Heights of Provenances and Progenies of Pinus contorta in Britain Correlated with Seedling Phenology and the Duration of Bud Development

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Summary

Differences in the duration of first-year seedling height growth among 15 provenances and groups of 16 and 10 open-pollinated progenies of *Pinus contorta* were correlated with 1 and 2-year seedling heights, and with 3 and 6-year heights after outplanting in 3 or 5 replicate forest trials in upland Britain. In all studies the correlations were positive, and became larger with age, accounting for 71—85% of the variation in mean heights by age 6 after outplanting. Observations on seasonal changes in the diameters of the apical domes of eight 7-year-old provenances showed that provenances with prolonged periods of growth as first-year seedlings also had prolonged periods of shoot apical meristematic activity in subsequent years.

Correlations between the duration of first-year seedling growth and 6-year heights were greatest when restricted to heights at sites favourable for growth. Furthermore, first-year seedling growth duration was significantly positively correlated with Finlay-Wilkinson (1963) regression coefficients evaluating height 'stabilities' at age 6 at different sites.

Thus, in Britain, the duration of first-year seedling height growth may be a useful criterion to select or reject provenances and progenies of *Pinus contorta* for both mean early height growth and for their likely contributions to genotype × site interactions.

Key words: Pinus contorta, early testing, phenology, provenance, genotype-environment interaction.

Zusammenfassung

Im englischen Hochland wurde bei 15 Provenienzen und 16 bzw. 10 frei abgeblühten Nachkommenschaften von *Pinus contorta* die unterschiedliche Dauer des Sämlingswachstums im ersten Jahr geprüft und mit der Sämlingshöhe im ersten und zweiten Jahr sowie im dritten und sechsten Jahr nach dem Auspflanzen in drei- bzw. fünffach wiederholten Versuchen korreliert. In allen Versuchen waren die Korrelationen positiv und nahmen im Alter zu, indem sie 71—85% an Variation in den Durchschnittshöhen sechs Jahre nach dem Auspflanzen ausmachten. Beobachtungen des jahreszeitlichen Wechsels im Durchmesser der Gipfelknospen von acht sieben Jahre alten Provenienzen zeigten, daß Provenienzen mit verlängerter Wachstumsperiode im ersten Sämlingsjahr auch in den folgenden Jahren eine verlängerte Meristemaktivität zeigten. Korrelationen zwischen der Wachstumsdauer im ersten Sämlingsjahr und den Sechsjahreshöhen waren am größten, wenn man sich auf die Höhen auf besseren Standorten beschränkte. Außerdem war die Dauer des Höhenwachstums im ersten Sämlingsjahr signifikant positiv mit dem Finlay-Wilkinson (1963) Regressionskoeffizienten korreliert, der die Stabilitäten der Höhen im Alter sechs an verschiedenen Standorten schätzte. So mag die Länge der Höhenwachstumsperiode im ersten Sämlingsjahr in England ein brauchbares Kriterium darstellen, um Provenienzen und Nachkommenschaften von *Pinus contorta* sowohl für das mittlere Höhenwachstum in der Jugend als auch für ihre wahrscheinlichen Verteilungen gegenüber den Genotyp × Umwelt Interaktionen zu selektieren.

Introduction

Several attempts have been made to find physiological seedling traits which can be used as early selection criteria. The traits examined include photosynthetic rates of *Populus* clones (Gordon and Promnitz 1976), seasonal growth phenology of some North American hardwoods (Farmer 1976), responses of *Pinus taeda* L. seedlings to water stress (Cannell *et al.* 1978) and frost hardening of *Pinus contorta* Dougl. seedlings in response to long nights (Jonsson *et al.* 1980). This paper concerns early screening of *P. contorta* for its ability to exploit the growing season in the British uplands (51—58° N) where provenances from the southerly parts of the natural range (especially the Oregon and Washington coasts, 43—49° N) grow faster, although with poorer stem form, than more northerly or inland provenances (Lines 1976) without suffering severe winter mortality, as occurs in parts of Scandinavia (e. g. Lindgren *et al.* 1980).

The hypothesis examined here is that, from the seedling stage up to at least 6 years after outplanting in Britain (8 years after germination) the heights of many *P. contorta* provenances and many sets of open-pollinated progenies have become more and more closely correlated with differences in their seasonal duration of shoot apical meristematic activity. That is, among the range of genotypes tested so far, the types which have become tallest have tended to be those that had prolonged periods of apical meristematic activity, producing new cataphylls, needle fascicles and stem units for relatively prolonged periods every autumn. This hypothesis was tested by (a) examining phenotypic correlations between the durations of first-year seedling height growth and mean tree heights at ages 1, 2, 5 and 8 after germination, and (b) by observing the duration of apical meristematic activity within the buds of 7-year-old provenances assuming that decreases in meristematic activity (i.e. in bud development) in the autumn were accompanied by decreases in apical dome diameters, as found in earlier studies (Cannell and Willett 1975, Cannell 1976). Note that differences in the duration of shoot elongation after the first year were ignored, because the shoots are then largely preformed and their elongation period is not then directly related to their period of apical meristematic activity.

Several workers have shown that the seasonal duration of first-year seedling height growth of *P. contorta* provenances increases with decrease in latitude and altitude of origin (Critchfield 1957, Sweet and Wareing 1968, Hagner 1970a, 1980), but this variation has not been related to subsequent tree growth. Ekberg *et al.* (1979) found that first-year seedlings of *P. contorta* provenances differed in their responses to photoperiod and temperature, while

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Table 1. — Provenances of *Pinus contorta* used to determine (a) dates of first-year seedling bud-set, (b) height up to 6 years after outplanting at 5 sites in Britain, and (c) the seasonal duration of bud development during the fifth growing season after outplanting in a nursery.
Provenances are listed in order of mean 6-year heights (8 years after germination) at 5 sites given in *Table 2*. Where provenances are bracketed together, the top one was used to assess first-year seedling traits, and the bottom one was used to assess heights after the first year.

Code in Fig. 1	See above		Location	Latitude (°N)	Longitude (°W)	Elevation (m)
A	a b -	Wash.	Long Beach	46°26'	124°03'	0-30
B	a - -	Oregon	Hauser Dunes	43°30'	124°14'	0-30
	- b c		Newport/Bandon	43°45'	ca 124°	0-50
	- - c	Wash.	Shelton	47°10'	123°05'	150
C	a - -	B.C.	Nanaimo	49°08'	123°58'	0-150
	- b c		Coombs	49°20'	124°30'	460
D	a - -	B.C.	Shuswap Lake	50°50'	119°20'	700-1160
	- b -		Chase Creek/ Harper Lake	50°42'	119°41'	ca 980
E	a b c	B.C.	Smithers	54°40'	127°20'	600
F	a b c	B.C.	Masset Q.C. Island	54°00'	132°39'	152
G	a - -	B.C.	Fort Fraser	54°03'	124°30'	750
	- b c		Fraser Lake	54°04'	124°51'	762
H	a b -	B.C.	Tofino Vanc. Is.	49°05'	125°47'	23
I	a b -	Alaska	Petersburg	56°47'	132°58'	15-30
J	a b -	Alaska	Sitka	57°04'	135°21'	150
K	a - -	Alaska	Yakutat	59°30'	139°10'	30-60
	- b c		Glacier Bay	58°27'	135°45'	10
L	a - -	Wash.	Trout Lake	46°04'	121°27'	1219
	- b -		Bird Creek	46°20'	121°26'	1220
M	a b -	Alaska	Skagway	59°27'	135°18'	0-61
N	a - -	B.C.	Pink Mountain	57°00'	122°24'	1097-1128
	- b -		Wonowon	56°40'	121°48'	914
O	a b c	Alberta	Crowsnest	49°23'	114°28'	1635

Cannell and Willett (1975) and Cannell (1976) reported provenance differences in the duration of shoot apical meristematic activity on young trees. Dietrichson (1964) stressed the potential importance of seasonal growth duration on the performance of *P. contorta* and *Pinus sylvestris L.* in Norway, and several workers have found significant positive correlations between seasonal growth duration and the mean heights of seedlings of north temperate conifer provenances (e.g. Mikola 1980, *P. sylvestris, Picea abies*). Correlations with mature tree performance are rarer; Hagner (1970b) correlated seasonal growth duration with the heights of single trees of *P. sylvestris* but he measured the elongation of preformed shoots. The potential value of first-year seedling height growth duration as an early selection criterion for *P. contorta* has not previously been explored.

Materials and Methods

Provenance experiments

In May 1975 stratified seeds of 25 provenances of *P. contorta* were germinated in peat/sand mixture in a glasshouse and, in early June, were moved to Teindland Forest, Morayshire (57°34'N, 3°12'W, 255 m) where they were grown in 12 cm diameter pots of nutrient-rich compost (John Innes No. 3) placed on sheltered raised flats. There were 24 to 40 seedlings per provenance, arranged in 10 randomized blocks. The presence or absence of developing buds within the terminal 'rosette' of each seedling was recorded every 1—2 weeks from 29 August to 28 November, when seedling heights were measured (taken as the length of the elongated epicotyls).

Fifteen of the provenances examined were the same as, or similar to, provenances that were evaluated at five forest sites (*Tables 1* and *2*). Seeds were sown in 1968 in raised beds at two lowland nurseries in southern Scotland, and the seedlings were planted as 1 + 1 bare-rooted stock in randomized blocks in 1970 (*Table 2*). Seedling heights, and the presence or absence of second-year lammas growth, were recorded before outplanting, and tree heights were measured 3 and 6 years after outplanting.

Observations were made on the seasonal duration of bud development on 8 provenances (see *Table 1*) which were planted in 1970 in unreplicated 25 tree rows in the nursery at Bush Estate, Penicuik (55°51' N, 3°12' W, 198 m). By 1974 the trees were 1.3 to 2.0 m tall. Branches 15—30 cm long were chosen for study from within the top two whorls. One branch terminal bud was cut off each of 12 trees per provenance on 12 June, 11 July, 16 August, 12 September and 17 October 1974, that is, during their fifth growing season since outplanting. The buds were fixed under partial vacuum in formalin-acetic acid-alcohol, and later dissected under a stereomicroscope to reveal the apical domes, which were measured in diameter to within ± 0.005 mm.

Table 2. — Details of forest sites in Britain where provenances and progenies of *Pinus contorta* were planted, together with mean heights at age 6 and F-ratios indicating differences among genotypes (G), sites (E) and G × E interactions.

	Site name	Latitude °N	Longitude	Elevation m	Soil type	Randomized block design	Mean tree heights 6 years after planting (m)	F-ratios †††
Provenances, planted 1971. Table 1, Figure 1.	Mabie	55°02'	3°31'W	12	Very deep peat	5, 30-tree blocks	1.9	
	Thetford	52°25'	0°41'E	40	Sandy loam	3, 25-tree blocks	1.2	G 103.3***
	Tywi	52°10'	3°51'E	400	Deep peaty gley	3, 25-tree blocks	0.9	E 219.0***
	Beddgelert	53°06'	4°11'W	350	Peaty gley	3, 25-tree blocks	0.9	G x E 3.5***
	Brendon	51°08'	3°28'W	350	Humus iron podzol	3, 25-tree blocks	0.8	
Open-pollinated progenies, planted 1971. Table 3, Figs. 2 & 3	Shin	58°06'	4°23'W	170	Peaty gley with indurations	2, 16-tree blocks	1.7 2.0 ††	G 6.7*** 2.3*
	Rumster	58°24'	3°34'W	122	Deep peat	2, 16-tree blocks	1.6 1.7	E 20.5*** 21.5***
	Coed Sarnau	52°23'	3°23'W	460	Shallow peat† over loam	4, 8-tree blocks	1.3 1.5	G x E 1.6* 1.1

† All sites except this one received 50 kg/ha of P at planting

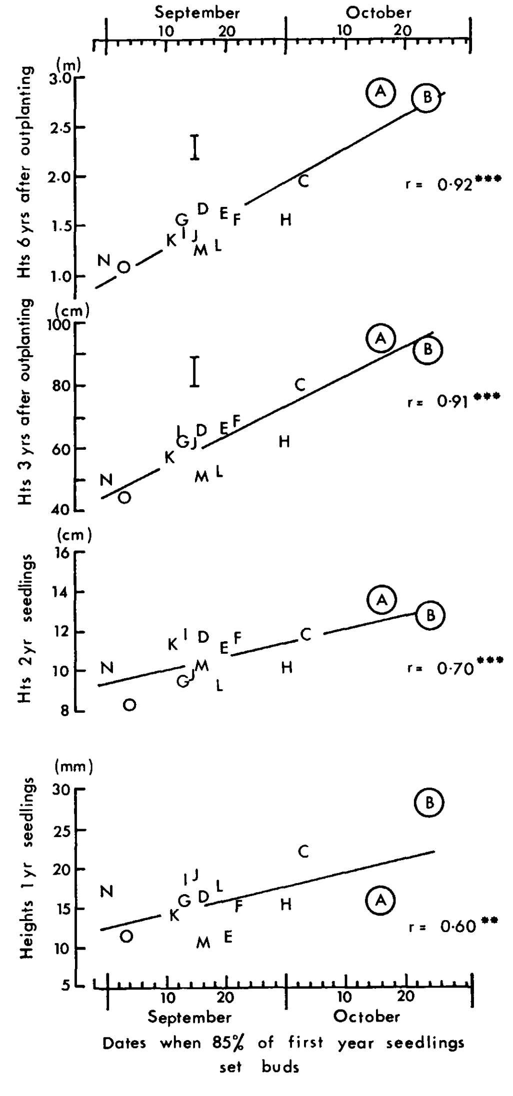
†† Heights on left refer to the 16 progenies in Fig. 2; values on right refer to 10 progenies in Fig. 3

††† *P = 0.05 ** P=0.01 *** P = 0.001

Open-pollinated progeny experiments

Seeds were collected from open-pollinated candidate plus trees growing in Britain*), mostly of known west American provenance. This seed was used in two seedling studies done in 1977 and 1979 using different progenies, as described below, and was also used to establish progeny tests at three sites (*Table 2*). These sites were planted in 1971 with 1 + 1 bare-rooted seedlings grown at the Bush Estate, Penicuik, and were measured in height 3 and 6 year after planting.

The first seedling study was done using 16 progenies of different parent provenance, the second using 10 progenies, nine of which were of Washington or Oregon coastal provenance (*Table 3*). In both studies stratified seeds were germinated in April—May in peat/sand mixture in a heated glasshouse. In early June ~~the~~ 16 progenies were transferred into 20 × 3 cm tubes and the 10 progenies were transferred into 13 cm square pots, all containing peat/sand/loam compost with added nutrients. These containers were placed outside in the nursery at Bush Estate, Penicuik. Twenty-five seedlings of each of the 16 progenies were arranged in a completely randomized design. Twelve seedlings of each of the 10 progenies were placed in each of eight randomized blocks. The heights of all seedlings of the 16 progenies, and 4 seedlings per block of the 10 progenies, were measured every 1—2 weeks from mid-July to mid-November. At the beginning of their second year the 16 progenies were transferred to 12 cm square pots and placed in the Bush Estate nursery in four 6-tree randomized blocks, while the 10 progenies were arranged in six 5-tree randomized blocks replicated in three environments: the Bush Estate nursery, an unheated glasshouse at the Bush Estate, and an exposed hillside at 275 m altitude on Turnhouse Hill, Penicuik.



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*) The work was done by the Genetics Branch of the Forestry Commission's Research and Development Section.

Table 3. — Open-pollinated progenies of *Pinus contorta* used to relate dates of first-year seedling height growth cessation with tree heights up to 6 years after outplanting.

			Parent Provenance				
Code in Fig.2	Code in Fig.3	Open-pollinated progeny no.	Location		Latitude °N	Longitude °W	Elevation m
A		Brenin 391	Wash.	Long Beach	46°26	124°03'	0-30
	A	Brenin 764	-do-				
B		Brenin 396	-do-				
	B	Borgie 240	Wash.	Coast	unknown		
C		Borgie 246	Wash.	Long Beach	46°26'	124°03'	0-30
	C	Brenin 395	-do-				
D		Brenin 761	-do-				
E	D	Standard	Wash.	Coast	unknown		
F		Strathy 232	-do-				
	E	Glenlivet 571	Wash.	Long Beach	46°26'	124°03'	0-30
G		Strathy 226	Wash.	Coast	unknown		
H		Culbin 26	Oregon	Coast	unknown		
	F	Brenin 394	Wash.	Long Beach	46°26'	124°03'	0-30
	G	Brenin 390	-do-				
	H	Brenin 398	-do-				
	I	Brenin 393	-do-				
	J	Inchnacardoch 344	B.C.	Hat Creek	50°32'	121°36'	1520
I		Millbuie 251	B.C.	Prince George	53°26'	122°43'	600
J		Millbuie 273	B.C.	Sonora Island	50°25'	128°20'	10
K		Morefield 263	Alaska	Hollis	55°27'	133°39'	15
L		Inchnacardoch 345	B.C.	Hat Creek	50'32'	121°36'	1520
M		Lael 423	Alaska	Hollis	55°27'	133°39'	15
N		Morefield 269	-do-				
O		Millbuie 258	B.C.	Prince George	53°56'	122°43'	570
P		Millbuie 189	B.C.	Terrace	54°30'	128°35'	60

Progenies are listed in order of 6-year heights (8 years after germination) at 3 sites given in *Table 2*. The names Brenin, Borgie etc. refer to forests in Britain in which numbered candidate plus trees were selected.

Statistical analysis

Analyses of variance were done, based on plot means, and simple phenotypic correlations were calculated between variates. The relative 'stability' in height of the provenances 6 years after outplanting at the 5 sites (*Table 2*) was assessed by calculating regression coefficients according to FINLAY and WILKINSON (1963): that is, individual provenance heights at each site (dependent variables) were regressed on the means of all provenances at each site (independent variables, used as a measure of site quality).

Results

First-year seedling height growth duration and 8-year heights

The 15 provenances differed by 55 days in dates of 85% bud-set, which accounted for 36% of the variation in first-year seedling heights (epicotyls only, r = 0.60, *Fig. 1*), 49% of the variation in 1 + 1 year seedling heights, 83% of the variation in 5-year heights, and 85% of the variation in 8-year heights (6 years after outplanting, *Fig. 1*). This improvement with age in the relationship between date of seedling bud-set and provenance heights was not associated with any marked effect of seed weight on early growth (seed weight-height correlation coefficients r = 0.3 and −0.1 at ages 1 and 8) nor with an increase with age in the relative heights of provenances. The relationship was significant at ages 5 and 8 with or without the two very vigorous south coastal provenances (A and B, encircled in *Fig. 1*) or the two very slow-growing ones (N and O in *Fig. 1*).

Figure 1. — Relationships, for 15 provenances of *Pinus contorta*, between the dates when first-year seedlings set buds, and tree heights up to 6 years after outplanting (means of 5 sites, *Table 2*) A, B, C . . . see *Table 1*; letters encircled denote Washington or Oregon coastal provenances. Vertical bars are least significant differences at P = 0.05 from analyses of variance using only the provenances in this study. There were no estimates of error for the percentage bud-set or seedling heights. First year seedling heights refer to epicotyl lengths only i.e. excluding hypocotyls and terminal buds * ** *** denote significance at P = 0.05, 0.01 and 0.001, respectively.

Significant provenance differences in the percentage (transformed to arcsine) of seedlings that produced lammas growth in their second year accounted for only 25% of the variation in 2-year seedling heights and 46% of the variation in 8-year heights. Also, the relationship was significant only when provenances A and B were included. When calculated for 42 provenances raised in the same nursery and planted in 1970, or for 25 IUFRO provenances planted in 1972 (LINES, pers comm.), the percentage lammas growth accounted for 59—61% of the variation in 8-year heights. That is, the ability of 2-year old seedlings of provenances to produce lammas growth was a poorer predictor of their future performance than the duration of first-year seedling height growth.

The 16 open-pollinated progenies differing in parent provenance completed 85% of their first-year seedling

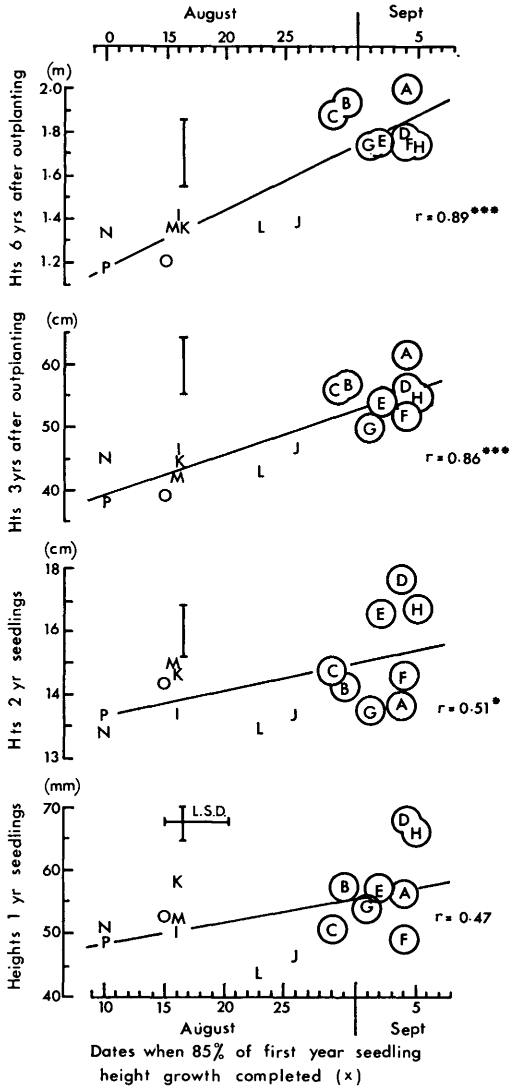

Figure 2. — Relationships, for 16 open-pollinated progenies of *Pinus contorta*, between the dates when first-year seedlings completed 85% of their height growth, and tree heights up to 6 years after outplanting (means of 3 sites, *Table 2*). A, B, C . . . see *Table 3*. See legend to *Fig. 1*.

height growth over a 26-day period. This variation in height growth duration was not significantly related to first-year seedling heights, but accounted for 26% of the variation in second-year seedling heights, 74% of the variation in 5-year heights and 79% of the variation in 8-year heights (*Fig. 2*). There was little increase in the spread of mean progeny heights with age, but in this experiment there was a significant apparent effect of seed weights on first-year seedling heights (r = 0.5) and a small residual or correlated effect to age 8 (r = 0.3). Also, the relationship between seedling height growth duration and 8-year heights was dependent on the inclusion of eight progenies of south coastal parentage (A to H, *Fig. 2*) which grew faster than all the other progenies and became very similar in height by age 8.

The other study on open-pollinated progenies included nine progenies of similar south coastal parentage which differed significantly in 8-year heights. Although their dates of 85% first-year seedling height growth completion spanned only 11 days and variation in this trait accounted for only 9% of the variation in first-year seedling heights, it accounted for 40% of the variation in 2-year seedling heights and 55% and 70% of the variation in 5 and 8-year heights, respectively (*Fig. 3*). This occurred despite the absence of any significant effects of seed weights on progeny heights, and a decrease with age in the relative spread of progeny heights. The relationship between dates of 85% first-year seedling height growth completion and 2-year seedling heights (and hence between 2-year seedling heights and 8-year heights) was not significantly improved by growing the seedlings at an upland site during their second year. The relationship was, in fact, slightly better when the seedlings were grown in a glasshouse.

Seasonal duration of bud development in provenances

During their 7th year after germination the diameters of the apical domes within developing branch buds on contrasting provenances differed markedly during the period July-October (*Fig. 4*), which, according to earlier studies (Cannell and Willett 1975) refected relative differences in the seasonal duration of bud development. Among coastal

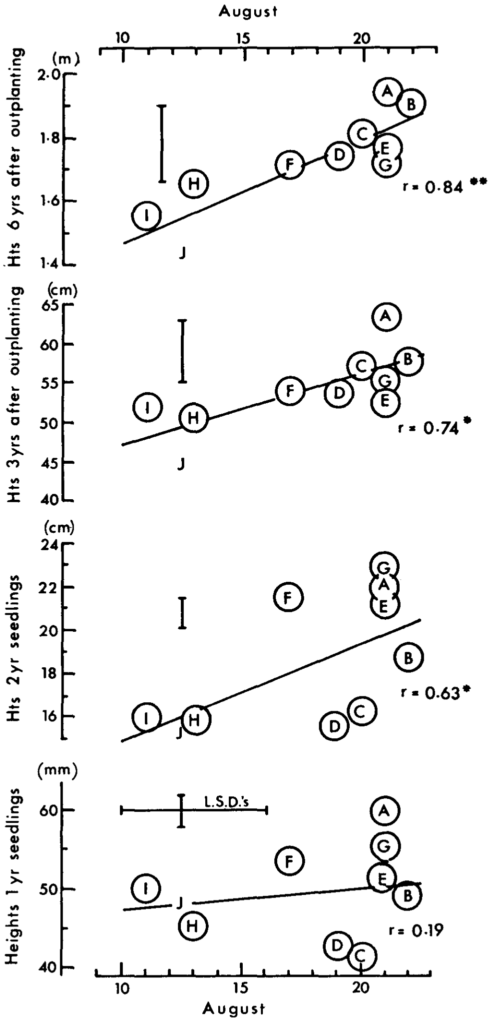

Figure 3. — Relationships, for 10 open-pollinated progenies of *Pinus contorta*, between the dates when first-year seedlings completed 85% of their height growth, and tree heights. Two-year seedling heights are the means for three sites (see materials and methods) and 3 and 6-year heights after outplanting are also the means of 3 sites (see *Table 2*). A, B, C . . . see *Table 3*. Note that all but J are of Washington or Oregon coastal provenance. See legend to *Fig. 1*.

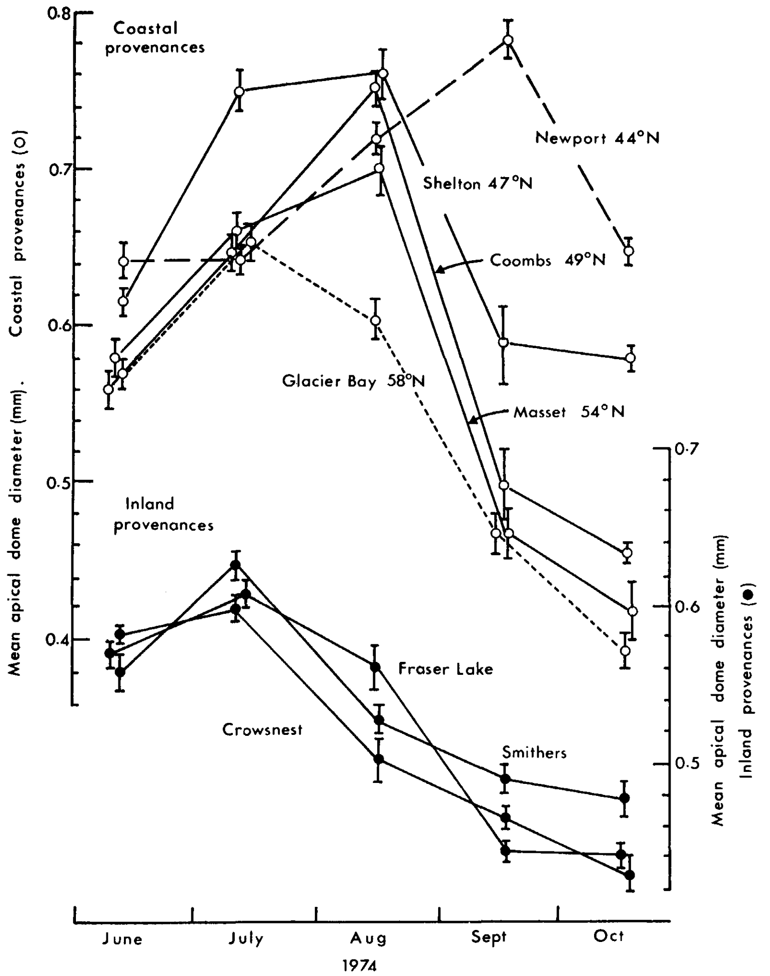

Figure 4. — Seasonal changes in the diameter of the shoot apical domes (meristems) within the terminal buds of first-order branches of 5 coastal and 3 inland provenances of *Pinus contorta* (see *Table 1*) during their fifth year after outplanting in a nursery (7 years after germination). Vertical bars denote ± one S.E..

provenances, the apical domes were larger, and remained larger for longer in the autumn, the further south the seed had been collected (*Fig. 4*). Three inland provenances behaved similarly to an Alaskan coastal provenance, Glacier Bay.

The five coastal provenances were ranked Newport > Shelton > Coombs > Masset > Glacier Bay, in (a) apical dome diameters in September (b) 7-year heights of the experimental trees from which buds were sampled, (c) mean heights of the same provenances at age 6 in the five forest trials (*Table 2*) and (d) the dates of 85% bud-set of first-year seedlings. That is, among these provenances. heights were closely related to the duration of apical meristematic activity which, in turn was correlated with the duration of first-year seedling height growth.

First-year seedling height growth duration and genotype × site interactions

There were significant differences between sites in 8-year heights in all experiments, associated with differences in altitude, soil type and fertilizer treatments (*Table 2*). There were also some significant genotype × site interactions (*Table 2*). This posed two questions: (i) did the relationship between first-year seedling height growth duration and 8-year heights differ between sites, and (ii) were differences in shoot apical growth duration associated with genetic differences in 'stability' in height growth as measured by Finlay-Wilkinson regression coefficients?

(i) In all experiments, the ability to predict differences in 8-year heights was most successful when the trees were planted at sites favouring rapid growth. Thus, considering the 15. provenances in *Fig. 1*, seedling height growth duration accounted for 80% of the variation in 6-year heights at Mabie (the best site) but only 62% at Brendon (the worst site). For the 16 open-pollinated progenies in *Fig. 2*, seedling height growth duration accounted for 81% of the variation in 6-year heights at Shin (the best site) but only 32% at Coed Sarnau. This was true for provenances and for progenies within provenances.

(ii) Finlay-Wilkinson regression coefficients calculated for the 15 provenances across 5 sites (*Table 2*) varied from 0.6 for Wonowon (which performed best relative to other provenances at the poor sites) to 2.0 for Coombs (which performed best relative to other provenances at the favourable sites), and all were significant at $P < 0.05$ with r values in the range 0.89 to 0.97. Over half of the variation in Finlay-Wilkinson regression coefficients was accounted for by dates of first-year seedling bud-set ($r = 0.72$ *Fig. 5*).

The progenies were grown at only 3 sites (*Table 2*) so it was not possible to accurately evaluate their stability in

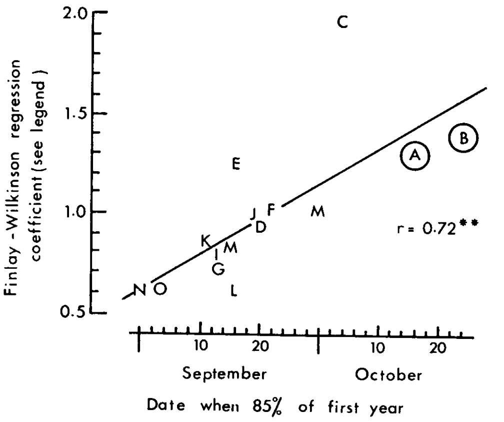

Figure 5. — Relationship between the dates of bud-set of first-year seedlings of 15 provenances of *Pinus contorta* (A, B . . . see *Table 1*) and Finlay-Wilkinson regression coefficients for provenance heights at age 8 (since germination) at 5 sites (*Table 2*). Provenances having greatest height growth potential at favourable sites have coefficients > 1.0, and those with greatest height growth potential at unfavourable sites have coefficients < 1.0 (Finlay and Wilkinson, 1963). Encircled letters denote Washington or Oregon coastal provenances.

8-year heights using Finlay-Wilkinson regression coefficients, because few coefficients were significant at P = 0.05. However, among the 16 progenies, 11 had coefficients in the range 0 to 2.5, and these values were significantly correlated with dates of first-year seedling height growth (r = 0.70), and among the 10 progenies, 9 had coefficients in the range 0 to 2.5, and these were also significantly correlated with dates of first-year seedling height growth (r = 0.80).

Discussion

The data presented here strongly suggests that, in Britain, both the mean height increment, and genotype × site interactions in height increment, of a wide range of *Pinus contorta* provenances and progenies, up to at least age 8 after germination, are closely correlated with the seasonal duration of shoot apical growth, which can be evaluated on first-year seedlings by recording their dates of height growth cessation in the autumn. The strength of the evidence lies in the observations that (a) the above correlations were found for both a wide range of provenances, and for open-pollinated progenies with similar provenance parentage, (b) the correlations between seedling growth duration and provenance or progeny heights improved with age, and (c) differences among provenances in the dates of first-year seedling bud-set were parallelled by differences in their heights and apparent durations of bud development at age 7.

Seedling heights alone are not closely correlated with 8-year heights, because many factors other than dates of bud-set, such as seed weights and times of germination, influence first-year heights. But inherent differences in the seasonal duration of shoot apical growth (presumably reflecting differences in temperature and/or photoperiodic responses) apparently become increasingly important with time, possibly because the effect is accumulative: types with prolonged apical growth each autumn may generate more stem units in their buds than other types, resulting in greater potential height growth, and a faster rate of increase in total foliage surface and tree mass (Cannell 1974). Previous studies showed that differences in the lengths of leaders on 15 provenances of 10-year-old *P. contorta* growing at two sites in upland Britain were closely correlated with numbers of stem units per leader (r = 0.8 to 0.9) (Cannell *et al.*, 1976).

Obviously, it would be unwise to suggest that genetic variation in the performance of a species is centred on one characteristic. The large correlations reported in these studies may occur only within genetic tests that include types with similar ranges of seasonal shoot apical growth duration, and our results may be confined to British upland sites, where Oregon-Washington coastal provenances of *P. contorta* only occasionally suffer severe winter damage. However, it does seem that most genotypes which have substantially shorter periods of shoot apical growth than Oregon-Washington coastal provenances will have a smaller height growth potential on most British sites, and this can be predicted on seedlings by comparing their seasonal height growth duration.

It should be added that the correlations reported here concern only tree heights, they do not include stem form and wind stability which tend to be poorest on provenances which grow rapidly in height (Lines 1980), although this is not necessarily true for progenies. Lastly, inherent differences in the dates of bud-set in the autumn are not always easy to detect: if the seedlings are sown too early in the spring or are grown in warm conditions, they set buds before the period August-October, whereas if they are sown too late all types may stop growing within a few days in response to falling temperatures.

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First-year height growth of southwestern Oregon Douglas-fir in three test environments[1])

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Summary

Douglas-fir seedlings from wind-pollinated seed collected from two trees at each of 36 locations throughout southwestern Oregon were grown in three test environments (growth room, greenhouse, and nursery) to assess environmental influence on genetic variation of first-year height growth.

The 36 populations differed markedly in first-year height growth; the estimated variance among populations was about four times greater than both the estimated family-within-population and population × environment variances.

Regression models showed populations originating from higher elevations and southerly latitudes in the sampled areas grew slower in all test environments. While trends were consistent in all environments, the model for the nursery was not as efficient in accounting for variation in population means. This may have resulted from poorer differentiation among populations owing to the shorter nursery growing season

Key words: Douglas-fir, genotype × environment interaction, clinal models, genocology.

Zusammenfassung

Douglasien-Sämlinge (*Pseudotsuga menziesii* Mirb. Franco) aus frei abgeblühten Samen, die von je 2 Bäumen an 36 Orten im südwestlichen Oregon stammen, wurden an drei Standorten (Klimaraum, Gewächshaus und Baumschule) angezogen, um den Einfluß der Umwelt auf die genetische Variation der Höhe im Alter 1 abzuschätzen.

Die 36 Populationen differierten markant in diesem Kriterium, die geschätzte Varianz zwischen den Populationen war etwa viermal größer als die Varianzen der Familien innerhalb der Populationen sowie zwischen den Interaktionen von Population und Umwelt.

Regressionsmodelle zeigten, daß Populationen, die aus höheren Lagen oder südlicheren Gebieten stammten, an allen Orten langsamer wuchsen. Während Trends an allen Versuchsorten vorhanden waren, war das Modell für die Baumschule nicht effizient genug, um die Varianten der Populationsmittel zu berechnen. Dies mag aus einer geringeren Differenzierung zwischen Populationen während der kürzeren Baumschul-Wachstumsperiode resultieren.

Introduction

Many studies have reported geographic variation in juvenile height growth of coastal Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco). Most of these have sampled provenances from the western portions of British Columbia, Washington, Oregon, (Campbell and Sorensen 1978, Rowe and Ching 1973) or California (Griffin and Ching 1977, Sweet 1965). Because southern Oregon, an important timber-producing area, has received less attention, we undertook a regional study there in cooperation with the Bureau of Land Management to investigate the patterns of genetic variation in Douglas-fir.

Campbell and Sorensen (1978) point out that studies to reveal and characterize adaptive genetic variation among plant populations should be initially attempted in environments (common gardens) with high resolution. By reducing environmental variation and by choosing test environments which discriminate among populations, we can better discern the patterns associated with population differences. For example, an environment with long photoperiods will tend to differentiate among populations which do and do not respond to such periods. Because genetic expression can vary in different test environments (genotype × environment interaction), more than one is necessary. We report results of an experiment examining genetic variation in

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