Provenance - Temperature Interactions in Four Coniferous Species

By F. MERGEN, J. BURLEY[1]) and G. M. FURNIVAL

School of Forestry and Environmental Studies
Yale University, New Haven
Connecticut, U.S.A. 06511

(Received July I October 1974)

Introduction

It is well established for msny commercial forest species that habitat-correlated, heritable differences occur between the genotypes of different populations (provenances, "sources"). These differences are demonstrated in designed provenance trials conducted in the field, nursery or greenhouse. When trials are carried out with the same provenances in two or more diverse environments, it is possible to detect the presence of interactions between the source population genetic effects and the environmental effects at the planting site. Such interactions are caused by the lack of additivity of the main effects and they are reflected in differential rankings or by differences in response of the provenances to the different sites. They are important because they reduce the silviculturist's ability to select and use an optimum provenance on all sites; each site could require a different provenance for maximum productivity. (The same problem arises with individual genotypic differences, as in selection and progeny testing, where genotype-environment interactions reduce heritability and genetic gain.) Interactions may also provide information on genetic affinities and evolutionary development of different populations. Historically work on genotype-environment interactions has been partitioned among two types of workers, the plant breeder who sought to minimise the effects and the geneticist who tried to explain them in terms of biometrical genetic parameters.

Although interactions can be demonstrated in field trials, many factors affect the growth of a plant and it is difficult to assess the contributions of individual factors; several factors may interact with each other to an extent that may itself vary with time. By growing material from different provenances in controlled environmental facilities, such as growth cabinets, it is possible to hold some factors constant while deliberately varying others and thus to investigate the interactions of genotypic and specific environmental effects.

This approach has been followed by many workers, using many species, several environmental factors, and a range of measured characteristics. A complete review of the extensive literature would be out of place here but the following references exemplify the development of research on provenance differences in controlled environments and (often implied) genotype-environment interactions, particularly with photoperiodic and thennoperiodic effects: — WENT (1948, 1958); **KRAMER** (1957a, b); **OLSON**, STEARNS and **NIENSTAEDT** (1959); DOWNS (1962); **HELLMERS** (1962, 1963a, b); **HELLMERS** and **ASHBY** (1958); **HELLMERS** and SUNDAHL (1959); **HELLMERS** and **ROOK** (1973); BURLEY (1965a, b); MERGEN (1963); MERGEN and **WORRALL** (1965); MERGEN, WORRALL and FURNIVAL (1967); YEATMAN (1966, 1967); LEDIG (1970); FRYER and LEDIG (1972).

Most of these and similar studies were concerned with differences between species or differences between provenances within one species. None of them examined the differential response of provenances in different species to the same range of environments. Further, none of them examined the contribution of individual provenances or environments to any interactions detected.

In this study we chose four coniferous species that are important commercially and have wide natural distributions. They have been shown (in the field or under controlled environments) to vary in several characters ecotypically or clinally in patterns closely related to the latitude, and hence the photoperiod or thermoperiod, of the seed source: —

1. Pinus banksiana LAMB., Jack Pine (**YEATMAN**, 1966)
2. Pinus silvestris L., Scots Pine (LANGLET, 1936, 1962; KING, 1965a, b)
3. Picea glauca (MOENCH) VOSS, White Spruce (**NIENSTAEDT**, 1968)
4. Picea sitchensis (BONG.) CARR., Sitka Spruce (**BURLEY**, 1965a, 1966).

The four species had been compared directly on the basis of cellular, genetic characteristics (nuclear volume, chromosome material or DNA content by **MERGEN** and **THIELGES** (1967) and **MIKSCHE** (1968) following **BURLEY'S** (1965b) observation of provenance variability in these traits; some indication of their susceptibility to genotype-environment interaction was given by WRIGHT (1973).

These species occur naturally in widely different geographic areas and habitats, yet they have similar latitudinal ranges. They are planted in many temperate countries and both national and international provenance trials have been initiated. There is still a need to compare them under closely controlled conditions; we chose a series of day and night temperature regimes that would (a) cover reasonably the range of temperatures the species would be expected to encounter in plantations during the growing season and (b) allow estimation of genotype-environment interactions.

Patterns of variation in tree growth related to daily temperature conditions vary greatly between species. The manifold interactions of temperature with all other plant processes create difficulties in the interpretation of these patterns. Growth is not related by chance to factors in the environment but represents the product of evolutionary processes. Studies of the responses of various species and provenances to controlled conditions of light and temperature are primarily attempts to elucidate this process and to interpret the results in terms of genetics, physiology and ecology.

Partitioning genotype-environment interactions *and* the concept *of stability*

When a statistically significant interaction is detected from variance ratios and variance components in the classical analysis of variance, and cannot be removed by scaling

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[1]) Present address: Commonwealth Forestry Institute, Oxford, England.

transformation, it is no longer meaningful to examine the means of main factors; the interaction implies that the difference between levels of one factor (*e. g.* provenances) itself differs between levels of another (*e. g.* temperatures). It is far more useful to partition the interaction among provenances in an attempt to determine those which contribute most to the interaction effects. Several techniques have been used for this though rarely with forest trees (Morgenstern and Teich, 1969; Snyder and Allen, 1971; see reviews by Squillace, 1970; Shelbourne, 1972 and Freeman and Dowker, 1973). Single degrees of freedom were estimated from interactions by Tukey (1949) and Mandel (1971). Individual contributions of potato varieties to variety x location interaction were estimated by omitting each variety in turn from the analysis (Plaisted, 1960). Wricke (1962) adjusted each variety's yield at one site by subtracting the mean of its performance on all sites, subtracting the mean of all varieties on the one site, and adding the grand mean. The resultant value was squared and the sum of such squares was considered the varietal contribution or ecovalence.

When several varieties (provenances) are represented at each location their mean may be considered a reasonable estimate of site productivity. The adaptability of the sources may be compared by linearly regressing their yield at each site on the site mean (Yates and Cochran, 1938; Finlay and Wilkinson, 1963); there have been semantic mis-uses of adaptability and stability and for our purposes a perfectly stable variety would have a regression coefficient (b) of zero while, in a source of average stability and hence good

Table 1. — Details of seed origin arranged by increasing latitude within each species.

Species	Provenance Serial no.	Provenance Code no.	Location	Latitude, N Actual Deg.	Latitude, N Actual Min.	Latitude, N Adjusted Decimal	Longitude Actual Deg.	Longitude Actual Min.	Altitude ft	Altitude m
1. Jack Pine	1	65	Lone Rock, Wisconsin	44	35	46.07	90	10W	830	253
	2	39	Twin Lakes, Ontario	44	39	47.05	77	53W	800	244
	3	79	Cloquet, Minnesota	46	20	50.53	94	10W	1150	351
	4	04	Victoria Co., Nova Scotia	46	45	47.95	60	21W	400	122
	5	31	Taillon Tp., Quebec	48	44	49.57	72	01W	275	84
	6	21	Sagunay Co., Quebec	49	40	49.97	67	15W	100	31
	7	84	Langton Tp., Ontario	49	51	53.75	93	21W	1300	397
	8	90	Cowan, Manitoba	52	03	55.65	100	23W	1200	366
	9	53	Kanaaupscow, Quebec	54	02	55.83	76	31W	600	183
	10	92	Kinoosao, Saskatchewan	57	05	60.68	102	01W	1200	366
	11	97(1)	Yellowknife, Northwest Territory	62	25	64.25	114	45W	720	220
	12	99	Wrigley, Northwest Territory	63	13	64.87	123	27W	550	168
2. Scots Pine	1	221	Turkey	40	30	55.20	32	42E	4900	1495
	2	621	Turkey	41	30	53.20	34	30E	3900	1190
	3	243	Greece	41	30	56.20	24	18E	49	15
	4	240	France	42	36	57.60	2	06E	50	15
	5	241	France	49	06	51.50	7	42E	8	2
	6	306	Czechoslovakia	49	12	53.70	14	—E	15	5
	7	527	Germany	50	54	56.30	13	42E	18	6
	8	222	Sweden	60	12	62.60	15	00E	8	2
	9	545	Sweden	60	24	62.80	12	54E	8	2
	10	546	Sweden	60	54	65.40	13	24E	15	5
	11	549	Sweden			66.90			(In last 3 treatments only)	
3. White Spruce	1	3071(2)	Chilson, New York	43	52	46.75	73	33W	960	293
	2	2572	Huron N.F., Michigan	44	30	46.60	83	45W	700	214
	3	2844	Acadia F.E.S., New Brunswick	46	01	46.77	66	22W	250	76
	4	2571	Grand Rapids, Minnesota	47	15	51.30	93	13W	1350	412
	5	2480	Kakabeka Falls, Ontario	48	30	51.35	89	30W	950	290
	6	2692	Moosonee, Ontario	51	16	51.42	80	39W	50	15
	7	2503	Summit Lake, British Columbia	54	18	61.80	122	40W	2500	763
	8	2557	York Fact., Manitoba	56	56	57.83	93	12W	100	31
	9	2490	Strg. Rapids, Saskatchewan	59	16	60.40	105	59W	710	217
	10	3141	Ft. Smith, Northwest Territory	60	02	61.83	111	55W	600	183
	11	4065	Ft. Smith, Northwest Territory	60	—	61.80	112	—W	600	183
	12	2496	Alaska Highway, Yukon	60	49	69.82	135	35W	3000	915
	1	37	Northwest California	41	45	42.05	124	45W	100	31
	2	15	North Bend, Oregon	43	24	43.40	124	15W	—	—
	3	24	Newport, Oregon	44	40	46.17	124	—W	500	153
	4	44	Montesano Co., Washington	46	57	47.55	124	02W	200	61
	5	6	Alberni, Vancouver Is., British Columbia	49	14	50.13	124	48W	250	76
	6	5	Bellacoola, British Columbia	52	24	52.48	126	40W	25	8
	7	3	Skeena River, British Columbia	54	30	55.25	128	34W	250	76
	8	19	Nass Valley, British Columbia	55	05	55.53	129	20W	150	46
	9	32(3)	Hollis, Alaska	55	28	56.07	132	42W	200	61
	10	33	Duck Creek, Juneau, Alaska	58	23	58.53	134	24W	50	15
	11	34	Homer, Alaska	59	36	59.75	151	28W	50	15
	12	31	Chugach N.F., Alaska	60	45	61.05	146	30W	100	31

(1) Replaced by 96 Ft. Smith, Northwest Territory, with equivalent adjusted latitude of 62.12 in three treatments.

(2) Replaced by 2437 with equivalent latitude of 46.43 in three treatments.

(3) In three treatments only.

adaptability, b = 1. An extension of this technique ("stability analysis") used both the regression coefficient and the deviations from regression to compare stabilities of different genotypes (Eberhardt and Russell, 1966; see also Freeman, 1973; Freeman and Dowker, 1973).

The joint regression technique is biassed, particularly when only a few genotypes are included, by the correlation between each individual genotype's value and the mean of all genotypes. Nevertheless it has proved successful in predicting genotypic performance over a wide range of species and environments. Possibly a preferable technique is to use an external measure of site mean productivity such as climatic or edaphic factors, and several external measures were recommended for multiple regression analysis by Hardwick and Wood (1972). The testing of multivariate methods, including factor analysis, canonical analysis and cluster analysis has been recommended and the use of principal component analysis has been demonstrated (Freeman, 1973; Freeman and Dowker, 1973).

When some form of joint regression technique is adopted there is a factorial arrangement of possible outcomes; firstly, there are internal or external measures of the environment; secondly, provenances can be classified into various types of stability based on the size of the regression coefficient; thirdly, a similar classification can be applied to the deviations from regression; fourthly, all these can be coupled with various classes of provenance mean value.

The final, common method of examining differential performance of populations is to compare the regressions of performance on seed source information for all environments individually. This method has been used for many tree species by many authors including the four tree species used in this study (*e. g.* Burley, 1966; Morgenstern and Teich, 1969; Eiche and Andersson, 1974; Yeatman, 1966). It tends to evaluate the stability of groups of provenances rather than of individual sources.

Materials and Methods

Provenances

Seeds from several provenances (origins within the natural range) of *Pinus banksiana, Pinus silvestris, Picea glauca* and *Picea sitchensis* were obtained from various agencies. The seeds were stored in glass vials in a refrigerator until used. To ensure a reasonably uniform but random sampling of the natural range of each species, it was divided into three latitudinal belts (north, central and south); four provenances were selected from each belt. Some seeds failed to germinate and some seedlots had poor survival; a list of the provenances finally represented is shown in *Table 1*. The actual latitudes were adjusted to a common altitude by a factor of 3^0 latitude per 1000 ft (305 m) of altitude. The treatment of missing data is discussed below.

Environments and experimental design

The experiment was designed to include 6 temperature treatments × 4 species × 12 provenances per species × 3 replications; thus 864 pots of seedlings were required. The experiment was done in two phases because of the large number of plants involved plus the limiting factor of space in the three controlled environment rooms (growth cabinets). Thus some planned differences between environments in the cabinets are also confounded with time differences between the two phases but this is not believed important. After having been disinfected with a 10% Chlorox solution and soaked overnight in distilled water to separate the filled from the unfilled seed, the seed for the first half of the experiment was sown in a 1 : 1 : 1 sand : soil : peat mixture. For the second phase the seed was planted in pots which had about 3 inches of vermiculite on the surface. Germination was much better in the vermiculite and damping off, a serious problem in the first phase, was eliminated.

Germination occurred after about 10 days and 10 seedlings were transplanted into each of the white plastic pots (10 cm diameter). Ferbam was applied to control damping off and later a shallow layer of quartz sand was applied. Two weeks after sowing, all seedlings were placed under a 16-hour photoperiod in the greenhouse; daylight was supplemented by tungsten lamps (500 watts).

When the seedlings were about one month old, they were placed in controlled environment rooms in a random arrangement of provenances and replications within species blocks. In addition, species positions were randomly assigned among treatments. The following conditions were maintained in all rooms: — 16-hour photoperiod; approximately 2000 fc light intensity; 50% humidity; and constant soil moisture content (watered twice weekly by weight loss). The temperature was the experimental variable, and for the first phase Cabinet I was maintained at 30^0 day/ 30^0 C night; Cabinet II — 30^0 day/20^0 C night, and Cabinet III — 30^0 day/10^0 C night. During the second part of the experiment Cabinet I had a 20^0 day/30^0 C night; Cabinet

Table 2. — Format for analysis of variance and expectation mean squares. (Components of variance for fixed effects are represented by Φ, those for random effects by V.)

Entry no.	Source of variation	Degrees of freedom		Test against entry no.	Expectation mean squares
		Planned	*Actual*		
1	Species	3	3	2	$V_E + 18V_P + 216\Phi_S$
2	Provenances in species	44	43	12	$V_E + 18V_P$
3	Day temperatures	1	1	9	$V_E + 9V_{DP} + 432\Phi_D$
4	Night temperatures	2	2	10	$V_E + 6V_{NP} + 288\Phi_N$
5	Days × Nights	2	2	11	$V_E + 3V_{DNP} + 4\ \Phi_{DN}$
6	Species × Days	3	3	9	$V_E + 9V_{DP} + 108\Phi_{SD}$
7	Species × Nights	6	6	10	$V_E + 6V_{NP} + 72\Phi_{SN}$
8	Species × Days × Nights	6	6	11	$V_E + 3V_{DNP} + 36\Phi_{SDN}$
9	Provs. in spp. × Days	44	41	12	$V_E + 9V_{DP}$
10	Provs. in spp. × Nights	88	86	12	$V_E + 6V_{NP}$
11	Provs. in spp. × D × N	88	81	12	$V_E + 3V_{DNP}$
12	Residual	576	532		V_E
	Total	863	806		

II — 20° day/20° C night; and Cabinet III — 20° day/10° C night.

After three months in the cabinets, the number of survivors was counted, the heights of the five tallest plants were measured to the nearest millimeter, and the presence or absence of a terminal bud was noted on each seedling. The seedlings were cut at soil level, and fresh weights to the nearest milligram were determined immediately. Each individual seedling was placed in a weighed aluminium foil bag and put into a forced-air oven at 80° C. After a minimum of 72 hours in the oven, the seedlings were removed and the dry weights were recorded to the nearest milligram. The ratios of dry weight/fresh weight were calculated. Mortality occurred mainly in Sitka Spruce, with less in White Spruce, particularly at the high temperatures; no further analysis of this characteristic was undertaken.

Mathematical model and analysis

For the statistical analyses of the resultant data the following linear model was adopted: —

$$Y = \mu + \alpha_1 S_i + \alpha_2 D_j + \alpha_3 N_k + \alpha_4 P_{il} + \alpha_5 SD_{ij} + \alpha_6 SN_{ik} + \alpha_7 DN_{jk} + \alpha_8 SDN_{ijk} + \alpha_9 DP_{jil} + \alpha_{10} NP_{kil} + \alpha_{11} DNP_{jkil} + e_{jkilm} \ldots\ldots\ldots\ldots\ldots \text{Equation 1}$$

where S, D, N, and P are the effects due to species, day temperature, night temperature, and provenance respectively,

i is the *ith* species (i = 1—4),

j is the *jth* day temperature (j = 1—2),

k is the k*th* night temperature (k = 1—3),

il is the l*th* provenance in the *ith* species (l = 1—12),

m is the m*th* replication in the ijkl*th* provenance-treatment combination,

μ is the general mean,

α_{1-11} are coefficients,

and e is the residual error term reflecting plot to plot variation between the replications of each provenance-treatment combination.

A mixed model is probably the most appropriate for these experimental conditions, with species and temperatures considered fixed (variance component Φ) and provenances random (V) (*Table 2*). It is always debatable whether provenances should be considered fixed or random since each is derived from a determinate location with fixed, known latitude, longitude and altitude. Nevertheless, they may reasonably be considered to represent the entire species so that if treated as random they may be used to draw inferences about the species. Similarily, although temperatures were considered to be fixed it is probably reasonable to make inferences about the temperatures within the range tested.

The statistical treatment was complicated by a number of missing values. Although it was planned to include 12 provenances from each species, only 11 were successful in Scots Pine. Further, one of these (11) was represented in only three treatments. Individual replications of specific source-treatment combinations were missing in White Spruce (5) and Sitka Spruce (25); most of these occurred at the high day/night temperature combination. Of the originally planned 864 plots only 807 yielded data, *i. e.* 7% missing. These represented means that should have been based on five seedlings per pot; however, insufficient seedlings survived in some pots and for them means were calculated from 1—4 plants. The total number of missing plants were 20 in Jack Pine, 52 in Scots Pine, 77 in White Spruce and 206 in Sitka Spruce giving a total of 355 missing out of 4320 planned, *i. e.* 8% missing.

Table 3. — Summary of analysis of variance for five characters. (F values are included only if significant at $<5.0\%$ probability level; variance components are expressed as actual values and as percentages of total variation.)

Source of Variation	d. f.	Fresh weight				Dry weight				Dry/Fresh weight				Height				Terminal buds			
		m. s. × 10^{-4}	F	component value	component %	× 10^{-3} m. s.	F	component value	component %	m. s. × 10^{-3}	F	component value	component %	m. s. × 10^{-1}	F	component value	component %	m. s. × 10^{2}	F	component value	component %
1. Species	3	372.0	19.9	1.64	7.6	440.2	24.2	2.04	8.8	108.7	38.8	0.49	20.1	314.3	10.0	1.31	8.0	870.5	20.6	3.83	19.0
2. Provenances in species	43	18.7	14.8	0.82	3.8	18.2	4.6	0.82	3.5	2.8	5.6	0.13	5.5	31.4	9.2	1.56	9.5	42.3	14.6	2.19	10.9
3. Day temperatures	1	88.1	11.0	0.19	0.9	13.6		0.01	0	35.3	27.2	0.08	3.4	1794.0	152.0	4.13	25.1	541.7	95.0	1.24	6.1
4. Night temperatures	2	765.5	119.6	2.63	12.2	615.1	150.0	2.12	9.1	75.7	84.1	0.26	11.1	729.7	130.3	2.51	15.3	665.9	78.3	2.28	11.3
5. Days × Nights	2	17.8	3.0	0.25	1.2	17.3	2.9	0.23	1.0	2.3	2.6	0.03	1.4	19.8	5.2	0.33	2.0	105.1	20.6	2.08	10.3
6. Species × Days	3	845.3	105.7	7.75	36.1	981.2	114.1	9.00	38.8	30.1	23.2	0.27	11.5	149.8	12.7	1.28	7.8	170.5	29.9	1.53	7.6
7. Species × Nights	6	73.5	11.5	0.93	4.3	89.3	12.5	1.14	4.9	10.6	11.8	0.13	5.5	29.4	5.3	0.33	2.0	84.9	10.0	1.06	5.3
8. Spp. × Days × Nights	6	71.1	12.1	1.81	8.4	82.2	13.9	2.12	9.2	7.8	8.7	0.19	8.0	10.0	2.6	0.17	1.0	44.2	8.7	1.09	5.4
9. Provs. in spp. × Days	41	8.0	2.1	0.46	2.1	8.6	2.1	0.50	2.2	1.3	2.6	0.09	3.8	11.8	3.5	0.93	5.7	5.7	2.0	0.31	1.5
10. Provs. in spp. × Nights	86	6.4	1.6	0.42	2.0	7.1	1.7	0.50	2.2	0.9	1.8	0.07	3.0	5.6	1.6	0.37	2.2	8.5	2.9	0.93	4.6
11. Provs. in spp. × D × N	81	5.9	1.5	0.67	3.1	5.9	1.4	0.60	2.6	0.9	1.8	0.13	5.5	3.8		0.13	0.8	5.1	1.8	0.73	3.6
12. Residual	532	3.9	—	3.90	18.2	4.1	—	4.10	17.7	0.5	—	0.50	21.2	3.4	—	3.40	20.6	2.9	—	2.90	14.4
TOTAL	806																				

Table 4. — Treatment means for five characters averaged over all provenances in each of four species

Day/Night temperature	Fresh weight, mg.	Dry weight, mg.	Dry/Fresh weight ratio	Height, mm	Terminal bud frequency
		Jack Pine			
30/30	170.83	55.44	0.34	30.06	0
30/20	333.26	99.70	0.31	34.29	0.06
30/10	456.33	134.17	0.30	35.41	0
Mean	320.14	96.44	0.32	33.25	0.02
20/30	303.91	96.97	0.33	32.14	0.37
20/20	659.84	197.85	0.30	39.46	0.87
20/10	688.18	219.96	0.32	41.43	0.15
Mean	550.64	171.59	0.32	37.68	0.46
Grand Mean	435.39	134.02	0.32	35.47	0.24
		Scots Pine			
30/30	311.87	96.70	0.32	33.53	0.52
30/20	333.73	104.99	0.32	40.01	0.73
30/10	512.27	156.15	0.31	41.52	0.25
Mean	385.96	119.28	0.32	38.35	0.50
20/30	487.60	158.03	0.33	36.58	0.78
20/20	803.42	244.87	0.31	49.24	0.88
20/10	622.18	206.88	0.33	44.98	0.27
Mean	637.73	203.26	0.32	43.60	0.64
Grand Mean	511.85	161.27	0.32	40.98	0.57
		White Spruce			
30/30	324.02	127.22	0.40	20.00	0.24
30/20	985.90	340.15	0.36	26.77	0.27
30/10	1225.73	425.97	0.36	28.60	0.46
Mean	845.22	297.78	0.37	25.12	0.32
20/30	94.69	35.14	0.39	28.10	0.33
20/20	287.37	99.54	0.37	37.94	0.50
20/10	515.48	160.12	0.33	43.41	0.09
Mean	299.18	98.27	0.36	36.48	0.31
Grand Mean	572.20	198.03	0.37	30.80	0.32
		Sitka Spruce			
30/30	22.18	65.54	0.41	17.73	0
30/20	98.23	31.67	0.33	30.42	0.05
30/10	114.22	39.03	0.35	30.99	0
Mean	78.21	45.41	0.36	26.38	0.02
20/30	106.57	35.17	0.34	32.58	0.01
20/20	492.61	139.50	0.29	49.58	0.02
20/10	552.84	156.72	0.29	46.21	0.01
Mean	384.01	110.46	0.31	42.79	0.01
Grand Mean	231.11	77.94	0.34	34.59	0.02

In the analysis of variance the sums of squares *(Table 3)* were computed by the application of least squares to Equation 1. The extremely large matrix (274 × 274) developed was inverted by an iterative technique. The coefficients for variance components shown in *Tables 2* and *3* assume an orthogonal, complete design and are, of course, approximate.

Variance components were expressed as percentages of total variation to examine the relative importance of the many sources of variation *(Table 3)*. Mean values were tabulated *(Table 4)* and typical examples of significant differences are shown in *Figures 1—2*. Where statistically significant provenance × temperature interactions were detected, they were partitioned among individual species. If these individual interaction effects were also significant they were examined within individual treatments *(Table 5)*.

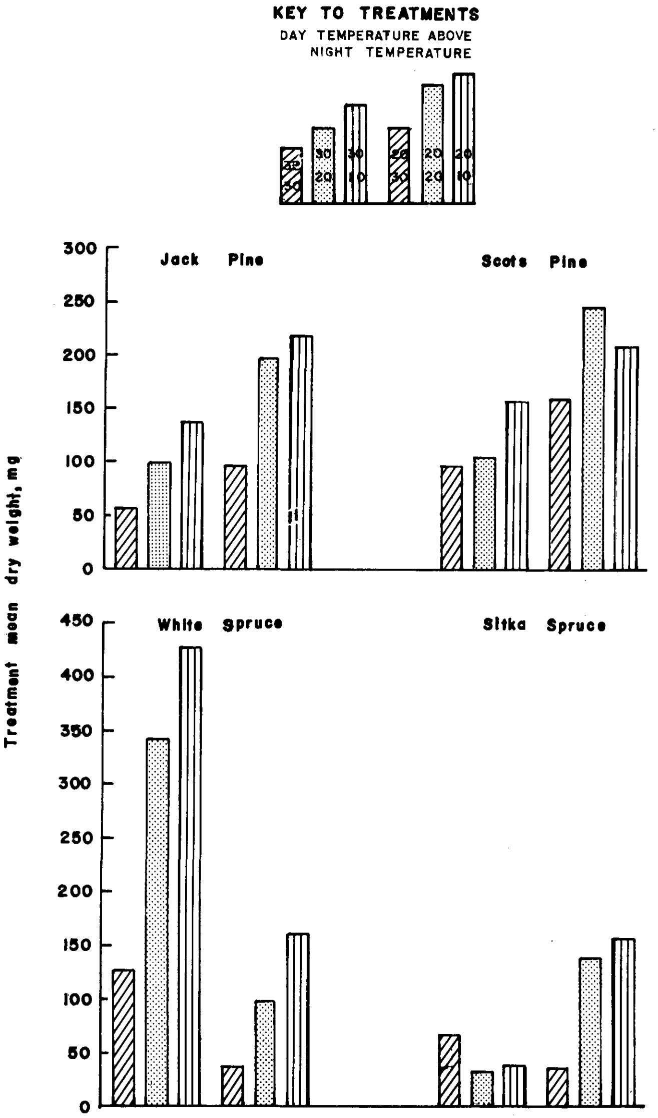
Linear regression analysis was used to deal with the unbalanced design and to relate seedling growth to the treatment temperature sum *(Figures 3—4)* and to the latitude of seed source within individual treatments and species (examples in *Figure 7*). It was also used in the joint regression technique to examine individual source contributions to significant interaction effects (Finlay and Wilkinson, 1963; Eberhart and Russell, 1966; Freeman, 1973) *(Table 6* and *Figures 5—6)*.

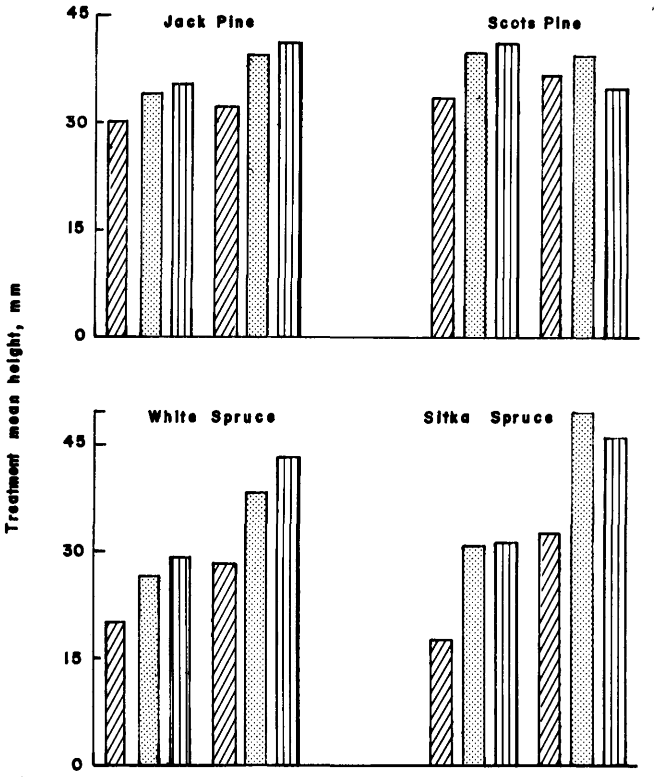
Results and Discussion

Species and temperature effects

Throughout the analysis of variance *(Table 2)* the large numbers of degrees of freedom associated with some factors and interactions produced such great precision that many factors appeared significant statistically *(Table 3)*. It is necessary to interpret them in the light of biologically or economically meaningful means and differences *(Table 4* and *Figures 1—2)* and of the proportion of total variation they explain (judged by their variance components expressed as a percentage of total variation, *Table3)*.

The simple and interacting of the main factors (species and temperatures) were clear and reasonably interpretable. Theoretically, means for the various levels of a single factor should not be examined in the presence of interaction effects; however, biologically the differences between the levels of single factors are of interest.





Figures 1—2. — Mean for six treatments in four species averaged over seedlings, replications and provenances. 1. Dry weight (mg). 2. Height (mm).

The four species obviously differed in most traits but they ranked in different orders for the different characters. White Spruce had the greatest fresh weight, dry weight and dry/fresh weight ratio but the smallest height; Scots Pine was consistently superior to Jack Pine while Sitka Spruce was the poorest in production. Of the total variation observed, the fixed effect of species accounted for 8—20% and this was commonly the second or third greatest source of variation after the residual variance.

Night temperatures accounted for an average of 12% of the total variation; a completely consistent trend of increasing growth with decreasing night temperature (*i. e.* a lack of species × night interaction effects) was interrupted only by:

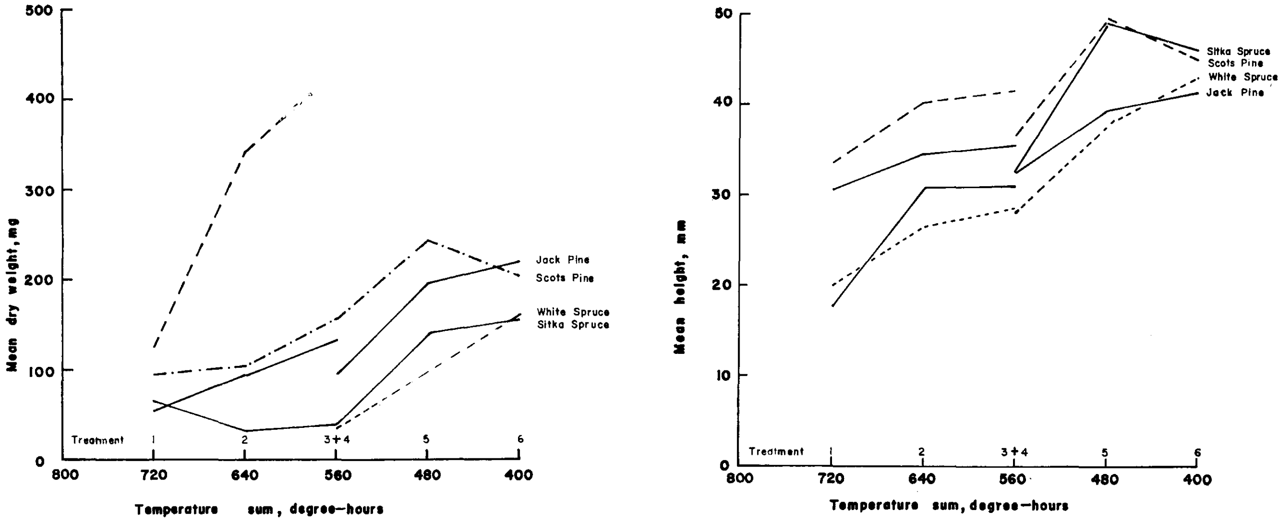
(a) 20⁰/20⁰ C treatment for Sitka Spruce (height) and Scots Pine (all values); values were greatest under this temperature regime (see *Figures 1—4),* suggesting that these species are not as dependent as the others on day/night temperature differentials. Certainly a leaf temperature of 20⁰ C was found optimal for net photosynthesis in Sitka Spruce (Ludlow and Jarvis, 1971; Neilson, Ludlow and Jarvis, 1972) although there was a trend for northern provenances to have higher photosynthetic rates and lower dark respiration rates; higher photosynthetic rates were associated with lower stomatal and mesophyll resistance.

(b) 30⁰/10⁰ C treatment for Sitka Spruce (height only).

(c) terminal buds, for which there were no consistencies and which did not lend themselves to complete analysis. An increase of growth with decreasing night temperature (at a given day temperature) could be expected because dark respiration decreases with decreasing temperature.

Day temperatures accounted for virtually no variation (except in height growth, 25%) and this is largely due to the species × day interaction, especially for fresh weight (36%). In both fresh and dry weight, White Spruce showed an opposite trend to that of the other species (*e. g. Figure 1).* At a given night temperature most species could be expected to increase productivity with increasing day temperature, up to the photosynthetic optimum; this optimum may itself vary with species and provenance (Hellmers and Sundahl, 1959; Hellmers, 1962; Fryer and Ledig, 1972) although this was less apparent in five provenances of Sitka Spruce examined by Neilson, Ludlow and Jarvis (1972). The present data suggest that 30⁰ C exceeds the optimum for Jack Pine, Scots Pine and Sitka Spruce; however, surprisingly, it did not exceed the optimum for White Spruce which covers a similar latitudinal range to all the other species and a similar geographic range to Jack Pine. No attempt was made to separate the many physiological processes that could be affected and interacting.

Temperatures may influence growth *inter alia* by affecting the rates of photosynthesis, light respiration and dark respiration through (a) temperature maxima as discussed above, (b) day-night differentials as shown in *Figure 1,* and (c) total heat sums. Differences between species were further examined in relation to daily temperature sums (the number of hours × the number of Centrigrade



Figures 3—4. — Relationship of growth to daily temperature sum (degree-hours) in four species. 3. Dry weight (mg). 4. Height (mm).

degrees at each period) and these are exemplified in *Figures 3—4* for dry weight and height.

In addition to the obvious differences between species in mean response, two important specific attributes are apparent. Firstly, only Scots Pine shows a clear maximum (480 degree-hours) for all traits within the range of heat sums tested. Sitka Spruce shows the same optimum for height while the other data from Sitka Spruce and Jack Pine suggest that maxima occur somewhat below 400 degree-hours. These values agree with those obtained for Jeffrey Pine (*Pinus jeffreyi* GREV. and BALF.), but are lower than those for Erectcone Pine (*Pinus brutia* TEN) and Eastern Hemlock (*Tsuga canadensis* (L.) CARR.) found by HELLMERS (1962), HELLMERS and ASHBY (1958) and OLSON, STEARNS and NIENSTAEDT (1959) respectively.

Secondly, the four species form two groups in relation to their response to the two treatments (3 and 4) represented by 560 degree-hours. White Spruce and Jack Pine demonstrate marked differences in their response to $30^0/10^0$ C and $20^0/30^0$ C treatments with significantly greater growth with the higher day/night differential. Sitka Spruce and Scots pine have virtually the same productivity in all three traits under both treatments, *i. e.* they are responsive to total heat sum regardless of day/night differential. It is understandable that Sitka Spruce should demonstrate this response as a reflection of the more equable diurnal and seasonal climatic patterns within the natural range of the species. Similarly, it is perhaps understandable that the more continental species, Jack Pine and White Spruce, should demonstrate a requirement for diurnal contrasts in temperature. It is not clear why the equally continental Scots Pine should show a closer affinity with Sitka Spruce. However, as stated above, no attempt was made to separate the component processes or structures such as the effect of leaf cuticle wax on gas exchange (JEFFREE, JOHNSON and JARVIS, 1971).

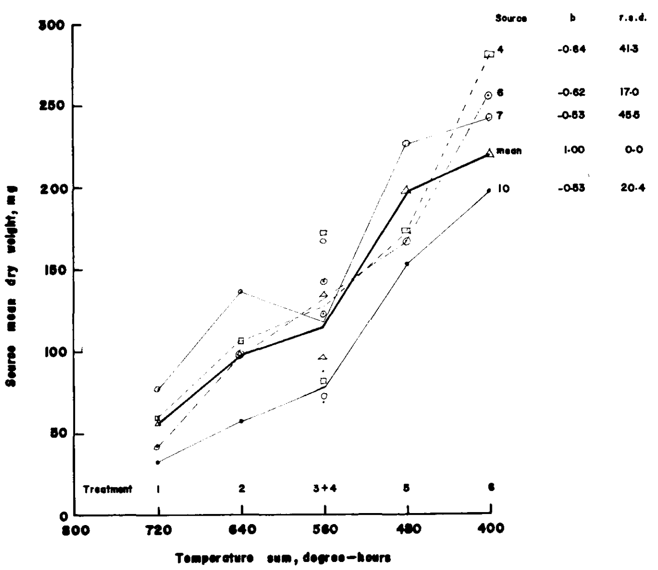


Figure 5. — Examples of relationship of provenance mean dry weight (mg) to daily temperature sum (degree-hours) in Jack Pine (b = regression coefficient; r.s.d. = residual standard deviation. Source numbers refer to origins listed in *Table 1.*)

Provenance effects and provenance-environment interactions

The biological importance of the statistically significant differences between provenances was confirmed by the size of the variance components which accounted for 0.5—1.1 times the species contribution (except for the ratio of dry/fresh weight). It was evident that some treatments allowed provenance variation to be demonstrated more than others, and that some species and characters exhibited more inter-provenance variability than others.

However, in this study the presence of interactions between provenance effects and temperature effects was obviously of more interest. Statistically all first- and second-order interactions involving provenances were significant at least at the 5.0% probability level for all traits (*Table 3*).

Because these interactions included all provenances nested within the four species, it was difficult to detect from two-way tables where the main interactions were occurring. Thus the interaction variances were partitioned among the four species as shown in *Table 5*.

White Spruce showed consistent provenance-temperature interactions for all traits and all environments. For Sitka Spruce both first-order interactions occurred for dry weight and height, while for the dry/fresh weight ratio only the provenance × day temperature interaction was significant. Scots Pine in contrast showed little evidence of interaction, while in Jack Pine height, the frequency of terminal buds and the dry/fresh weight ratio were affected.

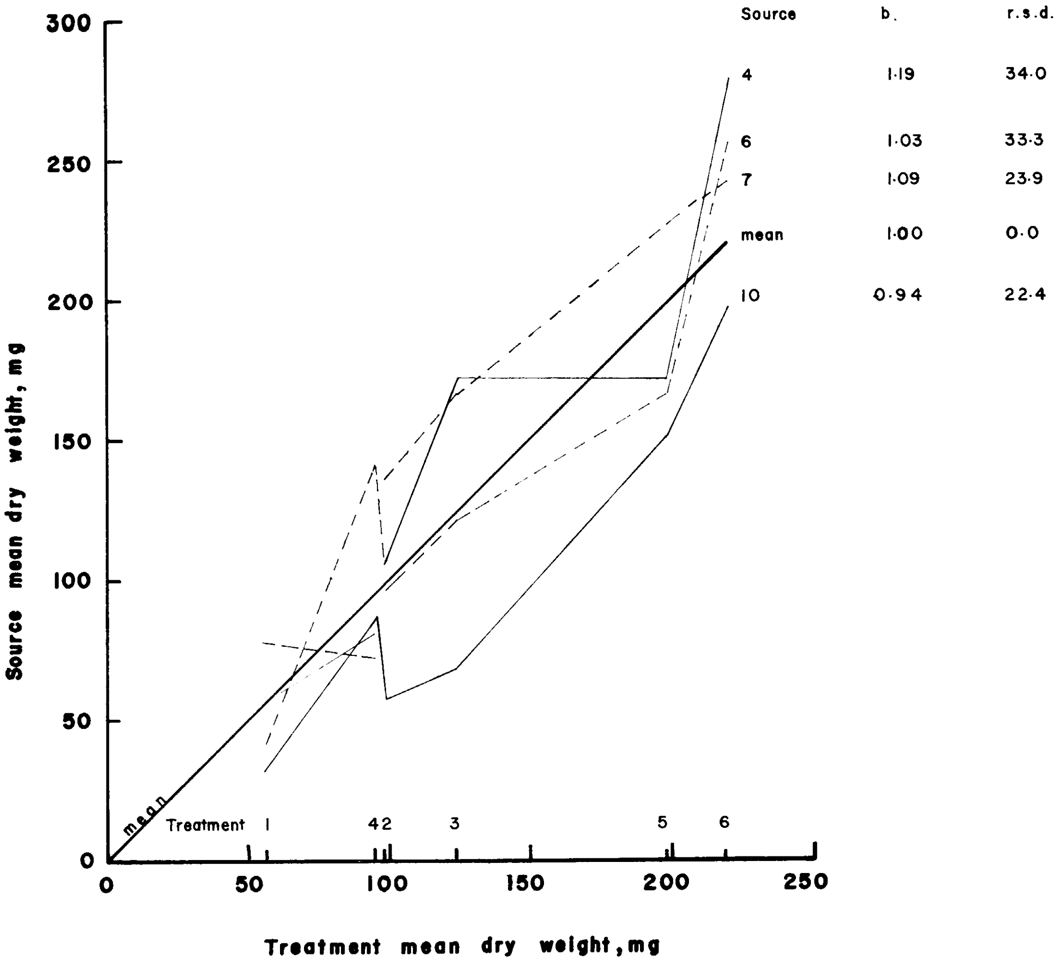


Figure 6. — Examples of relationship of provenance mean dry weight (mg) to treatment mean in Jack pine (b = regression coefficient; r.s.d. = residual standard deviation).

Among the many methods available for evaluation of genotype × environment interaction, the two that seemed most appropriate for our material were the joint regression technique over all six treatments and regression analysis of seedling growth on latitude of seed origin; as is well known, latitude, particularly when adjusted for differential altitude, reflects many of the climatic factors normally associated with population differentiation and evolution (*e. g.* diurnal and seasonal variations in photoperiod, thermoperiod, and precipitation).

Table 5. — Partition of provenance-temperature interaction variances for five characters between species. (F values are tabulated only if significant at <5.0% probability level)

Source of variation	Fresh weight	Dry weight	Dry/Fresh weight	Height	Terminal buds
Provenance × Day					
Jack Pine			2.8	2.8	2.6
Scots Pine					3.5
White Spruce	4.0	3.7		4.2	2.0
Sitka Spruce		2.7	4.7	5.1	
Provenance × Night					
Jack Pine					
Scots Pine					
White Spruce	2.8	4.2	2.6	2.2	5.5
Sitka Spruce		3.0		2.3	
Provenance × D × N					
Jack Pine					2.7
Scots Pine					2.1
White Spruce	4.2	4.3	3.5	2.0	2.0
Sitka Spruce					

The two traits for which consistent patterns were derived were dry weight and height; also these are the most commonly used descriptors of plant growth. For each provenance that was represented in all six treatments a separate regression analysis was calculated giving the slope (b) and residual standard deviation (r.s.d.) as well as the coefficient of determination (R^2%) for the relationship between provenance performance and (i) the mean of all provenances of that species in each treatment or (ii) the degree-hours for each treatment. As discussed above there was a poor correlation between growth and degree-hours, at least for White Spruce and Jack Pine *(Figures 3—5)*, because of the requirement for day/night temperature differential. Thus the regression on temperature sum was not as useful as that on treatment means *(e. g. Figure 6)*. Provenances differed significantly in the values of b:

	Range of b values	
	Dry weight	Height
Jack Pine	0.58 — 1.31	0.37 — 1.71
Scots Pine	0.69 — 1.93	0.65 — 1.48
White Spruce	0.62 — 1.96	0.18 — 1.40
Sitka Spruce	—0.23 — 1.74	0.17 — 1.37

Residual standard deviations varied also, though not necessarily with the same provenance rankings, and it would be possible to select individual populations that show high stability (low b value) to average stability (values near b = 1.0). To compare the species on the basis of random provenances the absolute values (moduli) of the differences (d) between actual b values and unity (b = 1.0) were averaged ($\bar{d}$) for the southern, central and northern groups of provenances in each species *(Table 6)*. Low values of d and r.s.d. indicate provenances of average phenotypic stability contributing little to genotype-environment interactions. For Jack Pine, Scots Pine and Sitka Spruce the central group of provenances appears to meet this criterion (at least for dry weight; differences in height growth were confounded with size of seedling crown). Within Jack Pine the pattern of deviation (d) values follows that described by MORGENSTERN and TEICH (1969), but the variation of b values was greater suggesting the environments we tested were more diverse or extreme.

As discussed by LEDIG (1970) provenances from optimal growth zones are able to adapt to a range of environmental conditions whereas provenances from marginal natural environments do not. It appears that provenances from optimal zones have more physiological homeostasis. Provenances from marginal or rigorous environments contribute more to interaction effects and show more differences in environmental response among themselves. We found stable provenances (b < 1.0) with below average performance over all tested environments, and adaptable provenances (b > 1.0) with better than average performance under the best environmental conditions; however, we did not locate stable provenance with superior performance over all environments *(i. e.* particularly favoured by poor conditions).

The various averages described above confirmed that provenances differ in their contribution to genotype-environment interactions. The patterns of differences themselves varied between species, reflecting their different evolutionary histories and geographic distributions. Also somewhat different patterns of stability and adaptability were observed for the different characters. The final type of analysis undertaken was the classical descriptive method of relating provenance performance to latitude of seed origin by linear regression analysis *(e. g. Figure 7)*. This allows speculation about the environments that contribute most to interaction effects.

For the least squares analysis of the anorthogonal design, a two-dimensional surface had been fitted to relate growth characters to latitude and temperature. However, for illustrative purposes regressions of seedling characters on latitude alone were computed for each trait in each environment separately.

In some cases there were no significant relationships and this was expected from the earlier analysis of variance within treatments. Regression parameters were not compared statistically between environments but it is clear from *Figure* 7 that the relationships changed in different environments. In the case of height of Jack Pine, treatments 3 and 4 ($30^0/10^0$ C and $20^0/30^0$ C with the same daily temperature sum) differed markedly from the others whereas, for dry weight of Scots Pine, treatment 6 was distinct. In White Spruce, treatment 1 showed no relationship between dry weight and latitude of seed source. Where linear trends were demonstrated they confirmed the pattern of decreasing growth with increasing latitude of seed origin previously reported for these four species.

Table 6. — Mean stability indices ($\bar{d}$ = deviation from b = 1; r.s.d. = residual standard deviation) from southern, central and northern groups of provenances based on regression of provenance mean on treatment mean.

Species	Provenance codes	Geographic group	Dry weight $\bar{d}$	Dry weight r. s. d.	Height $\bar{d}$	Height r. s. d.
1. Jack Pine	1—4	Southern	0.14	20.0	0.40	2.7
	5—8	Central	0.07	18.7	0.29	3.4
	9—12	Northern	0.21	23.0	0.16	2.4
2. Scots Pine	1—4	Southern	0.28	17.4	0.19	3.3
	5—7	Central	0.09	16.9	0.33	3.3
	8—10	Northern	0.21	32.8	0.28	3.4
3. White Spruce	1—4	Southern	0.04	62.7	0.21	5.3
	5—8	Central	0.15	39.6	0.21	4.5
	9—12	Northern	0.24	49.0	0.14	4.5
4. Sitka Spruce	1—4	Southern	0.54	23.5	0.21	3.8
	5—8	Central	0.15	32.2	0.16	3.5
	9—12	Northern*	0.45	44.4	0.32	5.0

* These values are greatly distorted by the atypical values of the most northern source.

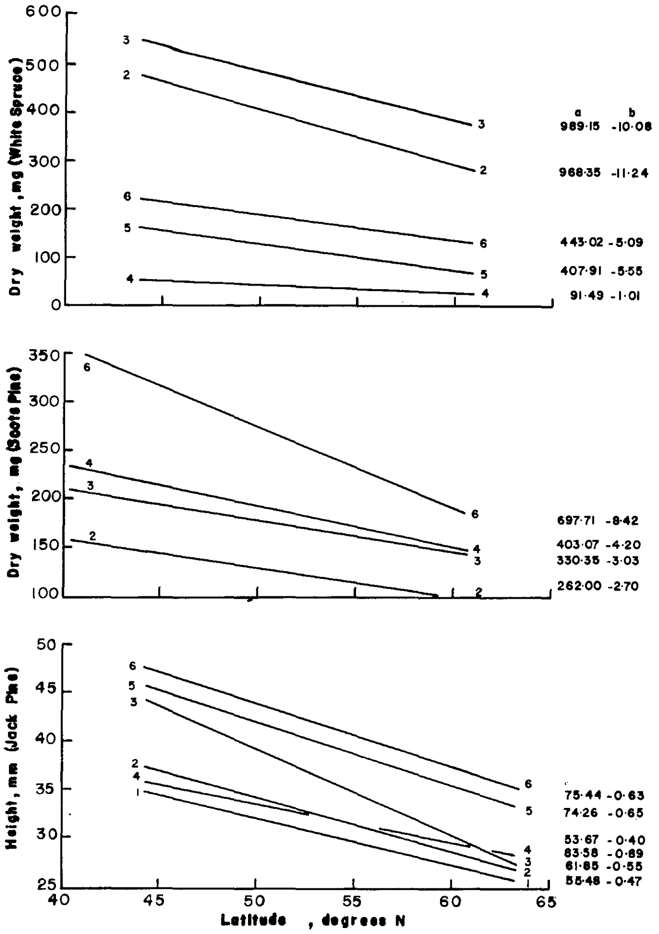


Figure 7. — Examples of regressions of provenance mean on latitude of seed origin (treatments are numbered 1—6).

Although the six environments tested did not permit separation of provenances for all the characters and species, they did demonstrate that some environments are more suitable than others for provenance discrimination. Because the environments were designed to compare only temperature effects it is not desirable to classify them as good or bad *in toto*, especially as their effects differ between species. However, the results confirm that, under suitable test conditions, the performance of a provenance may be predicted from its latitude; further, individual provenances may be selected not only on the basis of mean performance in one environment but on their contribution to genotype-environment interactions, *i. e.* their phenotypic stability or adaptability (*Table 7*).

Table 7. — Parameters of stability for dry weight and height in all provenances (regression on treatment mean).

Species Provenance	Dry weight R^2 %	b	r. s. d.	Height R^2 %	b	r. s. d.
1. Jack Pine						
1	99.4	1.31	7.0	84.8	1.71	3.5
2	92.6	1.05	21.1	83.7	0.74	1.6
3	94.3	1.01	17.7	75.4	1.30	3.6
4	86.0	1.19	34.0	88.7	1.31	2.2
5	98.0	1.08	10.8	75.2	0.71	2.0
6	82.8	1.03	33.3	84.1	1.16	2.4
7	91.4	1.09	23.9	6.4	0.37	6.7
8	99.2	1.09	6.8	82.1	1.06	2.4
9	84.6	0.69	20.8	88.8	0.96	1.6
10	89.9	0.94	22.4	84.9	0.78	1.6
11	86.4	0.95	26.8	66.0	1.17	4.0
12	78.0	0.58	21.8	72.1	0.81	2.4
2. Scots Pine						
1	95.5	1.04	14.5	71.3	1.00	4.0
2	92.3	0.87	16.1	87.6	0.68	1.6
3	97.5	1.03	10.5	79.5	1.27	4.1
4	95.0	1.93	28.4	71.3	0.82	3.3
5	85.7	0.99	25.8	91.5	1.48	2.9
6	93.1	0.85	14.9	85.6	1.15	3.0
7	98.1	1.12	10.0	81.8	1.35	4.0
8	91.0	1.13	22.8	81.2	1.32	4.0
9	69.8	0.69	29.2	51.9	0.65	4.0
10	55.1	0.80	46.3	92.3	1.16	2.1
11*						
3. White Spruce						
1	0.95	1.10	43.6	71.9	1.24	7.4
2	0.84	0.99	74.7	93.9	1.40	3.4
3	0.89	1.96	116.8	68.6	1.04	6.7
4	0.99	1.01	15.6	92.9	1.16	3.0
5	0.87	0.72	48.0	93.6	1.21	3.0
6	0.90	1.11	61.7	89.8	0.91	2.9
7	0.97	1.04	31.1	30.9	0.55	7.8
8	0.99	0.83	17.4	83.0	0.91	3.9
9	0.82	1.10	89.0	81.5	1.09	4.9
10	0.82	0.62	49.8	76.7	1.30	6.8
11	0.99	0.80	11.8	96.4	1.01	1.8
12	0.83	0.73	45.2	23.5	0.18	3.1
4. Sitka Spruce						
1	95.0	1.27	18.5	93.4	0.97	3.5
2	93.3	1.74	29.6	95.7	1.24	3.6
3*						
4	95.5	1.62	22.3	95.1	1.37	4.2
5	81.7	0.90	27.2	93.2	1.06	3.9
6	49.0	0.75	48.9	97.6	0.94	2.0
7	93.5	1.17	19.7	94.3	1.14	3.8
8	75.8	0.92	33.07	86.8	0.79	4.2
9*						
10	86.6	1.07	26.9	94.4	1.00	3.3
11	90.6	1.05	21.5	89.2	1.12	5.3
12	2.8	—0.23	84.9	12.1	0.17	6.3

(* Missing from some treatments)

Conclusion

Throughout the history of provenance evaluation in forest trees, intraspecific provenance-environment interactions have been observed, usually detected through the general analysis of variance. Few workers attempt to examine the contributions of individual provenances to the interactions, although numerical techniques have been developed, largely with agricultural crops. Further, in most field studies there is not an unequivocal independent unit of measurement that reflects the productivity of each site or that allows separation of the many interacting environmental factors.

In this study we chose to vary one major factor (temperature) while holding others constant. By using a reasonable number of provenances from each of four species with similar, natural, latitudinal ranges it was hoped to assess the contribution of individual species and provenances to any interaction effects.

The extent of interaction between genetic factors and temperature differences varied between species and between the growth characteristics assessed. However, once the presence of an interaction was detected, it was partitioned into contributions from single provenances by stability analysis (regression of provenance mean on treatment mean). This technique allowed the identification of adaptable provenances that react positively to environmental changes (as assessed by the mean of all provenances in a given environment). Also, regression of seedling growth on latitude of seed origin within each treatment separately showed that some environmental conditions facilitate this type of separation of provenances within a species; the usual north-south trends were confirmed but the stability analysis suggested that the distribution of stability parameters was not so straightforward. Depending upon the species and the character, maximum adaptability (b = 1.0) was found variously in northern, central or southern groups, although most frequently it occurred in the central group of four provenances. Northern and southern groups tended to deviate more from the average stability but the deviations were in both directions, *i. e.* in these groups some provenances were little affected by environmental changes while others responded more than the average to changes in environment.

These experiments were carried out in growth cabinets with only one environmental variable; clearly they cannot be extrapolated directly to field conditions. However, they do demonstrate that species differ in the extent of provenance-environment interaction and that individual provenances and environments contribute varying amounts to such interactions. Methods of analysing these contributions were tested and appear useful for experiments of this type with forest trees. They could certainly assist in the early screening of large numbers of provenances for which general patterns of variation were known.

Summary

Seedlings of up to 12 provenances in each of four species (*Pinus banksiana* Lamb., *Pinus silvestris* L., *Picea glauca* (Moench) Voss and *Picea sitchensis* (Bong.) Carr.) were grown for three months in growth cabinets under six temperature regimes (two day temperatures, 20 and 30^0 C, combined factorially with three night temperatures 10, 20 and 30^0 C). Seedling response was assessed by fresh weight, dry weight, dry/fresh weight ratio, height, and frequency of terminal buds. The presence and importance of provenance × temperature interaction effects were determined by analysis of variance. The contributions of individual provenances and treatments to these interactions were assessed by stability analysis and by regression of seedling growth characteristics on latitude of seed origin. The extent and pattern of provenance adaptability or stability varied between species and for different characters, with greater adaptability being demonstrated commonly by provenances near the centre of the natural distributions. The techniques would allow early discrimination on the basis of stability among large numbers of provenances of known or predictable mean performance.

Key words: Pinus banksiana, Pinus sylvestris, Picea glauca, Picea sitchensis, Provenance, Genotype — environment interation, Thermoperiod.

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