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Provenance Differences in Pacific Coast Douglas Fir

1. Seed and Seedling Characteristics

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1. Introduction

Many exotic species of value to New Zealand forestry have a wide natural distribution, and consequently provenance trials form an important part of this country's programme for tree improvement research. Next to Pinus radiata Douglas fir is New Zealand's most important exotic tree species, and its provenances are being quite intensively investigated. THULIN (14) detailed the existing knowledge of seed sources of New Zealand Douglas fir plantations and described steps which have been taken to establish provenance trials in this species. Among these was the sending, in 1956, of an officer to western North America to collect seed for trial purposes. The collections made included 30 seedlots of Douglas fir which have since been sown, raised in the nursery, and established in field trials. These lots have also been the subject of seed investigations and replicated nursery measurements; it is with the latter trials that this paper is concerned.

The importance 09 early measurements and observations is twofold. It is obviously important, in examining young trials, to know with some certainty the likelihood of early neight relationships changing with age. The literature does not throw much light on this question, and such information can 'be obtained for any species only if early measurements have 'been made. Secondly, it is important to be able to verify the origin of seed to be used for commercial establishment, to ensure that large areas are not planted with inferior provenances. Purchasers of seed are very dependent on the bonesty of their suppliers, and even where this is of a high order, mistakes are possible. It should be possible, by a combined study of seed and seedling characteristics, to check fairly closely the origin of any provenance, but this can be done only if adequate and reliable data are available on the expected behaviour of provenances.

2. Review of Relevant Literature

Reviewers of European literature on provenance trials of Douglas fir, e. g. JAHN (8), stress the extent to which the growth of this species is influenced by features of climate and site. Many provenances which have proved well suited to the coastal climates in the United States, and which are expected to suit New Zealand conditions, have failed completely in Europe because af spring frost damage and associated infection by the fungus Rhabdocline pseudotsugae (e. g. VEEN, 16). For this reason current European provenance research in this species is of less interest to New Zealand than that being carried out in North America.

Variations in seed size or seed weight due to provenance have been reported for several species, and these have been correlated with seed source, (e. g. 9, 15): no reference is known to any work correlating seed weight of Douglas fir with seed source, although ALLEN (1) has been able to separate coastal from interior seed in this species by differences in its gross morphology. Seed-weight differences caused by age, not provenance, have however been reported by J. W. DUFFIELD (1964, pers. comm.) who states that in the Pacific north-west, old trees of Douglas fir have smaller cones and lighter seed than young trees.

Only one reference (3), is known to have been published in which heights of Douglas fir in the nursery were measured in a climate comparable with that of New Zealand. CHING and BEVER examined 14 provenances from British Columbia, Washington, and Oregon. They raised seedlings at Corvallis in Oregon and reported significant height differences between provenances, those from higher latitudes being generally taller than those from lower latitudes. No correlation was found between seedling height and altitude af seed source. MUNGER and MORRIS (11) reported on the height growth of 13 provenances, 16 years after planting on several sites in Washington and Oregon. Some of these provenances showed a marked interaction with site, thus making difficult any general correlation between height growth and climate of seed source.

The phenology of Douglas fir has been more widely studied. The genetic component was examined by MORRIS, SILEN and IRGENS-MOLLER (10), who showed that the relative order of bud burst remained constant for many years, implying a high degree of genetic control. SILEN (12), working with grafted material, also found a high genetic component in time of bud burst, but WALTERS and SOOS (17) found more variation among individual trees in this feature.

MUNGER and MORRIS (11), assessing a number of provenances from the Pacific north-west on two sites in Oregon, found that the trees with earliest bud burst in spring came from areas with warm spring days and nights, such as low-altitude plains and wide valleys. Those that flushed next came from high-altitude areas with cold spring days and nights, while the last provenances to flush came from narrow valleys and foothill areas where cold-air drainage gave cold nights following warm spring days. CHING and

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Bever (3) also found a wide variation between provenances in order of bud burst, but were unable to relate this satisfactorily to climate. Irgens-Moller (6) studied differences in the date on which growth commenced, and also investigated the effect of photoperiod on bud burst. He reported that although the start of spring growth in high-altitude provenances could be altered photoperiodically, this was not possible with low-altitude lots.

Unfortunately the criterion for assessment of bud burst has varied; for example, whereas Irgens-Moller (6) recorded the date when the first bud burst, regardless of its position on the tree (in most cases this was the terminal), Ching and Bever (3) assessed the date of terminal bud burst only. The position is further confused by Walters and Soos' (17) report that in older trees, lateral buds normally begin to grow before the terminal. Regardless of the means of assessment employed, however, no significant relationship has been reported by any author between time of bud burst and amount of annual growth in Douglas fir.

Date of cessation of annual height growth in provenances has been less examined than date of bud burst, presumably because it is more difficult to measure. Irgens-Moller (7) assessed this feature by weekly height measurements, and also by counting the percentage of plants with dormant buds on a given date. He found that the two methods gave comparable results. High-altitude and inland provenances stopped growing earlier than coastal provenances, and plants which stopped growing early attained less height than those which continued to grow late in the season. Ching and Bever (3) assessed the percentage of bud set in their 14 provenances at weekly intervals. It is difficult to correlate their results with geography or climate of the seed source, and there was little apparent relationship between height growth and total length of growing season.

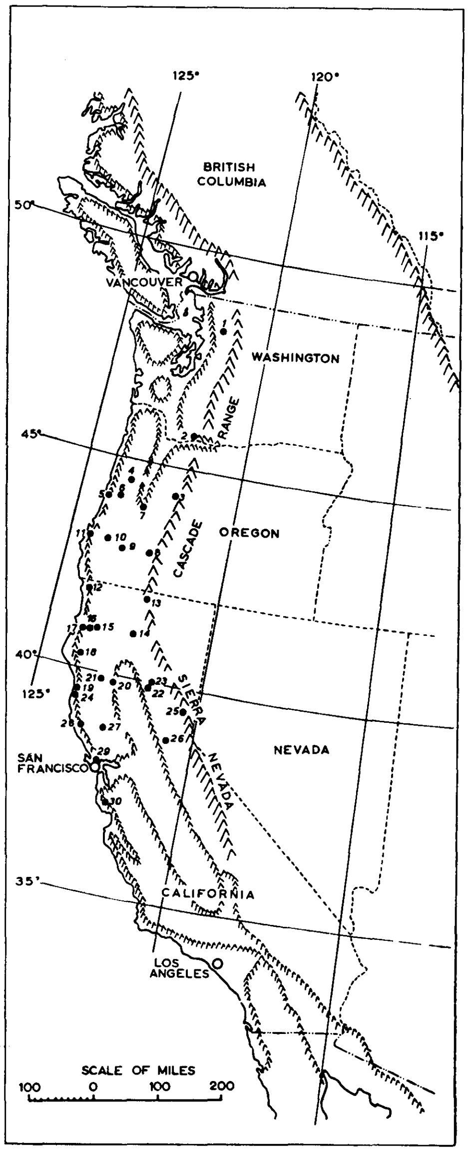

Fig. 1. — **Pacific Coast of North America, showing origin of provenances of Douglas fir.**

3. Material

The investigation concerned 30 provenances from North America and two from plantations in New Zealand, the latter being representative of routine seed collection for normal planting operations. Data on the origin of the provenances are presented in *Table 1,* together with such climatic and geographic data as are referred to in the text. Climatic data were obtained from the United States Weather Bureau records. The values for each provenance were taken from the nearest representative climatic station of comparable altitude; and, where seed source and climatic station differed in height by more than 300 ft, a correction factor was applied to the data (see *Table 1*). It is clear from *Fig. 1,* which illustrates the location of the provenances, that only the portion of the species range from west of the Cascade and Sierra Nevada ranges has been sampled. In almost every case, cones were collected from 10 trees of less than 50 years of age. Cones from individual trees were not kept separate, but were bulked to provide one representative lot for each provenance. Collections were made in 1956 except for one New Zealand lot which was collected in 1955.

In addition to these, data from a further 14 provenances (those reported on by Ching and Bever) have been examined in one part of this paper. Their collection was made in British Columbia, Washington, and Oregon between 1954 and 1956, 10 out of the 14 lots being collected in 1956. Full data on origin are given by Ching and Bever (3).

4. Experimental Design

Nursery studies were carried out at the Forest Research Institute nursery. Sufficient seed for these experiments was available in only 23 of the 30 North American provenances, and in the two New Zealand lots. A randomised block design was chosen, with three replications. Each replication occupied a single nursery bed, 3 ft wide, across which the seed lots were sown in individual bands 4 in. wide; each seed lot in a replication thus occupied a strip 1 sq ft in area. Adjacent bands were separated by a gap of 6 in. Sowing density was intended to aim at 50 seedlings per sq ft, to be evenly thinned to 30 per sq ft at the end of the first growing season. All seed was stratified at between 2^0 C and 3^0 C for four weeks prior to sowing, which was done in the spring of 1960.

5. Assessments

51. Seed Weight

511. Method

New Zealand Forest Service collection. The seed was cleaned by combined air current and vibrating screen to give an average of 94.3% full seeds in each seed lot, with a standard error of 0.84%. Five samples, each of 100 seeds,

Table 1. — Seed-Source Data.

Provenance no.	Origin	Latitude	Longitude	Altitude (ft)	Nearest representative weather station	Length of frost free growing season (days) [1]	Mean date of last spring frost [2]	Mean date of first autumn frost [2]	Mean temperature of coldest month (°F) [3]	Standard deviation of date of last spring frost (over 12 years) [4]
1	Darrington R. S., Washington	48° 15' N	121° 35' W	550	Darrington	151	12 May	10 Oct	34	20.86
2	Wind River, Washington	45° 48' N	121° 56' W	1100	Wind River	135	17 May	29 Sep	32	16.03
3	Willamette N. F., Oregon	44° 25' N	121° 58' W	3300	McKenzie Bridge R. S.	53	19 Jun	11 Aug	35	17.52
4	Suislaw N. F., Oregon	44° 28' N	123° 30' W	1300	Corvallis	169	28 Apr	14 Oct	37	13.73
5	Florence, Oregon	43° 58' N	124° 06' W	25	Canary	186	1 May	2 Nov	43	14.64
6	Deadwood, Oregon	44° 06' N	123° 45' W	250	Canary	186	1 May	2 Nov	43	14.64
7	Dexter, Oregon	43° 55' N	122° 58' W	700	Leaburg	208	9 Apr	11 Nov	40	13.62
8	Union Creek, Oregon	42° 54' N	122° 26' W	3350	Prospect	75	20 Jun	3 Sep	32	11.75
9	Rogue River N. F., Oregon	42° 54' N	123° 15' W	1000	Riddle	169	27 Apr	12 Oct	39	12.76
10	Siskiyou N. F., Oregon	43° 03' N	123° 51' W	500	Powers	187	25 Apr	28 Oct	42	21.71
11	Fourmile, Oregon	43° 02' N	124° 25' W	50	Bandon	256	2 Mar	13 Nov	44	12.53
12	Berteleda, California	41° 48' N	124° 04' W	300	Crescent City	254	18 Mar	27 Nov	44	26.83
13	Klamath N. F., California	41° 53' N	122° 12' W	4500	Mt. Hebron R. S.	30	26 Jun	26 Jul	27	3.58
14	Lamoine, California	40° 59' N	122° 26' W	1600	Lakeshore	183	25 Apr	25 Oct	39	17.11
15	Willow Creek, California	40° 57' N	123° 39' W	600	China Flat	247	7 Mar	9 Nov	42	29.18
16	Six Rivers, California	40° 55' N	123° 48' W	1600	China Flat	217	22 Mar	25 Oct	39	29.18
17	Mad River, California	40° 55' N	123° 55' W	700	China Flat	247	7 Mar	9 Nov	42	29.18
18	Miranda, California	40° 14' N	123° 52' W	1700	Alder Point	165	25 Apr	7 Oct	40	25.40
19	Dehaven, California	39° 36' N	123° 48' W	500	Fort Bragg	281	26 Feb	4 Dec	46	31.03
20	Mendocino N. F., California	39° 50' N	123° 03' W	2500	Covelo	142	12 May	1 Oct	36	14.86
21	Mendocino N. F., California	39° 51' N	123° 01' W	4500	Covelo	78	12 Jun	29 Aug	31	14.86
22	Magalia, California	39° 51' N	123° 36' W	2500	De Sabla	187	30 Apr	3 Nov	40	18.70
23	Inskip, California	39° 59' N	121° 32' W	4650	Quincy	28	21 Jun	19 Jul	29	13.99
24	Jackson S. F., California	39° 21' N	123° 43' W	500	Fort Bragg	281	26 Feb	4 Dec	46	30.90
25	Tahoe N. F., California	39° 28' N	120° 28' W	4000	Blue Canyon	184	3 May	3 Nov	40	12.87
26	Placerville, California	38° 45' N	120° 45' W	3000	Placerville	137	20 May	4 Oct	37	26.53
27	Middletown, California	38° 46' N	122° 41' W	1500	Clearlake Park	205	8 Apr	30 Oct	42	16.86
28	Stewart Point, California	38° 39' N	123° 22' W	500	Fort Ross	321	1 Feb	19 Dec	49	33.04
29	Stinson Beach, California	37° 53' N	122° 37' W	800	San Francisco	334	18 Jan	18 Dec	48	19.14
30	N. W. of Santa Cruz, California	37° 05' N	122° 15' W	1000	Ben Lomond	191	15 Apr	23 Oct	44	28.35
31	Kaingaroa Forest, New Zealand	38° 24' S	176° 34' E	1785	Kaingaroa	182	16 Oct	16 Apr	41	22.67
32	Forest Research Institute grounds, Rotorua, N. Z.	38° 10' S	176° 16' E	1006	Rotorua	250	11 Sep	19 May	44	21.66

[1]) Frost level is 32° F. Where altitude of provenance and of weather station differ by more than 300 ft, a correction was applied of the order of 30 days per 1000 ft.

[2]) Where altitude of provenance and of weather station differ by more than 300 ft, a correction was made of the order of 15 days per 1000 ft.

[3]) Where altitude of provenance and of weather station differ by more than 300 ft, a correction was made of the order of 3° F per 1000 ft. All figures have been rounded off to the nearest degree.

[4]) No correction has been made for differences in altitude between provenance and weather station.

were then counted from each provenance and weighed. An analysis of variance was calculated on the sample data, and the mean seed weight in mg was calculated for each seed lot.

Ching and Bever's collection. Ching and Bever (3) in their *Table 2* gave data on the number of seeds per gram in each of 14 seed lots which had been cleaned to give a cutting test of at least 85% sound seed. These figures were converted to individual seed weights in mg.

512. Results

Mean values for the New Zealand Forest Service collection and values converted from Ching and Bever (3) are presented in *Table 2*. The former range from 9.16 mg to 24.64 mg and the latter from 10.00 mg to 16.95 mg. Analysis of the data from the New Zealand Forest Service collection showed variance between seed lots to be significantly greater (0.1% level) than that between samples. The least difference for significance (calculated by Duncan's multiple range test [4] using a fixed rank difference of 10) is given in *Table 2* at the 5% and 1% levels.

513. Relationship between seed weight and climate and geography of seed source

Correlation analyses were carried out between seed weight of the New Zealand collected provenances from North America, and features of the climate and geography of their seed source. The highest correlations obtained were as follows:

Seed weight and altitude of seed source:

$$r = 0.7797, \text{ significant at } 0.1\%.$$

Seed weight and length of frost-free growing season at seed source:

$$r = -0.5977, \text{ significant at } 0.1\%.$$

Seed weight and mean temperature of coldest month at seed source:

$$r = -0.5775, \text{ significant at } 0.1\%.$$

Each correlation involved 28 degrees of freedom.

The correlation between seed weight and altitude of seed source was considerably higher than that between seed weight and features representative of temperature regime

Table 2. — Assessment Data.

Provenance no.		1. Mean seed weight (mg)	2. Mean height (in.) Age 1	3. Age 2	4. Median date of lateral bud burst	5. Median date of terminal bud burst	6. Lag between lateral and terminal bud burst (days)	7. Mean no. of trees (out of 15) with 2 growth flushes in 1962	8. Mean no. of trees (out of 15) with 3 growth flushes in 1962	9. Percentage of trees with terminal bud set on 5. 5. 1961	10. Mean no. of trees (out of 15) with terminal bud set on 21. 1. 1962
1		11.45	2.13	13.4	15 Oct	23 Oct	8	13.0	1.0	48	11.2
2		13.32	2.89	14.1	24 Sept	8 Oct	14	12.2	0.4	85	12.6
3		12.92									
4		12.97	2.54	17.8	2 Oct	10 Oct	8	9.8	0.7	27	8.8
5		10.09									
6		12.54	2.82	18.0	2 Oct	17 Oct	16	14.0	0	27	14.3
7		13.23									
8		17.14	1.79	14.0	2 Oct	7 Oct	5	10.5	0.4	92	11.5
9		14.04	3.01	15.5	3 Oct	11 Oct	8	11.7	0.3	78	12.3
10		11.92	3.11	17.4	3 Oct	15 Oct	12	13.6	1.4	20	9.5
11		9.16	3.60	21.1	28 Sept	13 Oct	15	13.3	0.4	27	10.9
12		10.74	3.14	21.6	25 Sept	13 Oct	18	12.0	1.7	3	2.3
13		15.04	1.41	5.7	12 Oct	16 Oct	4	8.4	0.9	87	13.1
14		18.61	2.22	11.8	23 Sept	2 Oct	8	11.2	0.3	76	13.1
15		13.93	2.91	15.9	30 Sept	12 Oct	12	14.1	0	33	9.6
16		13.27	3.70	19.2	7 Oct	20 Oct	13	9.4	0	4	6.9
17		12.62	3.48	20.3	28 Sept	13 Oct	15	12.6	1.7	6	8.9
18		13.11	4.29	22.3	22 Sept	3 Oct	11	12.3	0.3	16	10.2
19		10.65	5.46	24.8	24 Sept	10 Oct	16	12.3	0	7	9.7
20		15.63	3.40	18.6	26 Sept	9 Oct	13	12.0	0.3	20	10.6
21		18.67									
22		19.75	2.56	13.0	26 Sept	8 Oct	12	13.0	1.4	43	10.2
23		24.64									
24		12.25	5.18	24.5	27 Sept	20 Oct	23	12.9	1.0	7	7.5
25		17.80									
26		18.57	4.73	16.5	23 Sept	24 Sept	1	13.0	0	87	13.6
27		17.31	3.98	17.3	21 Sept	30 Sept	9	10.3	1.9	66	7.2
28		11.04	5.17	24.5	28 Sept	18 Oct	20	11.6	0.3	9	9.9
29		10.62									
30		13.96	8.22	30.2	24 Sept	8 Oct	14	8.5	0	19	10.2
31			3.72	19.0	6 Oct	19 Oct	13	12.9	0.4	34	9.5
32			3.64	19.0	2 Oct	13 Oct	11	14.0	0	61	13.2
					Values for least significant difference at 5% and 1%						
					(days)	(days)	(days)				
	5%	0.58	1.2	4.8	6	7	8	N. S.	N. S.	S.	4.4
	1%	0.73	1.6	6.3	8	9	11	N. S.	N. S.	S.	5.8
Ching and Bever's Provenances											
A		10.00									
B		10.87									
C		15.38									
D		10.99									
G		12.50									
H		13.33									
I		13.16									
J		10.20									
K		16.95									
L		12.20									
M		10.20									
N		13.89									
O		12.99									
P		14.92									

Values in column 1, provenances 1 to 30, represent the mean of 5 samples. Values in columns 2 to 10 represent the mean of 3 replications. Column 6 was not calculated directly from the difference between column 5 and column 4.

S. = significant
N. S. = not significant

at the seed source. Provenances from higher altitudes had heavier seeds than those from lower altitudes.

Climatic data were not available for Ching and Bever's seed lots, but the correlation coefficent between seed weight and mean altitude of seed source for their 14 provenances was 0.6900, significant at 1% for 12 degrees of freedom. Regressions of seed weight of the New Zealand collected provenances from North America, and of Ching and Bever's seed lots, on altitude of their seed sources are shown in *Figs. 2 A and 2 B* respectively. A t test shows that neither the values of the intercept nor those of the gradient in the regressions differ significantly from one another ($t_a = 0.72$ and $t_b = 0.25$ for 40 df), and the regression equation for the combined data is seed weight (mg) = 10.74 + 0.00179 altitude (ft).

52. Height Growth in the Nursery

521. Method

Every seedling was measured in the winter of 1961 and again in the winter of 1962, at which times they were aged 1 and 2 years respectively. At age 1, the number of surviving seedlings averaged 50 per replicate with a standard error of 3. At age 2, after thinning, the average number of seedlings was 26 per replicate with a standard error of 1 One-year heights were measured to the nearest 0.5 inch, and two-year heights to the nearest 1 inch.

522. Results

At age 1, provenance mean heights ranged from 1.41 in. to 8.22 in., while at age 2 the range was from 5.7 in. to 30.2 in.: in each year differences between provenances were

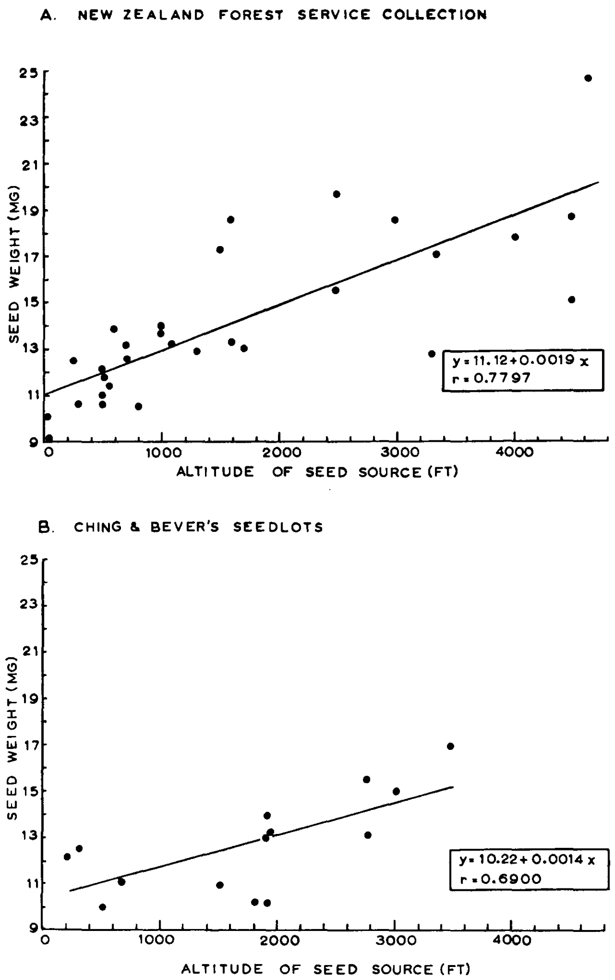

Fig. 2. — Regression of seed weight on altitude of seed source.

significant at the 0.1% level. Mean height values at both age 1 and age 2 are presented in *Table 2*, and the 2-year heights are shown photographically in *Fig. 3*. The least difference for significance calculated by DUNCAN's test (4) using a fixed rank difference of 10 is given at the 5% and 1% levels in *Table 2*.

A correlation analysis calculated between the height measurements at age 1 and age 2 gave r = 0.8715, which is significant at 0.1% for 23 degrees of freedom.

523. Relationship between 2-year nursery height and climate and geography of seed source

Correlation analyses were carried out between 2-year height of the provenances collected in North America, and features of the climate and geography of their seed source. The resulting correlation coefficients, all based on 21 degrees of freedom, illustrate some of the more significant relationships obtained.

2-year height and mean temperature of coldest month at seed source:

r = 0.7867, significant at 0.1%.

2-year height and length of frost-free growing season at seed source:

r = 0.6965, significant at 0.1%.

2-year height and date of last spring frost at seed source:

r = −0.6828, significant at 0.1%.

2-year height and date of first autumn frost at seed source:

r = 0.6796, significant at 0.1%.

2-year height and altitude of seed source:

r = −0.5858, significant at 1%.

2-year height and latitude of seed source:

r = −0.4883, significant at 5%.

Correlations with mean annual rainfall, growing-season rainfall, mean annual temperature, and mean temperature of the hottest month gave values lower than those quoted.

It is clear that provenances originating from milder climates with longer growing seasons in North America were taller at age 2 in the Forest Research Institute nursery than were those from more severe climates. In *Fig. 4*, regressions are shown of 2-year height in the nursery on (a) mean temperature of coldest month, (b) length of annual frost-free growing season, and (c) altitude of seed source. In each case it is evident that one provenance (No. 30) falls some distance off the regression line. The possible significance of this is discussed later in the paper.

53. Bud Burst in Spring

531. Method

In 1961, at the end of the seedlings' first growing season, 15 trees were randomly selected in each replicate and marked for subsequent identification. The following spring the marked trees were observed at two-day intervals, and a record was made of (a) date of terminal bud burst, and (b) date of burst of the first lateral bud. For purposes of the study, bud burst was defined as commencing when the first new needles emerged from the unfolding bud scales.

532. Results

Examination of the data showed the pattern of bud burst to be slightly skewed owing to delayed flushing of some buds that had been damaged by Tortricid insects. Because of this, the median date of bud burst was selected for analysis of data in preference to the mean. Median dates of both

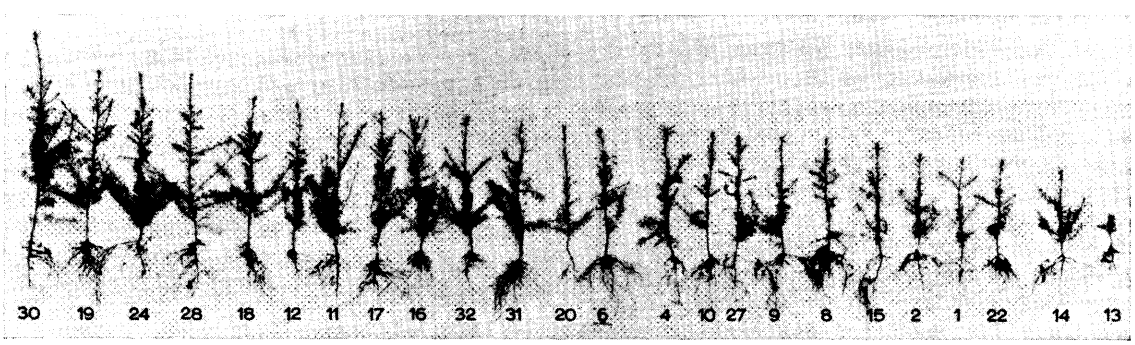

Fig. 3. — Two-year heights. — Each tree photographed represents the mean height of its provenance at age 2. Provenance 26 is not shown.

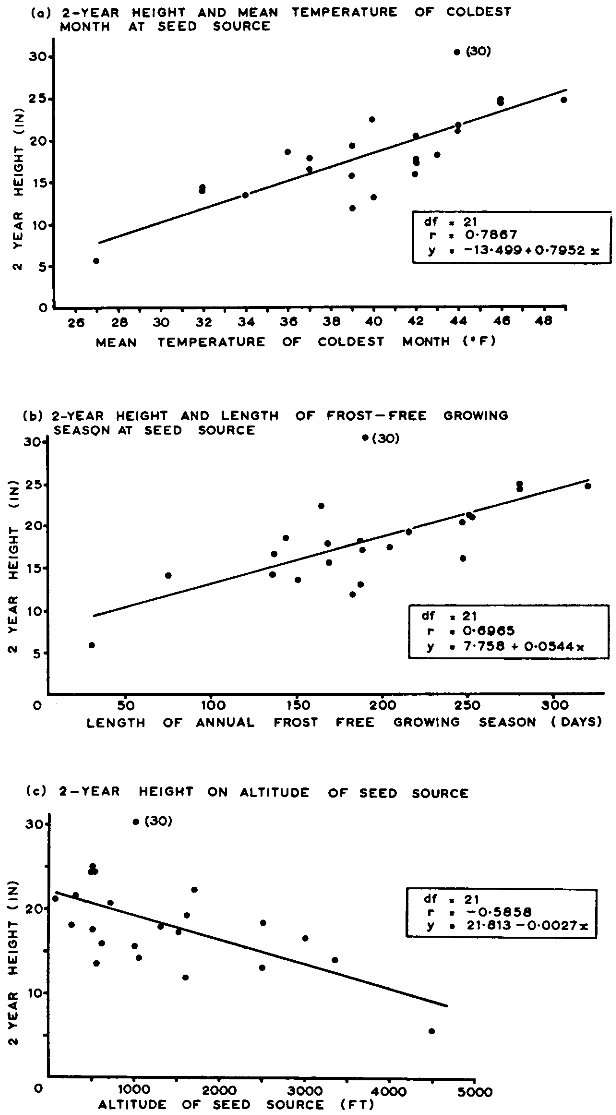

Fig. 4. — Regressions of two-year nursery height for 23 provenances.

lateral and terminal bud burst are presented in *Table 2:* differences between provenances were marked, and in every case the date of burst of the first lateral bud was earlier than that of the terminal bud. The time interval between lateral and terminal bud burst was also examined, and was found to range from 1 to 23 days according to provenance. These values also are presented in *Table 2.*

Analyses of variance were calculated using lateral and terminal bud burst data, and also data for time lag between lateral and terminal bud burst. In all cases differences between provenances were significant at the 0.1% level. Values for least significant difference at the 5% and 1% level have been calculated using DUNCAN's test (4) with a fixed rank difference of 10. These values are presented in *Table 2.*

533. Relationship between bud burst and climate and geography of seed source

Neither the average date of terminal bud burst in the provenances, nor that of lateral bud burst, showed any strong correlation with climate or geography of the seed source. The length of the time lag between lateral and terminal bud burst in each provenance, however, was strongly related to seed-source data, as is shown by the following correlations. These relate time lag between lateral and terminal bud burst in the provenances collected in North America to:

(i) Length of frost-free growing season at the seed source:

$r = 0.7863$, significant at 0.1%.

(ii) Date of last spring frost at the seed source:

$r = -0.7647$, significant at 0.1%.

(iii) Mean temperature of the coldest month at the seed source:

$r = 0.7331$, significant at 0.1%.

(iv) Altitude of seed source:

$r = -0.6980$, significant at 0.1%.

21 degrees of freedom were involved in all correlations.

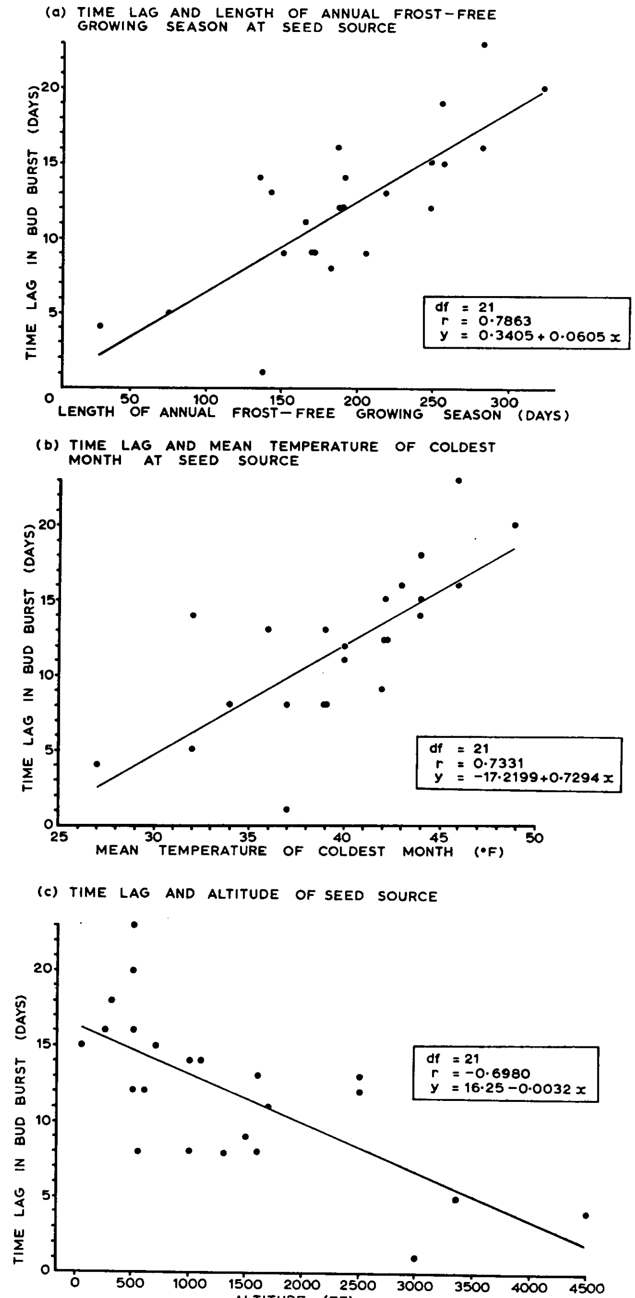

Fig. 5. — Regressions of time lag between lateral and terminal bud-burst for 23 provenances.

The correlations show that provenances with a long time interval between lateral and terminal bud burst came from milder climates than those with a short time interval. *Fig. 5* illustrates regressions between time lag in bud burst at the start of the second growing season in the nursery and (a) length of annual frost-free growing season, (b) mean temperature of coldest month, and (c) altitude of seed source.

54. Seasonal Growth Patterns

In the nursery, seedlings of Douglas fir frequently make two and sometimes three distinct flushes of growth in a year, each separated by a resting bud. The number of these growth flushes occurring in each provenance during its second growing season was examined.

541. Method

The 15 sample trees in each replicate which were assessed for spring bud burst were examined weekly during the second growing season. Record was made of the presence or absence of a terminal bud, and from these data figures were extracted on the number of growth flushes made during the growing season by each seedling.

542. Results

The mean number of trees per provenance having two and three growth flushes respectively during the growing season is shown in *Table 2.* An analysis of variance indicated that differences between provenances were not significant, either in the number of trees flushing twice, or in the number flushing three times. Over the whole trial 79.6% of the trees assessed made two separate flushes of growth, and 4% of the trees flushed three times.

55. Bud Setting

Data on the relative order of terminal-bud formation of the different provenances were obtained at the end of both the first and second growing seasons.

551. Method

On two dates towards the end of the first growing season (5 April and 5 May 1961) a count was made of the number of seedlings per provenance with clearly defined terminal buds. Every tree in the trial was assessed (an average of 50 per replicate with a standard error of 3), and the data were expressed as a percentage.

Similarly, counts were made on two dates towards the end of the second growing season (21 January and 7 February 1962). In this case, however, only the 15 sample trees per replicate whose date of bud burst had been recorded were assessed. In both years more than 98% of the buds recorded were overwintering buds which did not burst again until the following spring.

552. Results

First growing season. The relationship between data from the two assessment dates was tested by a correlation analysis. The correlation coefficient r is 0.8840, significant at 0.1% for 23 degrees of freedom. As a result of this close relationship, the decision was made to select one set of data at random to represent bud set at age 1. These values (those of 5 May) are presented in *Table 2.* Analysis of variance on angularly transformed data showed differences between provenances to be significant at the 0.1% level. The percentage of trees per provenance with terminal buds on 5 May ranged from 3 to 92.

Second growing season. The relationship between data from the two assessment dates was tested by correlation analysis; r equalled 0.9479, significant at 0.1% for 23 degrees of freedom. Based on this close relationship, the decision was again made to select one set of data at random to represent bud set at age 2. The mean number of trees per provenance with a terminal bud on this date (21 January) ranged from 2.3 to 14.3 out of 15, and an analysis of variance showed these differences to be significant at the 0.1% level. Values for individual provenances are presented in *Table 2,* together with values for the least significant difference calculated at the 5% and 1% level by DUNCAN's test (4) using a fixed rank difference of 10.

553. Relationship between bud setting at the end of the first and second growing seasons

A correlation analysis was calculated between the number of trees per provenance with terminal buds on 5 May 1961 and on 21 January 1962. The correlation coefficient r was 0.5895, which is significant at 1% for 23 degrees of freedom. That is, approximately 35% of the variation in oder of bud set at the end of the second growing season was related to that at the end of the first season.

554. Relationship between terminal bud setting at the end of the second growing season and climate of the seed source

Correlation analysis showed a significant relationship between time of bud setting at the end of the second growing season, and temperature regime at the seed source. This is illustrated by the following coefficients, calculated between number of trees with terminal buds in the nursery on 21 January 1962, and:

(i) Length of frost-free growing season at seed source: $r = -0.5227$, significant at 1%.

(ii) Date of first autumn frost at seed source: $r = -0.4968$, significant at 2%.

(iii) Mean temperature of coldest month at seed source: $r = -0.4384$, significant at 5%.

In all cases the correlations involved 21 degrees of freedom, and only the provenances collected in North America were included.

The correlations show that provenances from warmer climates with a longer growing season were later in forming terminal buds in New Zealand than were provenances from colder climates.

56. Relationship between Phenology and and Height Growth

It is logical to examine the relationship between the amount of height growth made in any one year by a provenance, and the length of time for which the trees grew in that year. In this experiment, the length of growing season in the nursery could not be measured directly for each provenance, but it was possible to relate height growth during the second year to other phenological features. Correlation analyses, each involving 23 degrees of freedom, were calculated with nursery data as follows:

(i) Between second-year height growth and median date of terminal bud burst in second year:

$r = 0.1565$, not significant.

(ii) Between second-year height growth and number of trees making two flushes of growth during second year:

$r = 0.0850$, not significant.

(iii) Between second-year height growth and number of trees making three flushes of growth during second year:

$r = -0.0433$, not significant.

(iv) Between second-year height growth and number of trees with terminal buds set at end of second growing season (21 Jan 1962):

$r = -0.4591$, significant at 5%.

The results show that date of terminal bud burst was less related to annual height growth than was the date of terminal bud set at the end of the growing season; the effect of the latter was significant at the 5% level. The average number of growth flushes made by the provenances during their second year was not significantly related to the height growth they made during that year.

6. Discussion

61. *Seed Weight*

The positive correlation shown between seed weight and altitude is contrary to that found by Mirov *et al.* (9) for *Pinus ponderosa* in the Pacific north-west. It does, however, parallel that found for larch in Europe (2, 5, 15), although the latter studies involved separate populations rather than a single cline. The difference between ponderosa pine and Douglas fir in seed-size relationships is unexpected and perhaps requires further investigation: it does appear, however, to be a genuine species difference. While the ponderosa pine data of Mirov *et al.* were based on 729 individual trees, the seeds from individual trees in each provenance were not kept separate in the present study of Douglas fir. It is unlikely, however, that this bulking of seed has affected the results in any way; and the reliability of the data is emphasised by the strong relationship between the seed weight/altitude regression from the New Zealand Forest Service collection and that from Ching and Bever's collection.

62. *Nursery Height in New Zealand*

The high correlation between 1- and 2-year heights of the provenances in the nursery indicates that there was little change in their height rankings during the second year. However, as it is likely that 1-year heights were influenced to some extent by variables such as rate of germination, 2-year heights were chosen for purposes of correlation with climatic and geographic features of the seed source.

The strong correlations between 2-year nursery height in New Zealand and measures of temperature regime at the seed source should be of value in indicating the type of adaptation to climate that may have occurred in Douglas fir. Most features of temperature climate are strongly interrelated, however, and thus the existence of a significant correlation between height growth and any one measure of temperature is no indication that this measure has in itself been of importance in natural selection. Neither is there any certainty that the feature of temperature regime showing the highest correlation with height growth of the provenances has had direct effect in selection. The applicaiton of corrected climatic data from the nearest weather station cannot, in this experiment, give a sufficiently precise picture of the climate at the seed source to enable soundly based deductions to be made on the exact mechanism through which selection pressure has acted. The application of more refined statistical techniques would therefore add nothing to the information available, and they have not been used.

While Ching and Bever (3) found no relationship between 2-year seedling height and altitude of seed source, they did report a positive correlation between 2-year height and latitude of seed source. This contrasts with the significant negative correlation obtained in this paper between 2-year heights in New Zealand, and both altitude and latitude of the seed source. The reason for this disagreement is uncertain, but it may indicate an interaction between provenance and site at Corvallis which did not occur in the milder climate of Rotorua.

The negative correlation shown in this paper between 2-year height in New Zealand and altitude of seed source contrasts with the positive correlation between seed weight and altitude of seed source. This suggests that seed weight should itself be negatively correlated with 2-year nursery height: the correlation coefficient r equals -0.5780, which is significant at 1% for 21 degrees of freedom. Such a relationship is contrary to that found in many other conifers and is obviously not a causal one. The observed effect almost certainly represents a confounding of direct effects of seed size on early growth, with provenance effects working in the opposite direction. A comparable finding was reported by Genys (5) for European larch.

The regressions in *Fig. 4* furnish good evidence of the clinal nature of the variation of Douglas fir from west of the Cascade and Sierra Nevada ranges. The only provenance which falls some distance off the regression lines is No. 30, the most southerly provenance tested. This lot was considerably taller at age 2 than would be expected on the basis of its altitude or the temperature climate at its seed source. It is interesting to note that it also has a very much faster germination rate than would be expected on the basis of its climate (Sweet, unpublished). The fact that its origin in the Santa Cruz mountains is close to the southern coastal limit of the species has led to speculation as to whether Douglas fir in this area has developed in response to different selection pressures from the remainder of the coastal Douglas fir. Further collection and testing would be necessary to clarify this point.

At age 2, the provenances from New Zealand plantations, typical of routine planting stock, were ranked 10th equal out of 25 for height. The best North American provenance was 59% taller than the New Zealand ones, which suggests that it may be possible to increase the growth rate of Douglas fir in New Zealand quite considerably by a change in provenance.

63. *Phenological Behaviour in New Zealand*

Phenological studies make it possible to relate magnitude of annual growth increment to length of growing season, and it was planned to investigate this relationship in the present study. Unfortunately it was not possible to obtain complete data on length of growing season for all sample trees individually, but data were forthcoming on the relationships between phenology and provenance, and phenology and growth.

631. Date of spring bud burst

As discussed earlier, workers recording phenological observations in Douglas fir have assessed bud-burst by differing methods. CHING and BEVER (3) recorded the date of burst of the terminal bud, while IRGENS-MOLLER (6) recorded the date of the first bud to burst on each seedling, regardless of its position. In the study reported here, in which lateral and terminal bud burst were examined separately, burst of the first lateral bud always preceded that of the terminal bud, and only 51.7% of the variation in one feature was related to that in the other. Thus, the use of CHING and BEVER's and of IRGENS-MOLLER's assessment methods would have given somewhat different results. In the New Zealand assessment, neither date of terminal bud burst, nor the bursting date of the first bud to flush on the tree, was very strongly related to climate or geography of the seed source. The feature that was highly correlated with seed-source data, however, was the time lag between lateral and terminal bud burst (see *Fig. 5*).

The closeness of the correlation between time lag in bud burst and temperature regime at the seed source suggests that the character of time lag may have developed in response to selection pressure from climatic features. The time lag is longest in mild climates, and these are also the climates where the date of last spring frost is most unpredictable. (For example, the correlation coefficient r between length of frost-free growing season and standard deviation of the annual date of last spring frost for the North American provenances in the trial is 0.7358, significant at 0.1% for 21 degrees of freedom.) Late spring frosts that kill new growth are a cause of mortality or reduced increment of Douglas fir in Europe (16), North America (11), and New Zealand (18). It has been observed in New Zealand, however, (SWEET, unpublished), that although the frosting of new terminal growth usually causes death or severe weakening of a seedling, frosting that is restricted to lateral shoot growth has relatively little effect on development. Frosting of lateral shoots of a seedling commonly occurs where there is a late spring frost after lateral growth has started but before the terminal bud has burst.

It is suggested, therefore, that the observed time lag in terminal bud burst of the provenances of Douglas fir may have developed as a survival mechanism in response to the selective action of late spring frosts; and that the more variable the date of last spring frost in a provenance, the greater is the time lag between lateral and terminal bud burst. The correlation coefficient r between time lag in bud burst in New Zealand and predictability (expressed as standard deviation over 12 years) of the date of last spring frost at the seed source is 0.5391, significant at 1% for 21 degrees of freedom. Such a hypothesis must immediately face two queries. First, why should the survival mechanism have developed as a time lag of the terminal bud only, rather than as a delay in bursting of all buds on the seedling?: and secondly, why is not the correlation between time lag in bud burst and predictability of date of last spring frost at the seed source higher than it is, in relation to other correlations obtained?

To answer the first question: It is likely that, in any one location, seedlings commencing growth (and therefore increasing their photosynthetic area) as soon as conditions are favourable in the spring, would have a selective advantage over their fellows which commence growth later. This advantage would persist, provided only that in the event of a further frost the growth potential of the whole seedling was not damaged. Selection pressure, then should favour a seedling commencing lateral growth early, but with terminal growth delayed for a safe period, rather than a seedling remaining fully dormant until the danger of late frosts is past. The second question is readily answered, in that it was not possible to correct predictability of date of last spring frost for differences in altitude between seed source and weather station. Such corrections were made for all other climatic data.

Over all, although the hypothesis that time lag in terminal bud burst in Douglas fir has developed as a response to the selective action of late spring frosts is not fully substantiated by the observed data, it fits them sufficiently well to warrant further investigation.

632. Bud setting

This was assessed by counting the number of plants with dormant terminal buds on two dates during the first growing season, and on two dates during the second. The close relationship of the counts within each year ($r = 0.8840$ in the first year and $r = 0.9479$ in the second year, both significant at 0.1%) is evidence that the method gave a reasonable indication of the order in which the provenances ceased terminal height growth. This is in agreement with the finding of IRGENS-MOLLER (7), who compared dormant bud counts with weekly height measurements to get this information.

The data showed only a moderately high relationship between the first and second years in order of bud set ($r = 0.5895$, significant at 1%). This result is somewhat similar to that obtained from a study of individual trees of one provenance over two years by WALTERS and SOOS (17).

Correlations between time of bud set at age two in the nursery, and climate of the seed source, showed that in New Zealand, provenances from areas with long growing seasons ceased height growth later than did those from areas with shorter growing seasons. This result agrees with that published by IRGENS-MOLLER (7). There was a marked overall difference in date of terminal bud set between the first and second years: in the first growing season, only 39% of the trees had set terminal buds by 5 May, whereas in the second season 76% of the trees had set terminal buds by as early as 21 January. In each case more than 98% of these buds were overwintering ones. The earlier cessation of growth in the second year is regarded as an effect of maturation, rather than a result of climatic differences between the two years.

633. Relation of phenology to height growth

In building up a knowledge of growth patterns in a species, it is of interest to investigate the relationship between its growth and phenology. The trial set out to provide data on three questions:

1. Do provenances with early spring bud burst in their second year make more height increment than provenances that commence growth later in spring?
2. Do provenances containing a high proportion of trees having more than one annual growth flush in their second year make greater height increment than provenances with fewer such trees?
3. Do provenances that grow on late into the autumn of their second year make more height growth than those that do not?

The correlation coefficients showed that, at a statistically significant level, the answers to questions 1 and 2 were "No", but it must be remembered with respect to question 2 that differences between provenances in number of growth flushes during the second year were not statistically significant either. The answer to question 3 was "Yes", but only 21% of the variation in height growth in the second year could be accounted for by variation in date of terminal bud set. While statistically significant, such a percentage is not high. This result, taken in conjunction with the answer to question 1 reinforces CHING and BEVER's (3) and WALTERS and SOOS' (17) findings that in Douglas fir magnitude of leader growth is not well related to length of growing period.

The phenological character most closely related to height growth during the second year was time lag between lateral and terminal bud burst. The correlation coefficient between height growth and time lag for the provenances tested was 0.6898 (significant at 0.1%). This correlation, almost certainly, does not express a dependent relationship, but rather is an incidental result of the relationship of each of these features to temperature regime at the seed source.

64. *The Potential Value of Correlations between Provenance and Climate*

It was stated in the introduction that one of the reasons for relating early measurements and observations of seedlings to climate was to establish relationships which could be used to check the source of seed quoted by suppliers. Two characters appear to be especially well related to climate and geography of the seed source, and would seem suitable for this purpose. Two-year height and time lag between lateral and terminal bud burst of the provenances were both highly significantly correlated with temperature climate and altitude of the seed source; in each case the highest sample correlation coefficient exceeded 0.75. It is suggested that these relationships, if used together, are sufficiently strong to be useful in checking the data accompanying purchased seed of Douglas fir collected from the area west of the Cascade and Sierra Nevada ranges in North America. Seed weight is not suggested as a usable character because, owing to the extent to which it may be affected by degree of cleaning, year of collection, and age of parent tree, it does not lend itself well to mathematical treatment. It should certainly have value, however, as a broad indicator of provenance.

The chief limitation of this method of checking provenances is the fact that both two-year height and time lag in bud burst may vary from year to year. The measurements are of importance not in themselves, but only in relation to those of other provenances measured at the same time. It is probable, then, that the most convenient way to use these relationships to obtain seed-source information would be to compare the unknown provenance with perhaps three provenances of accurately known origin. The relationships obtained could then be further related, by discriminatory analysis, to the regressions presented in this paper, and data obtained on altitude and temperature climate of the seed source. We are currently attempting at the Forest Research Institute to develop such a test.

The regressions shown in *Figs. 4 and 5* demonstrate that both two-year height and the time lag between lateral and terminal bud burst are under quite strong genetic control. This suggests that the relationships with climate might be put to a further use in determining the original seed source of first-crop plantation stands. For example, it is known that most New Zealand plantations of Douglas fir had their origin west of the Cascade Ranges in Washington and Oregon (e. g. SPURR 13), but further data on provenance are lacking. If the data for height growth and bud burst from the progeny of any New Zealand plantation be compared with those from provenances of accurately known origin, it should be possible to obtain information about the climate from which the plantation seed was originally collected. If this were done for a range of provenances of Douglas fir in New Zealand, data would become available on the behaviour in this country of mature stands of these provenances. This would anticipate by many years the collection of such data from our still comparatively young provenance trials.

The full application of such a method would again involve the use of discriminatory analysis, and the necessary techniques for this are currently being tested at the Forest Research Institute. It is possible, however, to use data from the two New Zealand plantation provenances in this trial to illustrate the type of results that may be forthcoming. If the data for two-year height and time lag in bud burst of the New Zealand provenances are incorporated into the appropriate regression equations *(Figs. 4 and 5)*, solution of the unknown gives the following results:

	Altitude (ft)	Length of frost-free growing season (days)	Mean temperature of coldest month (°F)
	Provenance 31		
From the height regressions	1042	207	40.8
From the bud-burst regressions	1016	209	41.4
	Provenance 32		
From the height regressions	1042	207	40.8
From the bud-burst regressions	1640	176	38.7

Data from the height and bud-burst regressions respectively gave very similar results in the case of provenance 31, and slightly less comparable results for provenance 32. Over all, the values appear sufficiently close to allow of a successful discriminatory analysis which would also, of course, qualify limits of error for the data.

The accuracy of such provenance diagnoses must depend largely on the accuracy of the climatic data on which the original regressions are based. It has been pointed out (J. W. DUFFIELD and K. K. CHING, pers. comm. 1964) that the weather stations over much of the area sampled are widely spaced, and that in the case of some provenances it is unlikely that the corrections applied to weather-station data are adequate. While this is fully recognised, it should also be emphasised that the derived relationships between provenance and climate are based on regressions involving 23 provenances, many of which are quite adequately supplied with weather data. It is likely, therefore, that inadequacies in data for the remaining provenances, although sufficient to enlarge the prevailing limits of error, will not invalidate the method.

Acknowledgement

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Summary

Seed characteristics and nursery behaviour of 30 provenances of Douglas fir from western North America and of two from New Zealand plantations were examined in Rotorua, New Zealand. (Rotorua, with a frost-free growing season of 250 days, has a climate comparable with parts of coastal Oregon and California.)

A significant positive correlation (r = 0.78) was established between seed weight of the provenances and altitude of their seed sources, indicating that provenances from higher altitudes in North America had larger seeds than those from lower altitudes.

In the nursery, height growth and phenology were assessed over a two-year period. Mean heights at age two ranged from 5.7 in. to 30.2 in., the two New Zealand provenances being 19.0 in. high. The heights of individual provenances from North America were significantly correlated with several climatic features representative of the temperature regime at the seed source. The highest correlation obtained, that between two-year height and mean temperature of the coldest month at the seed source, was 0.79.

Phenologically, significant differences between provenances were found in date of spring bud burst and date of autumn bud setting. During the second growing season, the height growth made by each provenance was more closely related to its date of bud setting than its date of bud burst. In every provenance, one or more lateral buds burst on the seedlings before the terminal bud. The time lag between lateral and terminal bud burst varied from one provenance to another, and was significantly correlated with the temperature regime at the seed source. Provenances from milder climates, where the date of the last spring frost varied considerably from year to year, displayed a longer time lag than provenances from more severe climates where the date of the last spring frost showed less annual variation. It is postulated that time lag in bud burst has developed in response to the selective action of late spring frosts.

The suggestion is made that both two-year height growth and time lag between lateral and terminal bud burst of the provenances in New Zealand are sufficiently strongly related to climate at the seed source to enable a check to be made on the data of origin supplied with commercial seed lots. Suitable statistical techniques for such a check are being devised.

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Tetrasome Spaltung bei Betula pubescens

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Ausleseversuche mit Herkünften und Individuen der *Betula pubescens*, die beim Institut für Forstgenetik in Schmalenbeck ausgeführt wurden, ergaben eine breite genetische Variation der wichtigsten Merkmale (unveröffentlichte Ergebnisse des Verf.). Für künftige Versuche, aber auch zum besseren Verständnis der Geschichte der tetraploiden Art (siehe: DIETERICH 1962 für Literaturzusammenstellung) wäre es gut, etwas über die Spaltungsverhältnisse zu wissen. JOHNSSON (1949 a) hat als einziger Untersuchungen hierüber angestellt. Sie zeigen die technischen Schwierigkeiten, die aus der Vielzahl und der geringen Größe der Chromosomen entstehen. An einem Versuch mit Frühblühern (JOHNSSON 1949 b) konnte er jedoch wahrscheinlich machen, daß der von ihm untersuchte Genort bei *B. pubescens* tetrasom spaltete.

In früheren Versuchen des Schmalenbecker Instituts (STERN 1960) wurde nun ein weiterer Erbfaktor bei *B. pubescens* identifiziert, der bei Kreuzung des Trägers mit einem bestimmten Baum von *B. cordifolia* einen epistatischen Effekt zeigte, der schon an Baumschulmaterial bonitiert werden kann („Krausblatt"). *B. cordifolia* ist ebenfalls tetraploid, und so waren es auch die im übrigen voll fertilen Hybriden. Auch die aus Rückkreuzungen und der Hybrid-F_2 zufallsmäßig ausgewählten und untersuchten Individuen waren tetraploid.

Die Spaltung beider Loci, sowohl des von *B .pubescens* wie des von *B. cordifolia* stammenden, zeigte im Hybriden keine Abweichungen von den jeweils erwarteten Verhältnissen (STERN 1960). Da dies jedoch nichts über die Spaltung innerhalb jeder der beiden Arten aussagt, wurde ein