Geographic Variation in Ponderosa Pine Leader Growth

BY
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Abstract. Growth of the shoot apices of 91 trees in a 45-year-old *Pinus ponderosa* Laws. provenance test was measured periodically with a transit. Analysis of the measurements led to the following conclusions: (1) 19 races of ponderosa pine planted near Priest River, Idaho, showed phenological, morphological, or physiological variation in six characters: date of beginning growth in the spring, date of ending growth, total seasonal elongation, duration of growth, length of dormant terminal bud, and rapidity of growth; (2) the variation described is continuous, although it was not possible to associate an environmental gradient to the variation pattern; (3) all trees except the local Kaniksu source achieved their maximum surge of growth during the same 7-day period, May 20-27, and this response closely paralleled temperature fluctuation; (4) simple correlations among the 19 progenies between total seasonal elongation and either beginning date, relative rapidity, or duration of growth were not significant. Correlation between dormant terminal bud length and total seasonal elongation was strong. Also, bud length was positively correlated with relative rapidity which was negatively correlated with duration of growth.

FEW CRITICAL OBSERVATIONS have been made of intraspecific variation in the seasonal activity of shoot growth on tall trees. A 45-year-old provenance test of ponderosa pine (*Pinus ponderosa* Laws.) provided a good source of material for measuring growth of mature tree apices with some environmental control. The objective was to determine whether provenances of ponderosa pine show variation in date of beginning or cessation of leader growth, duration of growth, rapidity of growth, total seasonal elongation, and length of dormant terminal bud. Measurements indicate that each of these growth characteristics vary significantly within the species. The variation is closely associated with seed source location.

Past Studies of Shoot Growth

Bud bursting of Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco, has received considerable attention. Munger and Morris (1936) and Morris *et al.* (1957) observed times of lateral bud bursting on 18- and 40-year-old Douglas-fir provenance plantations. They suggest that this characteristic is under strong genetic control. Irgens-Moller (1957) attempted to determine the degree of genetic control over time of bud bursting by measuring it on about 700 Douglas-fir seedlings, representing seven elevations from 60 to 4,000 feet. The measurements were made after the seedlings had overwintered in Corvallis, Oregon. His results indicated significant differences between certain sources in date of bud bursting the following spring and "some correlation" between this characteristic and elevation of seedling source. Ching and Bever (1960) observed dates of bud bursting of Douglas-fir nursery

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seedlings representing 14 sources varying in latitude (42° 20′ to 50° 30′) and elevation (100 to 4,100 feet). They found close relation between latitude or altitude of source and date of bud bursting, although the southernmost source was significantly earlier than other provenances.

Vaartaja (1954, 1959) has shown patterns of geographic variation in growth response for many tree species. Kriebel (1957) obtained evidence of clinal geographic variation in dates when sugar maple (*Acer saccharum* Marsh.) from 18 seed sources commenced growth. Irgens-Moller (1958) demonstrated geographic variation in time of height growth cessation among Douglas-fir seedlings. Critchfield (1957), working with lodgepole pine (*Pinus contorta* Dougl.) seedlings, associated a continuous variation in growth duration with changes in altitude and latitude of seed source. Langlet (1959) analyzed Wright and Baldwin's (1957) data on the growth rate of 46 Scotch pine (*Pinus sylvestris* L.) provenances. He interpreted the geographic variability in height increment as continuous and related to day length and temperature. Baldwin (1956) measured terminal growth during two seasons on 9- and 10-year-old trees of a European larch (*Larix decidua* Mill.) provenance plantation in New Hampshire but found no correlation between either altitude or latitude of seed source and amount of current height growth or midpoints of growth curves. He observed that: (1) all sources completed 50 percent of their growth at approximately the same date, (2) beginning date of growth varied as greatly within as between provenances, and (3) air temperature was associated with bud bursting. Kienholz (1941), Brown (1915), Friesner (1942), McMillan (1957), and others have attributed the inception of bud growth largely to temperature effects within certain photoperiodic and genetic limitations.

Several authors have compared terminal growth between species growing at one locality. The peak of seasonal growth for all species occurred about the same time. Tryon and Finn (1937) noted this when they observed growth curves for red pine (*Pinus resinosa* Ait.), white spruce (*Picea glauca* (Moench) Voss), and European larch in New York State. Friesner (1942) noted the similarity in dates of peak growth within trees of *Pinus banksiana* and *P. sylvestris* L. Fowells (1941) compared seasonal height growth of six conifers growing within a 10-acre area in California and reported differences in beginning, duration, and rapidity of growth.

This brief review of past work indicates clearly that the genetic makeup of the source material and a number of climatic factors may interact to produce geographic variation in shoot growth characteristics. Through natural selection, populations become adapted to each local environment. Sometimes the adaptation can be statistically correlated with environmental factors. In other cases this is not possible because interpopulation migration, limited population sizes, and slow genetic response to selection pressure tend to obscure phenotype correlations. Under growth chamber conditions or by appropriate sampling techniques and experimental design, the influence exerted on growth by any one environmental factor might be determined; but this would be difficult for the species and growth characteristics being considered here.

Experimental Materials

Seed or seedlings representing 22 provenances of ponderosa pine were planted at the Priest River Experimental Forest in northern Idaho from 1911 to 1917. Weidman (1939) has fully described the climate near the point of origin of each of the 22 seed sources and has also generally described the geographic areas of the seed sources (see also Table 1 and Fig. 1). The seed sources, or progenies, fairly well represent the broad range of ponderosa pine in the western United States. Since details of plot establishment were well de-

TABLE 1. Geographic location of ponderosa pine seed sources represented at Priest River Experimental Forest.[1]

General geographic area and national forest	Elevation	Latitude		Longitude	
	Feet				
North Pacific					
Siskiyou	2,000	42°	05′	123°	40′
North Plateau					
Boise	5,500	43°	30′	115°	00′
Payette	5,000	44°	30′	116°	00′
Whitman	5,000	44°	38′	118°	25′
Umatilla	3,500	46°	00′	117°	30′
Bitterroot	4,000	46°	00′	114°	20′
Bitterroot	5,000	46°	00′	114°	20′
Bitterroot	7,200	46°	00′	114°	20′
Lolo	3,000	47°	10′	114°	50′
Kaniksu	2,600	48°	20′	116°	50′
Colville	2,700	48°	40′	119°	00′
South Plateau					
Coconino	7,100	35°	10′	111°	50′
Santa Fe	8,000	35°	40′	105°	30′
East of Continental Divide					
Roosevelt	8,000	40°	30′	105°	40′
Ashley (Central Plateau)	7,500	40°	40′	109°	40′
Custer	3,200	45°	30′	104°	00′
Helena	4,500	46°	30′	111°	50′
Harney (Black Hills)	5,000	43°	40′	103°	30′
San Isabel	8,000	38°	00′	105°	00′

[1]Elevation 2,380 feet; latitude 48°20′; longitude 116°50′.

scribed by Weidman they are not elaborated here. Originally each progeny plot was composed of either 100 or 50 trees, but mortality of varying degrees has reduced the number of trees remaining to 10 to 50 per plot. All trees from one of the original sources (Mt. Shasta, California) were eliminated entirely by a severe temperature drop in December 1924 (Kempff 1928). Two sources of questionable origin also were omitted from this study.

The Priest River test of seed sources has received considerable study since its establishment. Individual progeny have been previously examined and compared for differences in vigor and frost resistance (Kempff 1928); external and internal foliage characteristics (Weidman 1939); total height and diameter growth (Weidman 1939, Squillace and Silen 1962); and season of cambial growth (Daubenmire 1950).

Methods and Definitions

Methods of measurement. Seasonal activity of shoot apices has never been described for these progenies. In March 1958 five dominant or codominant trees ranging from 25 to 65 ft in height were selected for measurement from each of the 19 plots. Their initial terminal bud length and subsequent height growth were measured throughout the course of the growing season.

The convenient method of direct measurement above a constant point, such as a pin inserted at the base of the terminal bud, was impractical because of the tree height and top flexibility. Therefore, the indirect method of angular measurements with a transit was adopted. Nine fixed instrument stations were established from which the tips and bases of all selected trees could be sighted clearly. The distance from each tree to a station was measured. Graduated sticks were nailed to the base of each tree to permit adjustment for height of instru-

ment at each remeasurement.

The only difficulty encountered in using this method was caused by wind. Any slight breeze considerably reduced the accuracy of an observation; consequently, all measurements were made only during calm periods of the day, usually early morning or evening. Error in measurement resulting from the experimental technique did not exceed ± 0.03 ft, well within the precision necessary for statistical validity. This value was determined by averaging

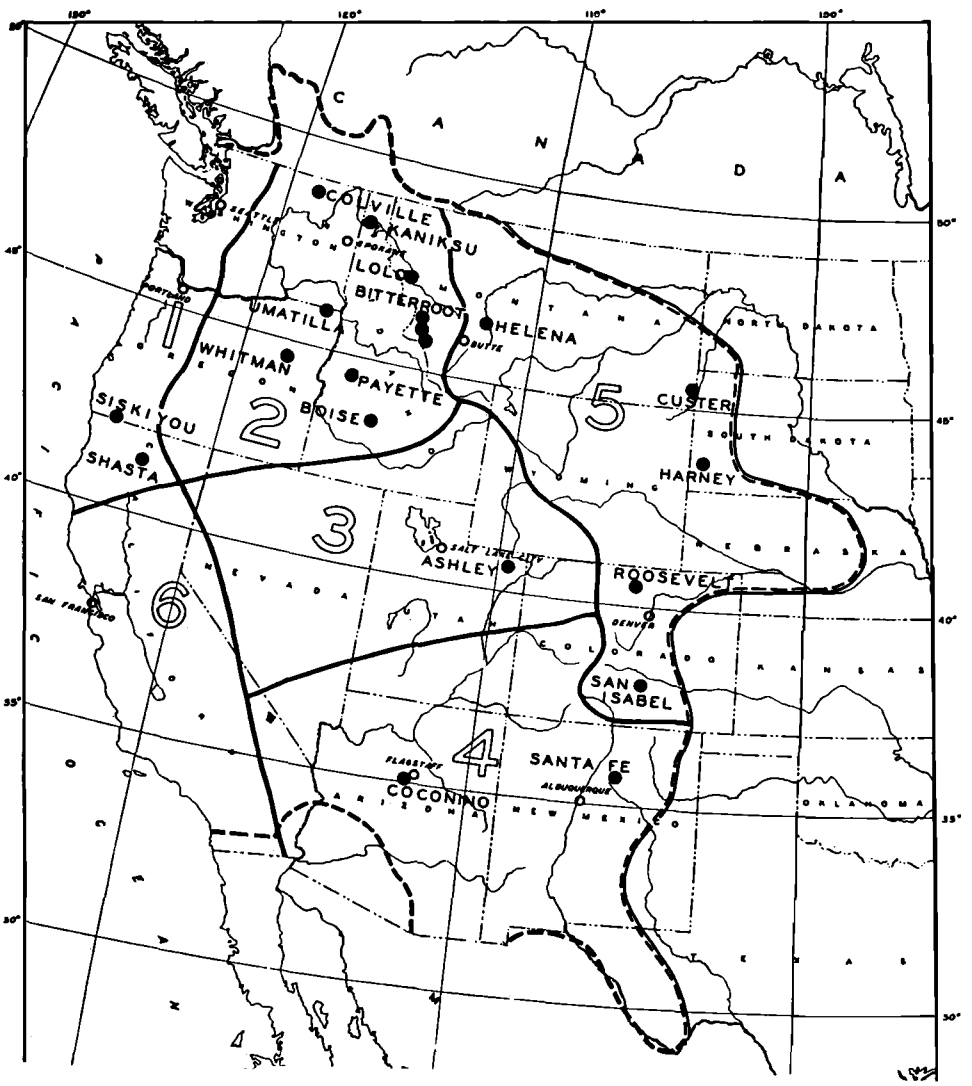

FIGURE 1. *Climatic regions of ponderosa pine range (north of Mexico): (1) North Pacific; (2) north plateau; (3) central plateau; (4) south plateau; (5) east of Continental Divide; (6) South Pacific. The broken line shows the range of ponderosa pine according to Sudworth (1917) and Munns (1938). Localities from which seed used in experiment was derived are indicated by black dots. The experimental site is located at the Kaniksu dot. (From Weidman 1939)*

the variation between readings obtained from successive measurements during the period when no growth was occurring. It includes error due to instrument resetting, residual tree lean after a wind, and human error.

Since the tips of four trees died during the observation period, complete measurements were obtained on only 91 trees. Trees were measured every 2 to 4 days beginning April 2. From May 13, when all trees were growing, until July 8, measurements were taken about every 7 days. Thereafter, until October 4, longer intervals between measurements sufficiently accounted for later growth and new bud formation.

Definitions. The beginning and ending dates of growth were determined by computing the points of time (expressed as consecutive days from January 1) at which 5 percent and 95 percent of the total seasonal growth had been completed. This was necessary because of the difficulty in pin-pointing actual growth beginning and cessation. Early growth seems to be sporadic at first because of daily weather variations and because small periodic increments may be obscured by error in measurement. Calculation of these base dates (or 0 percent and 100 percent) is necessary to arrive at the 5 percent and 95 percent points. The beginning base date height was taken as the average of the first and all successive measurements up to one showing a difference of greater than 0.05 ft between two consecutive readings followed by no successive readings differing by less than 0.05 ft. Ending base date height was determined by taking the average of successive measurements not differing by more than 0.10 ft after encountering a difference of less than 0.10 ft between two successive measurements. Rather than 0.05, 0.10 ft was used to adjust for the increased time between observations at the close of growth. Once the beginning and ending base dates were found, the 5 percent and 95 percent heights were calculated. The dates corresponding to these heights were used in the analyses.

Mirov *et al.* (1952) used a method based on lines of intersection of observed weekly increment values and average weekly increment over the entire growing period. Others have suggested obtaining the beginning and ending dates by constructing growth curves for each tree and determining the desired points on the curve. Depending on the nature of the data, any of these methods may be appropriate.

Duration of growth is the number of days elapsing between the 5 percent and 95 percent dates. *Total elongation* is total increment in feet between the beginning and ending base dates. *Bud length* in feet was computed from transit readings to the base and tip of the buds on April 1, when the first height measurements were made. *Rapidity of growth,* as used here, is the percent of the total season's growth completed within the 2-week period of most rapid growth. Rapidity may be thought of in two ways: (1) absolute, which is total elongation per unit of time, and (2) relative, which eliminates differences in total elongation and compares growth rate during the grand period of seasonal growth. The latter is more appropriate in this study because different genetic populations have different absolute growth rates (Tables 2 and 3). Absolute rapidity may be more applicable for most intraracial or intraspecific studies, since less genetic diversity is usually encountered. The *period of most rapid growth* for all the ponderosa pine progenies represented in this study was the 2-week period in which 38 to 58 percent of their total growth occurred. Fowells (1941) considered relative rapidity in his study of seasonal growth of young ponderosa pine in California. However, his methods of calculation were different. He used a constant percent of growth (50 percent) rather than a constant time interval, and he measured rapidity by the minimum number of days required to complete this amount of growth.

Method of analysis. From the data obtained, mean values for each provenance

TABLE 2. Ranking of ponderosa pine sources by date of beginning and ending of growth and duration of growth.[1]

Mean beginning date		Mean ending date		Mean duration	
Source	Day of year[2]	Source	Day of year[2]	Source	Days
Kaniksu	114	Bitterroot 7,200′	153	Boise	35
Ashley	115	Siskiyou	155	Helena	36
Siskiyou	116	Lolo	156	Lolo	37
Bitterroot 7,200′	117	Helena	156	Bitterroot 7,200′	37
Umatilla	117	Boise	157	Custer	37
Bitterroot 4,000′	118	Bitterroot 4,000′	158	Bitterroot 5,000′	38
Roosevelt	119	Kaniksu	158	Colville	39
San Isabel	119	Colville	158	Siskiyou	40
Colville	119	Custer	159	Whitman	40
Lolo	120	Bitterroot 5,000′	159	Bitterroot 4,000′	40
Helena	120	San Isabel	160	San Isabel	41
Payette	120	Roosevelt	161	Payette	41
Harney	120	Payette	161	Harney	42
Santa Fe	120	Harney	162	Roosevelt	43
Bitterroot 5,000′	121	Whitman	163	Kaniksu	44
Boise	121	Ashley	164	Santa Fe	49
Custer	122	Umatilla	167	Umatilla	50
Whitman	123	Santa Fe	169	Ashley	50
Coconino	124	Coconino	175	Coconino	52

[1]Any two means not included within the same line appearing to the right of each ranking of sources are significantly different.

[2]Days of the year numbered consecutively from January 1, 1958.

TABLE 3. Ranking of ponderosa pine sources by total elongation, terminal bud length (April 1958), and relative rapidity of growth.[1]

Mean total elongation		Mean terminal bud length		Rapidity	
Source	Feet	Source	Feet	Source	Percent
Harney	0.93	Roosevelt	0.11	Santa Fe	37.9
Roosevelt	.98	Ashley	.12	Coconino	42.3
Payette	1.06	Coconino	.13	Umatilla	43.5
Custer	1.08	Colville	.14	Payette	43.7
Bitterroot 7,200′	1.11	Custer	.14	Harney	44.6
Ashley	1.12	Santa Fe	.14	Bitterroot 5,000′	45.3
San Isabel	1.16	San Isabel	.14	Bitterroot 4,000′	45.6
Colville	1.22	Harney	.15	Ashley	46.2
Helena	1.23	Payette	.15	Lolo	47.1
Boise	1.23	Bitterroot 7,200′	.16	Siskiyou	47.3
Siskiyou	1.24	Bitterroot 5,000′	.16	San Isabel	47.6
Santa Fe	1.27	Boise	.17	Whitman	48.0
Bitterroot 4,000′	1.28	Bitterroot 4,000′	.18	Custer	48.6
Coconino	1.29	Siskiyou	.20	Roosevelt	48.7
Kaniksu	1.33	Kaniksu	.21	Colville	50.3
Bitterroot 5,000′	1.37	Umatilla	.23	Bitterroot 7,200′	51.4
Whitman	1.43	Helena	.23	Boise	51.9
Lolo	1.55	Whitman	.24	Kaniksu	55.0
Umatilla	1.64	Lolo	.24	Helena	58.1

[1]Any two means not included within the same line appearing to the right of each ranking of sources are significantly different.

were calculated for the traits observed (Tables 2 and 3). Either individual tree data, progeny means, or both were used for analysis of variance of each characteristic (Table 4). Bartlett's (1937) chi-square test for homogeneity of variance in

TABLE 4. Analyses of variance of characteristics of leader growth among 19 sources of ponderosa pine.

Growth characteristic[1]	*F*-value
Beginning date	2.09*
Ending date	2.80**
Duration	3.05**
Total elongation	1.97*
Bud length prior to growth	3.54**
Rapidity (relative)	2.39**

[1] Based on 5 percent and 95 percent points of seasonal growth completion.
* $p < 0.05$; ** $p < 0.01$.

TABLE 5. Coefficients of simple correlation (r) between shoot characteristics of ponderosa pine sources at Priest River.

Characteristics	*r*
Progeny or seed source basis ($n = 19$)	
Bud length and total elongation	0.724***
Duration and total elongation[1]	0.133
Beginning date and total elongation[1]	0.008
Bud length and relative rapidity	0.458*
Duration and relative rapidity	—0.599**
Beginning date and total height of progeny[1]	—0.135
Individual tree basis ($n = 91$)	
Bud length and total elongation	0.405***
Relative rapidity and total elongation	—0.126
Bud length and relative rapidity	0.257*

[1] Based on 5 percent and 95 percent of seasonal growth completion.
* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

progeny means showed that differences among individuals within provenances were nonsignificant at the 5-percent level. This was true for all characteristics except ending date and duration of growth, which were nonsignificant at the 1-percent level. That is, the five individual values from each provenance were consistent enough to justify use of a single statistic for the source. In the two exceptions, the individuals varied too much to permit assumption that they were from the same populations; but they have some value when aberrant individuals were removed.

Applying Kramer's (1956) extension of Duncan's (1955) multiple range test provided further analysis of the variation among the 19 progenies. Any two means (Tables 2 and 3) not included within the same line appearing at the right of each set of data are significantly different. For instance, in beginning date of growth the Siskiyou source is significantly different from the Custer but not from the Boise.

The data were also analyzed for simple correlations between measured attributes (Table 5).

Results and Discussion

The analyses of variance show significant differences among provenances for all the growth characteristics studied. Multiple range tests show that no two adjacently ranked provenances differ significantly, when arrayed according to magnitude of response, in any of the traits, i.e., under the conditions of this study, the variation is continuous.

The results of simple correlation analyses between attributes provide some indication as to the association between these responses and total seasonal growth. At least during the year of this study, neither beginning date, relative rapidity, duration of growth, nor ending date appeared to have any relation to total growth during the year. A strong positive correlation existed between bud length and total elongation. Bud length was also significantly correlated with relative rapidity of growth. Thus, total elongation seemed to depend more on inherent growth potential than on an endogenous rhythm mechanism that gave certain individuals or progenies an advantage over poorer performing ones.

Another interesting point revealed by simple correlation analysis was a highly significant negative correlation between relative rapidity and duration of growth.

An effort was made to relate the continuous variation patterns to geographic location of the seed sources. Weidman (1939) and Squillace and Silen (1962) established relations between morphology or height growth of the ponderosa pine

progenies at Priest River and certain climatic factors at the seed source localities. The many interacting factors involved and the inadequacy of the original plot design make it difficult to associate the responses studied here with seed source climatic factors.

Pictorial representation of several climatic factors and growth responses (Fig. 2) provides insight into causes of the variation. This method has been applied effectively in taxonomic studies of races or species when multiple attributes are involved (Anderson 1956). However, even by this method only certain trends are evidenced and no statistical significance is implied. For instance, the eastern sources tend to group into a sector of the diagram having a low total elongation and a late beginning date. Only the north plateau sources are in the upper portions of the total elongation scale, and among these the sources from higher elevations began growth later. Sources representing geographic regions in which September-through-June precipitation is relatively low, generally began growth later and grew less than seed sources from areas where precipitation is high for this period. It is interesting that the local Kaniksu source began growth considerably earlier than the two most southerly sources, Santa Fe and Coconino. Four sources—Ashley, Umatilla, Santa Fe, and Coconino—seem to have a distinctly longer period of growth than other sources. Such broad generalizations about progeny performance in relation to seed source are all that these data allow.

The period at which each tree and progeny achieved their maximum surge of

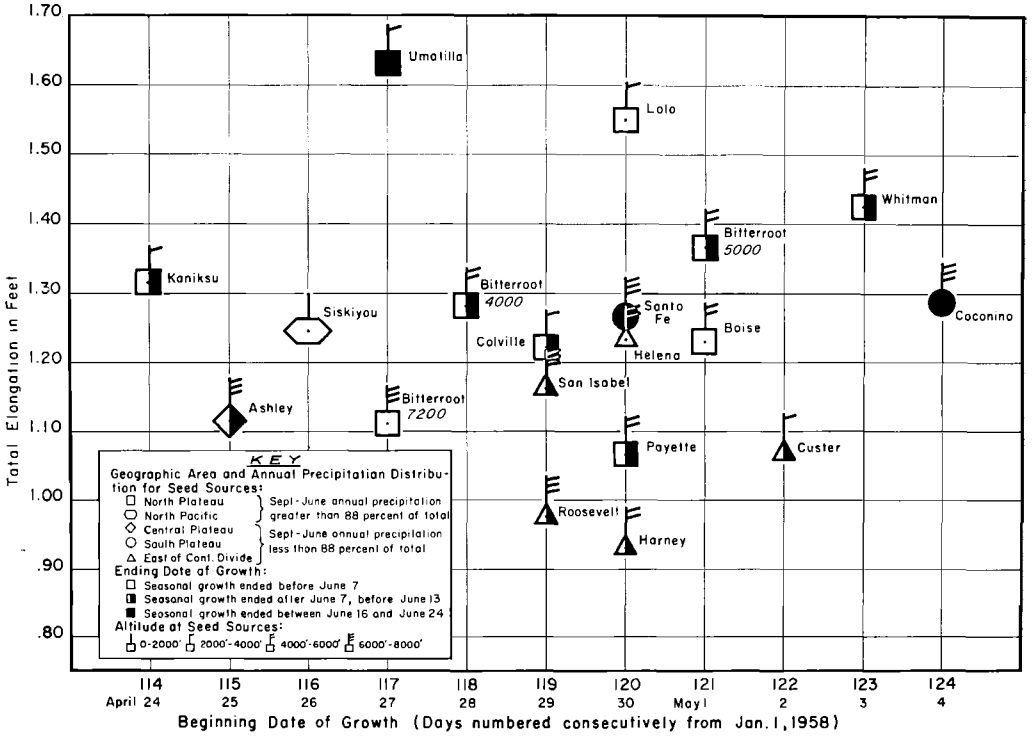

FIGURE 2. *Pictorialized scatter diagram showing variation in three growth factors and three climatic factors for ponderosa pine seed sources.*

TABLE 6. Weather at Priest River Experimental Forest in relation to growth of ponderosa pine sources.

Date	Temperatures		Precipitation	Cloud cover[1]
	Maximum	Minimum		
	°F	°F	*Inches*	
Week *preceding* maximum growth:				
May 13	63	30	Tr.	7
May 14	74	29	0	2
May 15	76	35	0	0
May 16	78	36	0	1
May 17	79	35	0	7
May 18	85	33	0	0
May 19	82	43	0	0
Mean	76.7	34.4	0	2.4
Week *of* maximum growth:				
May 20	85	44	0	0
May 21	88	55	0	2
May 22	88	46	0	1
May 23	85	47	0	10
May 24	86	55	0.01	2
May 25	85	51	0	4
May 26	90	50	0	5
Mean	86.7	49.7	0.00	3.4
Week *following* maximum growth:				
May 27	91	47	0	1
May 28	89	52	Tr.	6
May 29	73	46	0	9
May 30	76	41	0	5
May 31	73	42	0.19	10
June 1	69	41	0.20	4
June 2	72	38	0	6
Mean	77.6	43.9	0.06	5.9

[1] 0 = clear; 10 = overcast.

growth was related to local temperature. With few exceptions the period of most rapid growth for all trees was the same 7-day period, May 20-27. Only one progeny, the local Kaniksu source, averaged 1 week earlier. In an effort to relate an environmental factor to this response, weather records at the Priest River Experimental Forest headquarters (less than ¼-mile from the plantation) were examined. Temperature fluctuation closely paralleled this growth response. The week of maximum growth coincided with day and night temperatures higher than those of the weeks immediately preceding and immediately following the week of maximum growth (Table 6). The temperature pattern of this year could have obscured some differences between sources for this response or for any of the others considered here. However, Munger and Morris (1936), Friesner (1942), Tryon and Finn (1937), and Kienholz (1941) showed that though yearly variations occur in the absolute values for many phenological characteristics, different individuals, races, or species usually maintain the same relative positions during successive years.

All trees began growing in the spring before danger from frost had passed and ceased growing before the beginning of fall frosts. Also, growth was at least 95 percent completed before maximum day lengths and the July-August dry period were reached. This growth pattern is characteristic of many coniferous trees whose shoot elongation depends partly on stored carbohydrates but also on cell elon-

gation and division in buds formed during the previous year (Sacher 1954).

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