

Geographic Variation in Ponderosa Pine

II. Correlations Between Progeny Performance and Characteristics of the Native Habitat

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In a previous paper the results of a range-wide provenance test of ponderosa pine at East Lansing, Michigan were presented.²⁾ The geographic variation pattern, as interpreted from this test, was described as discontinuous. The seedling progenies fell into five more or less distinct groups and the distribution of these groups was given. The present paper gives the results of correlation analyses involving seedling traits and factors of the climate at the seed source. The evolutionary significance of these results is discussed.

Methods and Materials

Progenies from 60 different stands were grown in a replicated nursery test in East Lansing for 2 years. The seed collections sampled the range of *P. ponderosa* var. *ponderosa* and *P. ponderosa* var. *scopulorum* in the United States (Figure 1). Seed weight and 22 seedling characters were scored in the nursery.

Significant variation in each of these characters was demonstrated by analysis of variance. Simple correlation analyses were then computed among seedling characters and between seedling characters and climatic factors at the seed source origin. Seed weight, a parental character, was also included as a variable.

The climatic, seedling, and parental characters are listed below.

Climatic variables at seed source:

Average April-June temperature
July mean temperature
January mean temperature
July mean temperature minus January mean temperature.

Length of growing season
Date that growing season starts
Day length at start of growing season.

September-June precipitation
Annual precipitation
September precipitation-June precipitation.

Annual precipitation

Seedling variables at East Lansing:

Date of germination
Number of seedlings germinating in second year
Number of chlorotic seedlings.
Foliage color in July 1960, August 1960, October 1961, and June 1961
Stem color in June 1961
Number of seedlings forming secondary needles during the first growing season
Length of secondary needles
Extent of winter injury

Number of trees forming terminal buds during the first growing season

Terminal bud scale type

Number of seedlings having Lammas growth

First-year height

Second-year height.

Parental variable at seed source:

Seed weight.

The correlation coefficient between each climatic variable and each seedling and parental variable was computed separately for each region and ecotype. This involved seven computations of each correlation coefficient. Referring to the ecotype designations in figure 1, the seven analyses were performed on data from ecotypes (A + B), (A), (B), (C + D + E), (C), (D), and (E).

Stand-progeny means were used as items in all of the correlation analyses. Thus the correlation coefficients apply specifically to stand means.

Results

Correlations between Progeny Traits and Climatic Factors at the Place of Origin

The progeny-environment relationships in which significant correlation coefficients appear in at least one region or ecotype are presented in table 1. The three precipitation

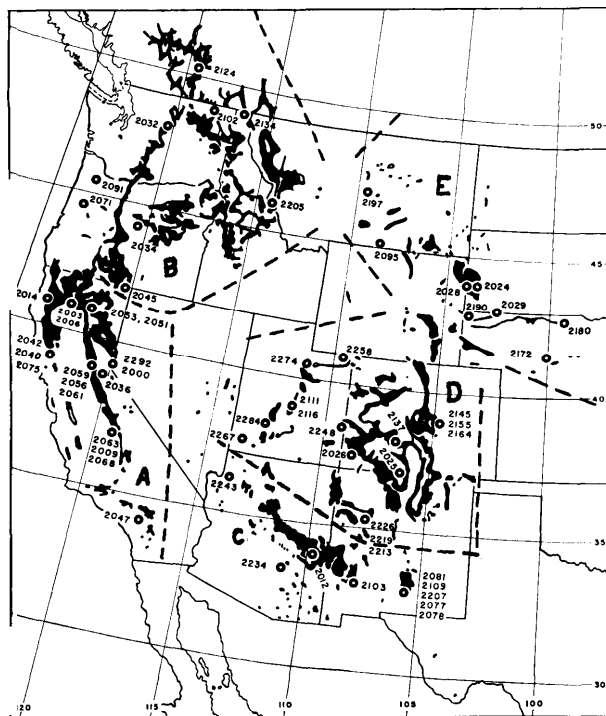


Figure 1. — Ecotypic division of Ponderosa pine progenies grown for two years at East Lansing. A = California, B = Northern Plateau and Willamette Valley, C = Southern Interior, D = Central Interior, E = Northern Interior. Numbers show the location of the stands which were sampled. (Distribution map by E. L. LITTLE Jr., U. S. Forest Service.)

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²⁾ WELLS, OSBORN O.: "Geographic variation in ponderosa pine. I. The ecotypes and their distribution." *Silvae Genetica* 13, 89-103 (1964).

factors were very strongly correlated with the same progeny characters. Therefore, only the correlations with annual precipitation are presented.

Thirty-two percent of the progeny-environment correlations were significant when calculated with data from an entire region. The same correlations were evident only 3 percent of the time when calculated with data from the ecotypes separately. This illustrates that many of the correlations were among ecotype means rather than among stand means. In a few instances the within-ecotype correlation coefficients were as high as the within-region

coefficients but were not significant because of the low number of degrees of freedom. It is probable that most of the correlations involving only progenies from the Pacific Northwest were also the result of discontinuous distribution and variation. The two Willamette Valley sources (MSFG-2071 and MSFG-2091) were different from the other Pacific Northwest sources in several characters and most of the significant correlations could be traced to this discontinuity.

Correlations involving average April-June temperature. — When all Pacific Coast sources were considered, an in-

Table 1. — Correlations between progeny traits and climatic factors at the place of origin in ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.).

Correlation applies to:		Pacific Coast Region			Interior Region			
Climatic factor	Seedling character	Entire region	Pacific Northwest	California	Entire region	Southern Interior	Central Interior	Northern Interior
Average spring temperature	(7) Foliage color, October, 1961	-.54**	-.60	.07	.00	.00	.00	.00
	(8) Stem color, June, 1961	-.25	.09	-.33	.52**	.09	.63**	.61
	(12) Basal needle mortality	.00	.00	.00	.49**	.67*	-.13	.75*
	(13) Winter injury	.62***	.61	.23	.42*	-.42	.00	.00
	(15) Terminal bud scale type	-.56**	-.52	.00	.00	.00	.00	.00
	(16) Number of lateral buds	--	--	--	.59***	.47	.38	.42
	(22) 2-year height	-.02	-.26	-.24	.60***	.67*	.42	.49
Average January temperature	(8) Stem color, June, 1961	-.11	-.22	-.30	.74***	-.07	.46	.36
	(10) Needle length	-.32	-.59	-.15	.54**	-.32	.27	.28
	(13) Winter injury	.53**	.94***	.52*	.73***	-.40	.35	.00
	(14) First year terminal buds	-.70***	-.72*	-.21	.08	.69*	.07	.56
	(16) Number of lateral buds	--	--	--	.43*	.15	.19	.09
	(17) Growth initiation	.71***	.73*	.30	.45**	-.02	.35	-.73*
	(21) 1-year height	.11	-.14	.50*	.50**	.09	.05	-.27
	(22) 2-year height	-.37	-.71*	-.26	.71***	.41	.20	.05
Average July temperature	(7) Foliage color, October, 1961	-.49**	-.36	.06	.00	.00	.00	.00
	(13) Winter injury	.50**	.29	.46	-.10	-.57	.00	.00
	(14) First year terminal buds	-.09	-.04	.07	.53**	.49	-.06	.33
	(15) Terminal bud scale type	-.52**	-.48	.00	.00	.00	.00	.00
	(21) 1-year height	.53**	-.18	.29	-.08	.70*	.09	-.30
Annual temperature range	(7) Foliage color, October, 1961	.69***	.63	.20	.00	.00	.00	.00
	(8) Stem color, June, 1961	.20	.34	.18	-.70***	-.20	-.31	.58
	(10) Needle length	.19	.08	.48	-.52**	.30	-.17	.74*
	(13) Winter injury	-.78***	-.88**	-.03	-.79***	-.52	.00	.00
	(14) First year terminal buds	.63***	.58	.45	.36*	-.03	.04	.53
	(15) Terminal bud scale type	.69***	.60	.00	.00	.00	.00	.00
	(17) Growth initiation	-.81***	-.84**	-.40	-.59***	-.20	-.11	-.72*
	(21) 1-year height	-.28	-.20	.08	-.54**	.62	.09	-.28
	(22) 2-year height	.20	.25	.69**	-.54**	.45	-.16	.37
Length of growing season	(7) Foliage color, October, 1961	-.59***	-.81**	.04	.00	.00	.00	.00
	(8) Stem color, June, 1961	-.32	-.09	-.40	.56***	-.14	.33	.59
	(10) Needle length	-.09	-.65	-.09	.38*	-.26	.21	.64
	(12) Basal needle mortality	.00	.00	.00	.47**	.67*	.02	.51
	(13) Winter injury	.71***	.92***	.41	.53**	-.60	.00	.00
	(15) Terminal bud scale type	-.60***	-.70*	.00	.00	.00	.00	.00
	(16) Number of lateral buds	--	--	--	.47**	.32	.06	.29
	(17) Growth initiation	.47*	.69*	.15	.21	.04	.24	.03
	(22) 2-year height	-.17	-.68*	-.29	.65***	.65	.14	.30
Date of growing season initiation	(7) Foliage color, October, 1961	.53**	.79*	-.17	.00	.00	.00	.00
	(8) Stem color, June, 1961	.35	.10	.44	-.52**	.12	-.22	-.57
	(12) Basal needle mortality	.00	.00	.00	.46**	-.67*	-.03	-.46
	(13) Winter injury	-.64***	-.87**	-.28	-.51**	.51	.00	.00
	(15) Terminal bud scale type	.56**	.69*	.00	.00	.00	.00	.00
	(16) Number of lateral buds	--	--	--	-.48**	-.31	-.12	-.27
	(22) 2-year height	.65***	.63	.08	-.63***	-.62	-.19	-.33
Day length at start of growing season	(7) Foliage color, October, 1961	.54**	.80**	-.14	.00	.00	.00	.00
	(8) Stem color, June, 1961	.35	.10	.47	-.67***	.11	-.38	-.65
	(10) Needle length	.04	.61	-.16	-.51**	.36	-.35	-.54
	(12) Basal needle mortality	.00	.00	.00	-.51**	-.67*	-.77***	-.54
	(13) Winter injury	-.65***	-.89***	-.25	-.60***	.48	.00	.00
	(15) Terminal bud scale type	.58**	.73*	.00	.00	.00	.00	.00
	(16) Number of lateral buds	--	--	--	-.46**	-.33	-.17	-.34
	(17) Growth initiation	.47*	-.62	-.02	-.36*	-.06	-.34	.66
	(22) 2-year height	.10	.64	.01	-.72***	-.62	-.32	-.46
Annual precipitation	(7) Foliage color, October, 1961	-.49**	-.71*	.02	.00	.00	.00	.00
	(13) Winter injury	.62***	.93***	.06	.46**	.78*	.00	.00
	(14) First year terminal buds	-.55***	-.62	.58*	-.26	-.52	-.11	.60
	(15) Terminal bud scale type	-.52**	-.67*	.00	.00	.00	.00	.00
	(17) Growth initiation	.63***	.89**	.49	.19	.27	-.19	-.16
Number of progenies in analysis		27	9	16	33	9	16	8
Value of r significant at 5 percent level (= *)		.38	.67	.50	.35	.67	.50	.71
Value of r significant at 1 percent level (= **)		.48	.80	.62	.44	.80	.62	.83
Value of r significant at 0.1 percent level (= ***)		.59	.90	.74	.55	.90	.74	.92

crease in spring temperature at the place of origin was accompanied by an increase in the amount of winter injury among the progenies in the nursery. Also, with higher spring temperatures there were fewer trees with exserted scales on the terminal buds and the foliage was lighter green.

When all Interior sources were considered, an increase in spring temperature at place of origin was accompanied by increased basal needle mortality, number of lateral buds, and 2-year height of the progenies in the nursery. In addition, progenies from localities with low spring temperatures had bright green stems in June whereas those from warm localities had gray stems.

In general, most of the significant correlations involving spring temperature were a result of discontinuous variation. Few of the within-ecotype correlations were significant and all of them were weak.

Correlations involving average January temperature. — When all Pacific Coast sources were considered, an increase in January temperature was accompanied by an increase in amount of winter injury and a decrease in percent of trees forming terminal buds during the first growing season. These relationships also held true for the progenies from the Pacific Northwest. The relationship between January temperature and winter injury holds true for the progenies from California.

When all Interior sources were considered, an increase in January temperature at the place of origin was accompanied by increases in needle length, amount of winter injury, number of lateral buds, 1-year height, and 2-year height. Also, seedlings from areas having low January temperatures had green stems in June and started growth later in the nursery. In the Interior region January temperature accounted for much more variation in seedling characters than did July temperature.

When the subdivisions within the Interior region were considered separately, the only relationship with January temperature that held true was the one involving growth initiation.

Correlations involving average July temperature. — When all Pacific Coast sources were considered, an increase in July temperature was accompanied by increased 1-year height and winter injury. There was also a tendency for those progenies that came from localities with low July temperatures to have darker green foliage in November and to form exserted bud scales. July temperature accounted for only about 25 percent of the variation in these characters.

When all Interior sources were considered, an increase in July temperature was accompanied by an increase in number of trees forming terminal buds the first year.

When the ecotypes were considered individually, a single strong correlation was evident. In the Southern Interior ecotype, as the July temperature rose the 1-year height of the progeny increased. The coefficient of determination ($= r^2$) is .49 in this case, indicating that 49 percent of the variation in 1-year height was accounted for by variation in July temperature, indicative of a clinal variation pattern.

Correlations involving the difference between average July and average January temperature. — When all Pacific Coast sources were considered, an increase in annual temperature range at the place of origin was accompanied by a decrease in winter injury and an increase in the percent of trees that formed terminal buds the first year.

Progenies from localities with a small temperature range had light green foliage in November whereas those from localities with a large temperature range had dark green foliage. In addition, progenies from areas with a small temperature range had little tendency to form exserted scales on the terminal buds. These relationships were strong.

If only the Pacific Northwest sources were considered, the temperature range-seedling character correlations were significant and very strong for amount of winter injury ($r^2 = 0.78$) and date of growth initiation ($r^2 = 0.70$) but not for other seedling characters.

When all Interior sources were considered, an increase in annual temperature range was accompanied by decreases in needle length, winter injury, 1-year height, and 2-year height. In addition, progenies from localities with a small temperature range had gray stems in June and started growth late whereas those from localities with a large temperature range had bright green stems and started growth early. The relationship between annual temperature range and needle length was reversed if only the Northern Interior sources were considered.

Correlations involving length of growing season. — If all Pacific Coast sources were considered, an increase in length of growing season at the place of origin was accompanied by an increase in winter injury. There was also a tendency for those progenies from localities having short growing seasons to have dark green foliage in November and exserted scales on the terminal buds.

All of these relationships held true when the Pacific Northwest sources were considered separately. None of them held true when only the California sources were considered. The relationships were considerably stronger in the Pacific Northwest than they were over the region as a whole.

When all Interior sources were considered, an increase in length of growing season was accompanied by increases in winter injury, 2-year height, needle length, basal needle mortality, and number of lateral buds. Also, seedlings from areas that have short growing seasons had bright green stems whereas those from areas with long growing seasons had gray stems.

The relationship with basal needle mortality holds true in the Southern Interior ecotype. Other ecotypic correlations involving length of growing season were not significant.

Correlations involving date of growing season initiation.

— When all Pacific Coast sources were considered, those progenies from localities where the growing season starts early tended to have light green foliage in November, terminal buds with appressed scales, and heavy winter injury. The seedlings from areas where the growing season starts early were taller at the end of the second year in spite of severe injury during the first winter.

All relationships except that with 2-year height were significant if only the Pacific Northwest progenies were considered. None were significant if only the California sources were considered.

When all Interior sources were considered, the progenies from areas with a long growing season tended to have gray foliage in November of the second year, more winter injury, greater 2-year heights, and more lateral buds.

Correlations involving day length at start of growing season. — When all the Pacific Coast sources were considered, short day length at start of growing season was

accompanied by slight winter injury, light green foliage in November, and a slight tendency to form exserted scales on the terminal buds. All of these relationships held true if only the Pacific Northwest sources were considered but none held true if only the California sources were considered.

When all Interior sources were considered, an increase in day length at the start of growing season was accompanied by decreases in needle length, basal needle mortality, and number of lateral buds. In addition, progenies from localities with short days at the beginning of the growing season had gray stems in June whereas those from localities with long days at the beginning of the growing season had bright green stems.

The relationship with basal needle mortality held true in the Southern Interior ecotype. Other ecotype correlations involving day length at start of growing season were not significant.

Correlations involving annual precipitation. — When all Pacific Coast sources were considered, progenies from areas with high annual precipitation suffered most winter injury, started growth latest, had light green foliage, and had a high percent of trees forming terminal buds the first year.

The relationship involving first-year terminal buds was the only one which was not significant if only the Pacific Northwest sources were considered and was the only one which was significant if only the California sources were considered.

Annual precipitation was associated only with amount of winter injury within the Rocky Mountain variety.

Seed Weight — Climatic Factor Correlations

The seed weight-climate correlations are presented in table 2. There were higher correlations between seed weight and climate at the place of origin than between seedling characters and climate at the place of origin. Forty-one percent of all possible seed weight-climate correlations were significant at the 5 percent level whereas only 15 percent of the seedling character-climate correlations were significant. This is probably due to the fact that seed weight is a parental character and is subject to

phenotypic modification by the climate at the place of origin.

In the Interior region and the Southern Interior ecotype seed weight was significantly and strongly correlated with several climatic factors. Seeds from areas with warm climates, long growing seasons, or low precipitation were largest. In the Pacific Northwest seeds from areas with low precipitation were also the largest but the relationships with growing season and temperature factors were reversed. The largest seeds came from areas with cold climates and short growing seasons. The relationship between seed weight and annual precipitation, however, is positive in both the Pacific Northwest and the Southwest. This indicates the presence of a direct cause-and-effect relationship. It lends support to the observation first reported by TOUMEX (1916)³⁾ that conifers from low spring rainfall areas tend to have large seed. One would logically expect natural selection to have favored the development of large-seeded types in low-rainfall areas. Seeds germinating in moisture-deficient soil would benefit from large food reserves and the ability of the roots to penetrate the soil rapidly.

The seed weight-winter temperature and seed weight-length of growing season correlations were reversed between the Pacific Northwest and the Interior. This in itself is indicative that there was no direct cause-and-effect relationship between seed weight and either climatic factor. Instead, it is more logical to assume that the relationships are indirect through precipitation. In the Pacific Northwest the high winter and spring temperatures occur near the coast where the precipitation is higher than it is inland. In the Interior region the higher temperatures occur at low elevations where the precipitation is less than it is at higher elevations.

Correlations among Progeny Traits

All possible simple correlations were calculated among seed weight and the 13 progeny characters. Stand-progeny means were used as items and the analysis was repeated for each of the seven regions and ecotypes. All correla-

³⁾ TOUMEX, J. W., 1916: Seeding and planting in the practice of silviculture. New York: John Wiley and Sons, Inc. London: Chapman and Hall, Ltd. 455 pp.

Table 2. — Correlations between seed weight and climatic factors at place of origin for regions and ecotypes

Correlation between seed weight and:	Region or ecotype to which correlation applies						
	Pacific Coast region			Interior region			
	Entire region	Pacific Northwest	California	Entire region	Southern Interior	Central Interior	Northern Interior
Average spring temperature	-.02	-.66	.18	.69***	.85***	-.03	.72*
Average January temperature	-.22	-.91***	.02	.55***	.87**	.11	.26
Average July temperature	.05	-.43	.22	.62***	.75*	.32	.75*
Annual temperature range	.41*	.78*	.42	-.04	.10	.26	.80*
Length of growing season	-.16	-.86**	.07	.77***	.93***	.40	.65
Date of growing season initiation	.17	.82**	-.17	.76***	-.93***	-.41	-.59
Day length at start of growing season	.17	.85**	-.15	-.66***	-.92***	-.27	-.55
Annual precipitation	-.26	-.86**	-.21	.05	-.82**	.12	.51
Number of progenies in analysis	27	9	16	33	9	16	8
Value of r significant at 5 percent level	.38	.67	.50	.35	.67	.50	.71
Value of r significant at 1 percent level	.48	.80	.62	.44	.80	.62	.83
Value of r significant at 0.1 percent level	.59	.90	.74	.55	.90	.74	.92

Significant at 5 percent level = *
Significant at 1 percent level = **
Significant at 0.1 percent level = ***

tion coefficients that were significant in at least one region or ecotype are presented in table 3. A total of 98 were significant at the 5, 1, or 0.1 percent levels.

Forty-six percent of the correlations among progeny traits were significant when calculated with data from an entire region. The same correlations were evident only 18

percent of the time when calculated with data from separate ecotypes. Thus, many of the correlations were among ecotype means rather than among stand means.

Those correlations which are of value in predicting the most important economic characters (winter injury and height) are discussed below.

Table 3. — Correlations among progeny traits in ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.).

Characters to which correlation applies		Pacific Coast Region			:	Interior Region			
		Entire region	Pacific Northwest	California		Entire region	Southern-Interior	Central-Interior	Northern-Interior
(1) Seed weight	(5) Foliage color Aug., 1960	.11	.19	-.15		.49**	.60	.33	.87**
	(6) Foliage color Oct., 1960	-.15	.06	-.38		-.47**	-.17	-.43	-.31
	(12) Basal needle mortality	.00	.00	.00		.55***	.68***	.68*	.65
	(13) Winter injury	-.15	-.92***	.33		.37*	-.71*	-.23	.00
	(14) First year terminal buds	.27	.36	.75***		.50**	.72*	.32	.31
	(15) Terminal bud scale type	.24	.00	.83***		.00	.00	.00	.00
	(16) Number of lateral buds	--	--	--		.47**	.37	-.14	.34
	(17) Growth initiation	-.24	-.33	-.66**		-.16	-.11	-.39	-.74*
	(22) 2-year height	.27	.54	.22		.44**	.55	-.32	.23
	(21) 1-year height	.28	-.11	.47		.30	.20	.02	.15
(5) Foliage color Aug., 1960	(6) Foliage color Oct., 1960	.09	-.24	.27		-.48**	-.11	-.49	-.22
	(17) Growth initiation	.05	.31	.11		-.40*	-.01	.13	-.88**
(6) Foliage color Oct., 1960	(10) Needle length	-.39*	-.70*	-.16		.29	-.20	.67***	-.69
	(14) First year terminal buds	.18	.15	-.33		-.48**	.02	-.44	-.42
	(17) Growth initiation	-.21	-.26	.33		.52**	.62	.48	.42
(7) Foliage color Oct., 1961	(14) First year terminal buds	.62***	.45	-.10		.00	.00	.00	.00
	(15) Terminal bud scale type	.83***	.66	.00		.00	.00	.00	.00
	(17) Growth initiation	-.76***	-.83**	.03		.00	.00	.00	.00
	(18) Lammas growth	-.45*	-.21	.05		.00	.00	.00	.00
	(13) Winter injury	-.85***	-.82**	.09		.00	.00	.00	.00
(8) Stem color June, 1961	(10) Needle length	-.06	.35	.10		.80***	.68*	.53*	.66
	(13) Winter injury	-.12	-.07	-.19		.87***	.66	.33	.00
	(16) Number of lateral buds	--	--	--		.08	.16	.86***	
	(17) Growth initiation	-.17	-.57	-.31		.66***	.35	.63**	.45
	(21) 1-year height	.10	.19	.38		.59***	-.14	.02	.07
	(22) 2-year height	.15	.22	.17		.81***	.10	.47	.86***
(10) Needle length	(13) Winter injury	-.03	.42	-.14		.70***	.33	.43	.00
	(14) First year terminal buds	.22	-.33	.38		-.42*	.05	-.67**	.12
	(16) Number of lateral buds	--	--	--		.45**	-.43	.57*	.72*
	(17) Growth initiation	-.14	.33	-.46		.80***	-.15	.88***	-.38
	(21) 1-year height	.23	.50	.04		.53**	-.04	.54*	-.41
	(22) 2-year height	.42	.74	.31		.80***	.15	.92***	.63
(12) Basal needle mortality	(14) First year terminal buds	.00	.00	.00		.46**	.71*	.56*	.58
(13) Winter injury	(14) First year terminal buds	-.77***	-.20	-.70**		-.21	-.32	-.24	.00
	(15) Terminal bud scale type	-.89***	.00	-.79***		.00	.00	.00	.00
	(16) Number of lateral buds	--	--	--		.45**	-.04	.27	.00
	(17) Growth initiation	.83***	.32	.85***		.55***	.50	.39	.00
	(21) 1-year height	.57**	.78*	-.07		.67***	-.27	.22	.00
	(22) 2-year height	.07	-.71*	.29		.74***	-.49	.28	.00
(14) Trees forming terminal buds at age 1	(15) Terminal bud scale type	.75***	.00	.70**		.00	.00	.00	.00
	(16) Number of lateral buds	--	--	--		.04	.33	-.63**	.16
	(17) Growth initiation	-.79***	-.95***	-.51*		-.64***	-.18	-.76***	-.55
(15) Terminal bud scale type	(17) Growth initiation	-.71***	.00	-.60*		.00	.00	.00	.00
	(18) Lammas growth	-.56**	.00	-.52*		.00	.00	.00	.00
	(22) 2-year height	-.03	.68*	.00		.00	.00	.00	.00
(16) Number of lateral buds	(20) Amount of lean	--	--	--		-.54**	.00	-.49	.00
	(21) 1-year height	--	--	--		.47**	.36	.78***	.16
	(22) 2-year height	--	--	--		.65***	.30	.67**	.85**
(17) Date of growth initiation	(21) 1-year height	.26	.00	-.07		.54**	.35	.78***	-.23
	(22) 2-year height	-.14	-.63	-.06		.61***	.01	.64**	-.21
(20) Amount of lean	(21) 1-year height	.00	.00	.00		-.32	.00	-.71**	.00
	(22) 2-year height	.00	.00	.00		-.48**	.00	-.74***	.00
(21) 1-year height	(22) 2-year height	.32	.51	.15		.69***	.53	.65***	.06
Number of progenies in analysis		27	9	16		33	9	16	8
Value of r significant at 5 percent level (= *)		.38	.67	.50		.35	.67	.50	.71
Value of r significant at 1 percent level (= **)		.48	.80	.62		.44	.80	.62	.83
Value of r significant at 0.1 percent level (= ***)		.59	.90	.74		.55	.90	.74	.92

Within the Interior variety and within the California ecotype seed weight was correlated with 1-year height at the 10 percent level and with 2-year height at the 1 percent level of significance. There are three reasons for suspecting that these were not direct cause-and-effect relationships. First, both characters are correlated with a number of climatic factors of the parental habitat. Second, albino seedlings which depend for their entire growth on food reserves stored in the seed grew to only a small fraction of the size attained by green seedlings in one year. Third was the absence of significant seed weight-height correlations within the individual Interior ecotypes.

Other significant character-character correlations are:

1. June stem color progressed from green to gray as winter injury, 1-year height, and 2-year height increased in the Interior variety. June stem color and 2-year height were also associated in the Northern Interior ecotype.
2. Needle length increased as 1- and 2-year height increased in the Interior variety and the Central Interior ecotype.
3. Percent of trees forming terminal buds the first year increased as winter injury decreased in the Pacific Coast variety and the California ecotype.
4. Winter injury increased as 1-year height increased in the Pacific Coast and Interior varieties and in the Pacific Northwest progenies. Winter injury increased as 2-year height increased in the Interior variety and the Pacific Northwest progenies.
5. One- and two-year heights were significantly correlated in the Interior variety and the Central Interior ecotype. The heavy winter damage suffered by the California seedlings precluded finding such a significant correlation within the Pacific Coast population.

Evolution of the Ecotypes

The numerous significant associations between seedling characters and factors of the climate indicate that selection pressure has been a primary differentiating force responsible for the present characteristics of the ecotypes. A number of characters are obviously adaptive and the selection mechanism responsible for their evolution can be easily postulated. Growth rate, cold resistance, presence or absence of first-year terminal buds, and date of growth initiation are examples of these characters.

A number of characters which are of equal importance in distinguishing the ecotypes are very difficult to explain on the basis of selection pressure. Foliage and stem color are in this category. The Northern Plateau ecotype was most easily identified by the distinctive dark-green color of its foliage. The character was common to all sources from the Northern Plateau which indicates that it is probably adaptive or linked to genes which control an important character that is adaptive. The physiological link between the selective factor of the climate and expression of the dark-green color in the foliage of the seedlings is not clear, however.

Number of needles per fascicle and needle length are other diagnostic characters which cannot be explained easily on the basis of selection pressure. Some other factor, such as geographic or reproductive isolation, population size, population density, or genetic drift, must have had a part in the evolution of these characters.

The differences between the typical variety of the Pacific Coast and the Rocky Mountain variety is one case where factors other than selection pressure have determined evolution. When the climatic factors in the regions

occupied by the two varieties are compared the only climatic factor that shows a distinct break is the seasonal distribution of precipitation ^(Sept.—June) _{annual}. This contrasts

with the results of the correlation analysis which showed that many characteristics of the varieties could be related to factors of the environment within the region occupied by each variety. Moreover, it does not seem reasonable to attribute the relatively large differences in morphology and growth behavior that distinguish the two varieties to the seasonal distribution of the precipitation. If there is a physiological link between this climatic factor and the development of these particular differences it is not apparent. It seems more likely that the large differences between the two varieties are of a more ancient origin than the differences between ecotypes within either one of the varieties. Whereas the smaller differences between ecotypes are reflected in climatic differences in the modern climate the larger differences between the two varieties stem from more ancient causes that are not reflected in relatively ephemeral weather records of the past 70 years.

The distinct differences among the central Colorado progenies is an example of the combined effects of selection pressure, population density, and reproductive isolation. MSFG-2137 is from 9000 feet elevation in the mountainous country about 100 miles southwest of Colorado Springs. MSFG-2164 is from 9000 feet elevation about 10 miles northwest of Colorado Springs. Progenies from these two sources are very similar when grown in the East Lansing nursery. MSFG-2155, which is from 7200 feet elevation about 3 miles northwest of Colorado Springs is similar to them in all characters even though the climatic conditions in which they grow are quite different. This is probably due to the fact that there is a lateral distance of only seven miles between MSFG-2155 and MSFG-2164 with continuous forest between. Gene flow between generations of trees growing in these two areas must have been considerable. This would have tended to negate the differentiating effects of differing selection pressures.

The third progeny from this area (MSFG-2145) is from a small stand in the relatively flat country northeast of Colorado Springs and is isolated from the continuous forest in the more precipitous country to the west by about 4 miles. It differs from the other central Colorado progenies in rate of height growth and date of growth initiation. A reproductive isolation barrier is indicated by the fact that the growing season starts about two and one-half weeks earlier in the parent vicinity of MSFG-2145 than it does in the parent vicinity of MSFG-2155. Presumably, these geographic and reproductive isolation barriers have allowed this population to differentiate genetically in response to the selection forces in its particular environment without being swamped by gene flow from neighboring stands.

The break in northeastern California between the California and Northern Plateau ecotypes seems to be due to the combined effects of selection pressure and reproductive isolation. Pronounced differences between MSFG-2045 and the other California progenies indicate that the boundary between the California and Northern Plateau ecotypes is sharply defined in northeastern California. The break in seedling characters across the crest of the Sierra Nevada in northeastern California corresponds to a sharp break in January temperature. None of the other climatic factors show such a degree of discontinuity. Apparently, low temperatures have been a strong selection force. The available distribution data, however, indicate that the distribution

of the species is continuous in this area. In order for the pronounced discontinuity between the two ecotypes to develop, an isolation barrier of some sort would have had to be present. The climatic data indicate that this barrier is reproductive in nature. The growing season starts approximately three weeks later in the vicinity of MSFG-2045 than it does in the parent vicinities of the other northern California progenies. This indicates a difference in flowering times which would effectively isolate the two ecotypes.

The effects of selection pressure and geographic isolation are evident in the break between the Southern and Central Interior ecotypes and in central Utah. The selective force which caused differentiation between the Southern Interior and Central Interior ecotypes is probably minimum temperature. There are two lines of evidence to support this hypothesis. First, in the Interior region there are seven significant correlations between January temperature and progeny traits. This was more than with any other climatic factor (table 1). Second, there is a temperature break across the dividing line between the Southern Interior and Central Interior ecotypes. The average minimum temperature in the area occupied by the Southern Interior ecotype ranges from 0 to -10° F. In northern New Mexico and in Colorado the minimum temperatures are generally lower (Atlas of American Agriculture, 1936). The extensive lowland area between the Mogollon plateau of Arizona and New Mexico and the central Colorado plateau has apparently restricted gene flow enough to permit genetic differentiation of the two ecotypes.

In Utah, the point where the progenies begin to show some affinities to those from the Northern Interior ecotype corresponds to a break in average minimum temperature. Southeastern and central Utah have minimum temperatures from -5° F. to -10° F. Northeastern Utah has lower minimum temperatures that approach those found in the Northern Interior ecotype. Thus, the selective effect of minimum temperature is again indicated. The isolation which has allowed these populations to differentiate in response to this selection pressure is geographic. The ponderosa pine in central Utah occurs in scattered stands which are separated by areas of low elevation.

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Summary

Two hundred and ninety eight individual-tree progenies of ponderosa pine from 60 different stands were grown in East Lansing, Michigan, for 2 years. The collections sampled the range of *P. ponderosa* var. *ponderosa* and *P. ponderosa* var. *scopulorum* in the United States. The stock was grown in a replicated nursery test.

Seed weight and 22 seedling characters were scored in the nursery. The data were subjected to analyses of variance in order to determine the amount of genetic variance present, summation-of-difference analyses in order to determine the multi-character relationships between pro-

venances, and correlation analyses. The latter analyses were made between seedling characters and 10 climatic factors at the place of origin, and among seedling characters.

These analyses, in addition to general observation in the nursery, all indicated the presence of a predominantly discontinuous genetic variation pattern both between and within the two varieties of ponderosa pine in the United States.

The correlation analyses indicated that many of the seedling characters were significantly associated with factors of the climate. This indicates that selection pressure has been the primary differentiating force responsible for the present characteristics of the ecotypes. Minimum winter temperature, especially, was significantly correlated with seedling characters.

The isolation barriers which allowed the ecotypes to differentiate genetically in response to different selection pressures were geographic for the most part. The crest of the Sierra Nevada separates the California and Pacific Northwest ecotypes in northeastern California. The Cascade Mountains isolate the Willamette Valley populations from the more extensive inland populations of the Pacific Northwest. The extensive treeless area between the Mogollon Plateau in southern New Mexico and Arizona, and the Colorado Plateaus to the north, separates the Southern Interior and Central Interior ecotypes. The combined effects of selection pressure due to minimum winter temperature and geographic isolation was postulated to be responsible for genetic differentiation among the Utah progenies. The combined effects of selection pressure, population density, and reproductive isolation appear to be responsible for differences among progenies from near Colorado Springs, Colorado.

Although the differences in seedling characters within a variety were often associated with factors of the climate the larger differences between progenies from the typical variety and the progenies from the Rocky Mountain variety were not. This indicates that the two varieties arose earlier in geological time than the ecotypes. The selection forces and other factors responsible for their evolution are not reflected in modern weather records.

Résumé

Titre de l'article: *Variation géographique chez Pinus ponderosa. II. Corrélations entre le comportement des descendance et les caractéristiques de la station d'origine.*

298 descendance individuelles de *Pinus ponderosa* venant de 60 peuplements différents ont été élevées à East Lansing, Michigan pendant 2 ans. Ces descendance représentaient un échantillonnage de l'aire de *Pinus ponderosa* var. *ponderosa* et *Pinus ponderosa* var. *scopulorum* aux Etats-Unis. Les plants ont été élevés dans un test de pépinière avec répétitions.

On a mesuré le poids des graines et, en pépinière, 22 caractères des semis. Les données ont été soumises à des analyses de variance afin de déterminer la proportion de variance génétique; d'autres analyses ont permis de déterminer les relations multiples entre caractères pour les différentes provenances. Les analyses de corrélation ont été faites entre les caractères des semis et 10 facteurs climatiques du lieu d'origine, ainsi qu'entre les caractères relevés sur les semis.

Ces analyses, de même que l'observation directe en pépinière, indiquent la présence d'une variation génétique

de nature nettement discontinue aussi bien entre les deux variétés qu'à l'intérieur de chacune d'elles.

Les analyses de corrélation indiquent que beaucoup de caractères des semis sont liés de façon significative avec des éléments du climat. Cela montre que la pression de sélection a été le facteur primordial de différenciation, responsable des caractères actuels des écotypes. En particulier, les températures minima hivernales sont liées de façon significative avec les caractéristiques des semis.

Les barrières d'isolement, qui permettent la différenciation génétique des écotypes en réponse aux différentes pressions de sélection, sont surtout de nature géographique. La crête de la Sierra Nevada sépare les écotypes de Californie et ceux du «Pacifique Nord-Ouest» dans le Nord-Est de la Californie. Les Monts Cascade isolent les populations de Williamette Valley des populations intérieures plus étendues du «Pacifique Nord-Ouest». La grande zone sans forêt entre le Plateau Mogollon dans le Sud du Nouveau Mexique et de l'Arizona, et le Plateau du Colorado vers le nord, sépare les écotypes de la zone intérieure du Sud et de la zone intérieure du Centre. Les effets combinés de la pression de sélection dus aux températures minima et de l'isolement géographique sont supposés responsables de la différenciation génétique dans les descendances de l'Utah. Les effets combinés de la pression de sélection et de l'effectif de la population paraissent responsables des différences entre les descendances de Colorado Springs, Colorado.

Bien que les différences dans les caractères des semis à l'intérieur d'une variété soient très souvent liées avec les facteurs du climat, il n'en est pas de même pour les différences plus grandes entre les descendances du type et celles de la variété des Montagnes rocheuses. Cela indique que les deux variétés se sont différenciées dans les temps géologiques plus tôt que les écotypes. Les forces de sélection et autres facteurs responsables de leur évolution ne se retrouvent plus dans les données climatiques actuelles.

Zusammenfassung

Titel der Arbeit: *Geographische Variation bei der Ponderosa-Kiefer. II. Korrelationen zwischen der Leistung der Nachkommenschaft und Merkmalen ihres Herkunftsortes.*

298 Einzelbaum-Nachkommenschaften der Ponderosa-Kiefer von 60 verschiedenen Beständen stockten in East-Lansing, Michigan, seit 2 Jahren. Diese Sammlung enthielt Proben des Verbreitungsgebietes von *Pinus ponderosa* var. *ponderosa* und *P. ponderosa* var. *scopulorum* in den U.S.A. Das Pflanzenmaterial entstammte einem wiederholten Baumschultest.

Samengewichte und 22 Sämlingsmerkmale waren in der Baumschule festgestellt worden. Die Daten waren zu einer Varianz-Analyse verwendet worden, um die Summe der vorhandenen genetischen Varianz festzustellen, ferner zu "summation-of-difference"-Analysen zur Ermittlung von "multi-character"-Beziehungen zwischen den Herkunftsorten und zu Korrelations-Analysen. Letztere wurden zwischen Sämlingsmerkmalen und 10 Klimafaktoren des Herkunftsortes und den Sämlingsmerkmalen durchgeführt.

Diese Analysen zeigen alle in Ergänzung zu den allgemeinen Beobachtungen in der Baumschule das Vorhandensein einer ausgeprägten diskontinuierlichen genetischen Variation sowohl zwischen den 2 Ponderosa-Varietäten als auch innerhalb derselben in den U. S. A. an.

Die Korrelationsanalysen wiesen nach, daß viele Sämlingsmerkmale signifikant mit Klimafaktoren assoziiert waren. Dies besagt, daß der Selektionsdruck die primäre Kraft für die Differenzierung der gegenwärtigen Ökotypenmerkmale gewesen war. Besonders die Tiefsttemperatur im Winter war mit solchen Sämlingsmerkmalen eng korreliert.

Die Isolierungsbarrieren, die eine genetische Differenzierung der Ökotypen als Folge verschiedenen Selektionsdruckes erlaubten, waren meist geographischer Natur. Der Kamm der Sierra Nevada trennt die kalifornischen und die nordwest-pazifischen Ökotypen in NO-California. Die Cascaden isolieren die Williamette-Tal-Populationen von den verbreiteten Inlandpopulationen des pazifischen Nordwestens. Das ausgedehnte baumlose Gebiet zwischen dem Mogollon-Plateau in Süd-Neumexiko und Arizona und die Colorado-Ebenen im Norden trennen die südlichen Inlands- von den zentralen Inlands-Ökotypen. Die kombinierten Effekte des Selektionsdruckes, der Tiefsttemperatur im Winter und der geographischen Isolierung müssen auch für die genetische Differenzierung der Nachkommenschaften aus Utah verantwortlich sein. Die kombinierten Effekte von Selektionsdruck, Populationsdichte und reproduktiver Isolierung scheinen ferner für die Unterschiede zwischen den Nachkommenschaften der Gegend nahe den Colorado-Springs verantwortlich zu sein.

Obwohl die Unterschiede in den Sämlingsmerkmalen innerhalb der Varietät oft mit Klimafaktoren assoziiert gewesen waren, so waren dies doch die weit größeren Unterschiede zwischen den Nachkommenschaften der typischen Varietät und denen der Rocky-Mountain-Varietät nicht. Dies deutet darauf hin, daß diese 2 Varietäten in einer früheren geologischen Zeit entstanden sein mußten als die Ökotypen. Diese Selektionskräfte und andere Faktoren der Evolution spiegeln sich also nicht in den heutigen Witterungsverhältnissen wider.