES and MITCHELL, 1966), both of which were positively correlated with height in *P. sitchensis*.

Higher numbers and greater lengths of branches in southerly provenances have been shown in many cases to be a function of their superior height growth (CANNELL, 1974), and the characters were correlated in *P. sitchensis*. Inland sources of *P. contorta*, however, are more sparsely branched than coastal provenances (CRITCHFIELD, 1957), and there was no significant correlation between branching and height in the pine species.

Clonal variation within provenances was significant in nearly all cases, and equalled that due to provenances in some branching and phenological characteristics. Within provenance variation has been described in *P. contorta* (ILLINGWORTH, 1976) as well as in several other species (*Picea abies*, WORRALL, 1975; KLEINSCHMIT and SAUER, 1976; SAUER-STEGMANN *et al.*, 1978; *Pinus radiata*, BURDON 1971). In *P. sitchensis*, results from a diallel cross between trees of a single provenance suggest that form characters are largely under additive genetic control, but that growth traits show both additive and non-additive variation (SAMUEL *et al.*, 1972), both of which could be captured by vegetative propagation.

It is possible to calculate the genetic gain which is expected from selection and propagation of the best clones within a provenance from $\Delta G = i \cdot h^2(c) \cdot \sqrt{V_{c(p)}}$, where ΔG

is the genetic gain, i the selection intensity, $h^2(c)$ the repeatability of clone means and $\sqrt{V_{c(p)}}$ the square root of

the variance of clone means. By selecting the tallest 5% of *P. sitchensis* clones at the lowland site and growing them in a similar environment, a 38% gain in fifth year height compared with the trial mean is anticipated, and a smaller gain of 23% from selection of the best 5% at the upland site. Expected gains in other traits are shown in Table 6.

Both selection gain and repeatability values must be interpreted with care, since they are applicable only to a particular set of clones and the environments used to estimate the genetic parameters for their calculation. In addition, if clone performance is influenced by persistent non-genetic "c" effects arising from a common shared environment on the mother tree, clone variance, repeatability of clone means and genetic gain can all be overestimated (LIBBY and JUND, 1962; BURDON and SHELBOURNE, 1974).

Table 6. — Mean, square root of the clonal variance ($\sqrt{V_{c(p)}}$), genetic gain (ΔG) and percentage gain over the mean from clonal selection in *Picea sitchensis* and *Pinus contorta*. Gains calculated from $\Delta G = i \cdot \sqrt{V_{c(p)}} \cdot h^2(c)$ where i is the selection intensity, here taking a value of 2.06 (top 5% of clones selected), and $h^2(c)$ is the repeatability of clone means.

Character	Mean	$\sqrt{V_{c(p)}}$	ΔG	% gain
<i>Picea sitchensis</i>				
Height (m): lowland	2.03	0.45	0.77	38
upland	1.06	0.21	0.25	23
Diameter (cm): lowland	3.80	0.73	1.14	30
upland	2.17	0.41	0.48	22
Branch number	21.38	7.58	13.27	62
Branch angle (°)	68.16	5.43	8.05	12
Lammas growth (cm)	3.98	4.05	6.01	151
Flushing date (days)	140.06	3.48	5.45	4
Date bud set (days)	243.30	29.63	51.27	21
Frost damage	11.37	5.87	9.19	81
<i>Pinus contorta</i>				
Height (m): lowland	2.24	0.20	0.22	10
upland	0.77	0.09	0.04	6
Diameter (cm): lowland	5.21	0.63	0.75	14
upland	2.11	0.23	0.12	6
Branch number	8.18	1.26	0.80	10
Branch angle (°)	55.20	6.80	6.58	12
Whorl number	1.47	0.26	0.50	34

In this test there was no evidence that differences in rooting ability between clones influenced their subsequent growth, but other non-genetic effects may have been important in determining clone performance, and second generation trials are currently underway to assess the magnitude of all "c" effects.

Differences between the repeatabilities at the two sites are a reflection of the genotype \times environment interactions also detected in the analysis of variance of combined height data. Genotype \times environment interactions have been reported in *P. contorta* (ILLINGWORTH, 1976) and in *P. sitchensis* by JOHNSTONE and SAMUEL (1978), who suggest that there may be justification in breeding for specific sites and in using vegetatively propagated planting material if seed is in short supply.

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Variation of *Alnus rubra* for Nitrogen Fixation Capacity and Biomass Production¹⁾

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Summary

To test half-sib families of *Alnus rubra* BONG. for biomass production and nitrogen assimilation capacity, seeds were collected from two parent trees selected from each of five natural populations between Newport and Corvallis in western Oregon. The seedlings were germinated and grown in a greenhouse with or without indigenous inoculant at two nitrogen fertilizer levels. At age 5 weeks before inoculation, seedling size and weight among families and sources differed little. However, at age 14 weeks, seedlings inoculated with indigenous endophyte grew 10 to 15 times larger than noninoculated seedlings. Differences in biomass production and nitrogen assimilation between families and sources in the inoculated group indicate genetic variability and the possibility of gain by selection. Because progeny from sources with site indices of 95 and 65 performed better in this experiment than those from sites with indices of 100 and 110, site index should not be the sole selection criterion for nitrogen-fixing capacity and biomass production in *A. rubra*.

Key words: *Alnus rubra*, tree improvement, genetic selection, nitrogen-fixation.

Zusammenfassung

Samen von je zwei selektierten Elternbäumen aus fünf natürlichen Populationen von *Alnus rubra* BONG. zwischen Newport und Corvallis in West-Oregon wurden gesammelt, um Halbgeschwister-Familien bezüglich ihrer Biomasse-Produktion und Stickstoff-Assimilationskapazität

zu testen. Nach dem Auskeimen wurden die Samen im Gewächshaus mit oder ohne am Standort gewonnene Strahlenpilz-Suspension bei zwei Stickstoffdüngerstufen angezogen. Im Alter von fünf Wochen vor der Beimpfung differierten die Sämlingshöhen und -gewichte zwischen Familien und Herkünften nur gering. Im Alter von 14 Wochen waren die mit standort eigener Pilzsuspension beimpften Sämlinge 10 bis 15 mal so groß wie die nicht beimpften. Unterschiede in der Biomasse-Produktion und Stickstoffassimilation zwischen Familien und Herkünften in der beimpften Gruppe deuten auf eine genetische Variation und die Möglichkeit eines Selektionsgewinnes hin. Weil die Nachkommenschaft von Herkünften mit Standortindexen von 95 und 65 in diesem Versuch besser abschnitten, als die von Standorten mit einem Index von 100 und 110, sollte der Standortindex nicht das alleinige Selektionskriterium für die Stickstoff-Fixierungskapazität und Biomasseproduktion bei *Alnus rubra* sein.

Introduction

Nitrogen-fixing plants in managed forests may increase wood production for timber, fiber, and energy (BOND, 1977; SMITH, 1978; STETTLER, 1978). *Alnus rubra* BONG. or red alder is a moderately fastgrowing and widely distributed nitrogen-fixing hardwood tree in the Pacific Northwest (BURNS and HARDY, 1975; FRANKLIN and PECHANEC, 1968; TARRANT, 1978). As predominant hardwood in the Northwest, *A. rubra* may be a useful silvicultural tool for maximizing forest yield (BERG and DOERKSEN, 1975; DEBELL, STRAND, and REUKEMA, 1978; GORDON, 1978). Oregon alone has 79 million m³ of *A. rubra* (U.S. Forest Service, 1977). In addition to economic value as sawtimber, *A. rubra* is an efficient and valuable nonleguminous nitrogen-fixer. The fixed nitrogen causes the rapid growth of *A. rubra*, and the accretion of nitrogen to the soils increases the productivity of associated species (ATKINSON and HAMILTON, 1978; FRANKLIN and PECHANEC, 1968; MILLER and MURRAY, 1978).

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