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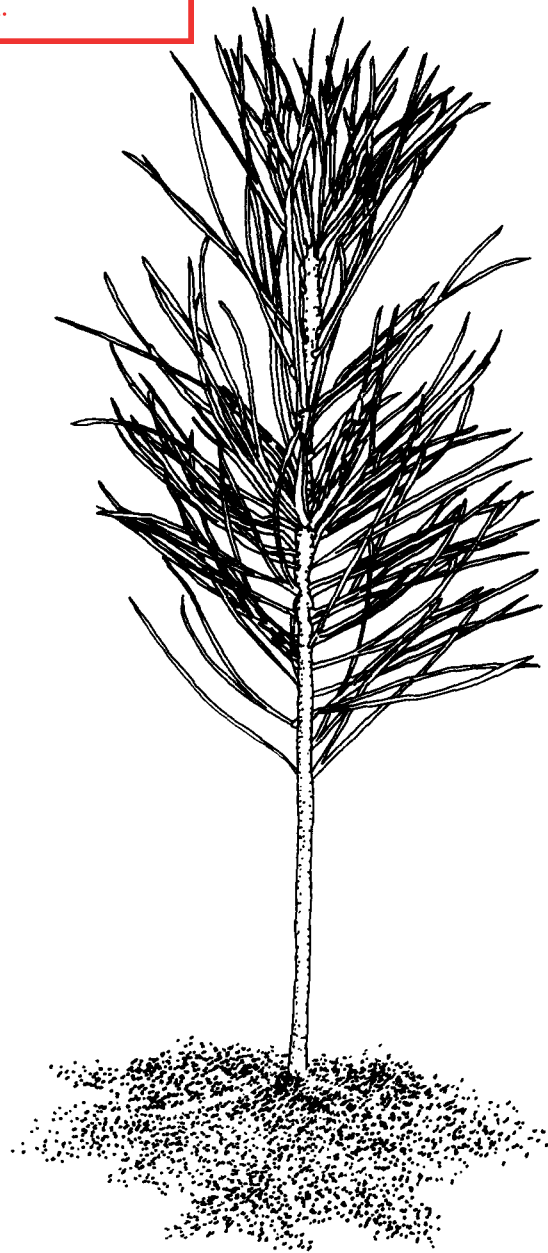


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Geographic Variation in Speed of Seed Germination in Central Oregon Ponderosa Pine (*Pinus ponderosa* Dougl. ex Laws.)

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Abstract

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Variation in speed of seed germination was investigated among ponderosa pine trees representing 225 locations in central Oregon. Results suggested that at least some of the geographic variation is related to the severity of summer drought. In general, germination speed was greater in locations with short, drought-limited growing seasons. Levels of geographic variation were highest in the region having the steepest precipitation gradients. Most of the variation occurred, however, within locations.

Keywords: Geographic variation, seed germination, ponderosa pine, adaptation, drought, central Oregon.

Summary

Variation in speed of seed germination was investigated among 296 ponderosa pine trees (*Pinus ponderosa* Dougl. ex Laws.) representing 225 locations in five geographically disjunct regions of central Oregon. Mean rates of embryo development toward germination (reciprocal of days to 50-percent germination) were estimated for each tree in two replicated, controlled environments differing in stratification period and incubation temperature. Higher mean rates were equated with greater average germination speed. Results suggested that at least some of the geographic variation in germination speed is adaptively related to the severity of summer drought. In general, germination speed was greater in locations with short, drought-limited growing seasons. The region with the steepest precipitation gradients among locations had the highest relative levels of geographic variation and the strongest geographic trend in germination speed. Most of the variation in germination speed occurred, however, within locations.

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Introduction

Geographic variation in germination speed may be adaptively related to the length of the growing season in general (Flint 1974) and to the severity of summer drought in particular in the Pacific Northwest¹ (Campbell and Ritland 1982). In this paper, we investigate this hypothesis for ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) in central Oregon.

Ponderosa pine is an early successional conifer that flourishes in the relatively dry, lower montane zones in the Pacific Northwest and elsewhere in Western North America (Wang 1977). Its seeds are wind dispersed in late summer and early autumn during reproductive years, but the size of the seed crop differs among stands and trees within stands, and from year to year. Seeds experience a period of moist chilling (stratification) in the winter that affects the rate of embryo development toward germination. The response to stratification differs among seed sources in ponderosa pine and other species (Schopmeyer 1974) and apparently serves as an adaptive mechanism for timing seed germination (Vegis 1964). Seeds typically germinate between March and June in central Oregon.²

Ponderosa pine is genetically diverse (Wang 1977), but there are few published reports of variation in seed germination in this species. Investigations outside the Pacific Northwest suggest, in general, that there is relatively little variation in germination speed (or similar measures) among seeds sampled from the same tree compared to the variation among seedlots from different trees and that there is geographic variation in germination speed in some regions (Callaham and Hasel 1961, Curtis 1955, Jenkinson 1977, Moore and Kidd 1982, Read 1980, Woods and Blake 1981). Most of the reports cited above focus on variation patterns in seedling characters and pay little attention to variation in seed germination. Our study is the most intensive investigation to date of patterns of geographic variation in seed germination speed in ponderosa pine.

When the safe growing period begins, seeds that germinate rapidly provide their seedlings with a competitive advantage (Angevine and Chabot 1979). Rapid germination in spring may be particularly adaptive in dry locations in the Pacific Northwest because the growing season generally is limited by summer drought. Precipitation gradients occur with latitude, longitude, and elevation in central Oregon, but the steepness of these gradients differs among regions (USDA Soil Conservation Service 1964). If geographic variation in germination speed of ponderosa pine seed is adaptively related to the severity of summer drought, we might expect central Oregon regions with steep precipitation gradients to have relatively greater geographic variation and steeper clines in germination speed than regions with milder precipitation gradients (Endler 1977).

¹ Sorensen, F.C. The ecological genetics of germination rate and timing in Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco). Manuscript in preparation. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Forestry Sciences Laboratory, 3200 S.W. Jefferson Way, Corvallis, Oregon 97331.

² Personal communication, Duane Ecker, U.S. Department of Agriculture, Forest Service, Ochoco National Forest, P.O. Box 490, Prineville, Oregon 97754.

Methods

Sample Collection and Geographic Variables

The major objectives of this study were to (1) determine if geographic variation in germination speed occurred in central Oregon ponderosa pine; (2) determine if germination speed was correlated with latitude, longitude, and elevation (and, by inference, with precipitation); and (3) compare the three largest sample regions in terms of location-related geographic variation and correlations with latitude, longitude, and elevation.

Mature cones were collected from 299 trees distributed among 225 locations in five geographically disjunct regions of central Oregon (fig. 1). Sampling intensity was about one location per 4600 hectares (one-half of a township) within the ponderosa pine zones of three larger regions (referred to as Malheur, Ochoco, and Deschutes) and two smaller regions (referred to as Maury and Lost Forest). Sampling intensity differed slightly within and among regions, which reflected the availability of cones. The Malheur region includes five districts in two National Forests (NF): Burns, Bear Valley, Long Creek, and Prairie City of Malheur NF; and Snow Mountain of Ochoco NF. The Ochoco region includes three districts in the Ochoco NF: Paulina, Big Summit, and Prineville. The Deschutes region includes four districts in the Deschutes NF: Fort Rock, Crescent, Bend, and Sisters. The Maury region includes the Maury district in the Ochoco NF. The Lost Forest region is managed by the Bureau of Land Management. One tree per location was sampled at 151 locations. Two trees per location, at least 100 meters apart, were sampled at 74 locations. Locations with two sample trees provided an estimate of variation within locations.

About 70 percent of sample trees were "select trees." The USDA Forest Service and the Bureau of Land Management use seeds from select trees for reforestation because the trees exhibit phenotypic characteristics in the field that are considered desirable for timber production. The other trees were randomly chosen from those producing an adequate cone supply and that were relatively easy to climb. Select trees generally were less than 75 years old when sampled; age of the other trees was not determined, but they were similar in size to the select trees.

Cones were collected from most trees in 1981, but cone production was inadequate in some areas that year. Gaps in the sample (mainly in the Deschutes, Malheur, and Lost Forest regions) were filled by obtaining seed samples from cone collections made in 1978 and 1983. The number of trees sampled in 1978, 1981, and 1983 was 71, 200, and 28, respectively. Seeds were extracted after cones had dried to a constant weight. Empty seeds and seeds with a poorly developed embryo and gametophyte were identified by weight and x ray and were discarded. About 140 full seeds were subsampled from the cones of most trees, but as few as 60 full seeds were obtained from some trees. The 140 seeds, if available, were randomly selected from the remaining full seeds. Seed subsamples were stored at -10 °C until the germination tests; storage time differed with collection year.

Latitude (degrees N.) and longitude (degrees W.) were determined from map location and converted to a decimal scale. Elevation was estimated directly with an altimeter. Ranges in location latitude and longitude are illustrated in figure 1. Elevation of sample locations ranged from 850 to 2010 meters with an average of 1510 meters. Elevation increases in general from north to south and especially from west to east over the entire sample area. The range and average elevation (in parentheses) in the three larger sample regions were 1300 to 2010 meters (1610 meters) in the Malheur, 1120 to 1860 meters (1510 meters) in the Ochoco, and 850 to 1700 meters (1360 meters) in the Deschutes.

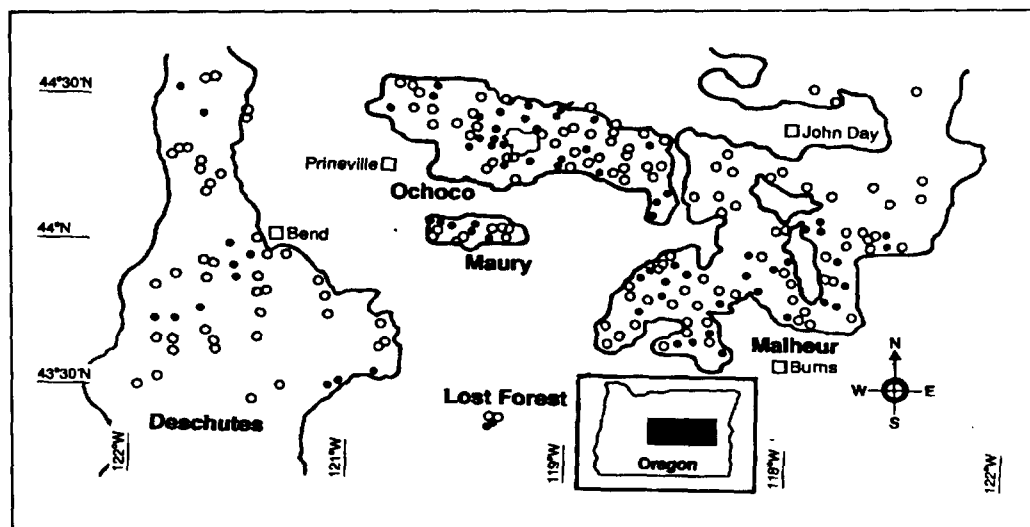


Figure 1—Geographic distribution of 225 ponderosa pine sample locations in central Oregon. Locations were sampled in five regions: Deschutes, Ochoco, Malheur, Maury, and Lost Forest. Each location was represented by either one or two sample trees (open and closed circles, respectively). The crest of the Cascade Range extends along the western boundary of the Deschutes region. Location of the sample area is shown on the inset map.

Germination Test Procedures

The timing of seed germination differs with environmental conditions and genetically controlled responses to environmental conditions (Bewley and Black 1985). The period of moist chilling in the winter (stratification) and the seedbed temperature during germination (incubation temperature) are two major environmental conditions that may uncover adaptive genetic variation in many forest-tree species from temperate climates (Flint 1974, Vegis 1964). In a preliminary study, we investigated the general effects of stratification period (range 15 to 120 days) and incubation temperature (range 10 to 25 °C) on germination speed in central Oregon ponderosa pine (Weber and Sorensen 1990). Based on that study, we chose two controlled environments for testing variation among individual trees.

Test environments are referred to below by their relative incubation temperature: WARM is 30.5 days stratification followed by 16 °C incubation, and COLD is 61.5 days followed by 11.3 °C. Incubation temperature was lower after the longer stratification period because longer stratification seems to lower the minimum temperature requirement for germination (Vegis 1964, Weber and Sorensen 1990). Test environments were chosen to represent two fairly extreme stratification and temperature conditions that we thought would (1) occur naturally in central Oregon, (2) produce adequate germination, (3) produce a similar distribution in germination speed, and (4) uncover variation in relative germination speed among trees. Tests were not designed to estimate absolute differences in stratification and temperature requirements for germination among tree seedlots. Germination was tested in only two environments as a result of limited seed samples from many trees. Tests were conducted in spring 1984 (WARM) and winter 1984-85 (COLD); tests were not conducted simultaneously because of limited staff and equipment.

The experimental design included two replications per tree in each test environment. Sample size was generally 35 seeds per tree per replication per treatment but was as low as 15 seeds in some cases. Seedlots were removed from cold storage and transferred to mesh bags (two seedlots per tree). Seedlots were soaked in aerated, distilled water (about 22 °C) for 24 hours, then dipped in fungicide for 30 seconds (4 grams Captan powder per liter distilled water) and air dried for 30 minutes.³ Replications were placed in separate polyethylene bags containing moist paper towels and stratified at 2-3 °C for the designated period (30.5 or 61.5 days). Bags were rotated daily during stratification to minimize potential microenvironmental effects in the cold room. After stratification, each seedlot was transferred to a separate petri dish (9 centimeters in diameter, 1.5 centimeters deep) containing 25 milliliters vermiculite and 20 milliliters distilled water covered by filter paper. Seeds were spread out on the filter paper (Whatman no. 2). To ensure adequate aeration within petri dishes, plastic ties were used to maintain a gap between the dish and lid.⁴ Replications were placed in separate germinators (blocks) calibrated to the designated temperature (16 or 11.3 °C, ± 1 °C, with constant illumination). The 299 dishes in each germinator were randomly assigned to positions within 30 stacks, and dishes were rotated systematically every day to minimize potential microenvironmental effects in the germinator. Distilled water was added as needed to maintain the filter paper at a visually constant moisture level (no meniscus between paper and seed, upper surface of seed coat not shiny). Filter paper and vermiculite were changed in moldy seedlots at 30 days of incubation.

Germinated seeds were counted on a variable schedule, beginning at 1.33 days in the germinator and ending at 50 days. A seed was considered to have germinated when the radicle appeared to be about 1 millimeter long. Germinants were counted more frequently in the first week of incubation, when most seeds germinated, than later in the incubation period. The total number of counts was 22 in the WARM environment and 25 in the COLD environment.

Analyses of Germination Data

Mean rates of embryo development towards germination (MEANS) were estimated for each petri dish in the two environments (WARMMEAN, COLDMEAN) by using a procedure suggested by Campbell and Sorensen (1979). Cumulative percentages of germination at each counting time were transformed to probits, and mean rates were estimated with a maximum likelihood procedure.⁵ Mean rates were estimated in units of the reciprocal of days to 50-percent germination; thus, if 50-percent germination occurred in 4 days, the mean embryo development rate was 0.25 units per day.

³ The use of trade names in this publication is for the information and convenience of the reader. Such use does not constitute an official endorsement or approval by the U.S. Department of Agriculture of any product to the exclusion of others that may be suitable.

⁴ Recommended by J.L. Jenkinson, U.S. Department of Agriculture, Forest Service, Pacific Southwest Forest and Range Experiment Station, 1960 Addison St., Berkeley, California 94704.

⁵ GRPNORM computer program and documentation. On file with: R.K. Campbell and F.C. Sorensen, U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Forestry Sciences Laboratory, 3200 S.W. Jefferson Way, Corvallis, Oregon 97331.

Higher mean rates were equated with greater average germination speed (that is, fewer days to 50-percent germination). Mean rates were estimated from germinated seeds only; ungerminated seeds were counted but not included in the estimation of mean rates.

COLDMEAN was recoded and transformed ($\log_{10}[\text{rate} \times 10^4]$), and WARMMEAN was recoded ($\text{rate} \times 10^2$). Rates were recoded to improve computation efficiency, and COLDMEAN was transformed to reduce heterogeneity in variances (Snedecor and Cochran 1967). On these scales of analysis, there was no significant correlation between mean and variance for trees or locations, but distributions were significantly leptokurtic ($P < 0.01$) and skewed (WARMMEAN positive $P < 0.05$, COLDMEAN negative $P < 0.01$).

Variation in MEANs was partitioned into four sources by analysis of variance (ANOVA): locations, trees nested within locations, blocks, and residual. All sources of variation were considered random in this partially nested model. Variance components were estimated for each source of variation and expressed as a percentage of total variance.

Variation in MEANs was analyzed over the entire sample area and separately within the three largest sample regions (Malheur, Ochoco, Deschutes). One tree in the Malheur region and two trees in the Deschutes region were excluded because of a low percentage of germination, which left 296 trees for ANOVAs over the entire sample area. The three trees from the extreme northern Malheur region were excluded from the separate analysis within the Malheur because they were distant geographically from the main body of the Malheur sample (fig. 1). The separate ANOVAs within the Malheur, Ochoco, and Deschutes regions included 110, 94, and 63 trees, respectively.

Regional differences in MEANs were tested among the Malheur, Ochoco, and Deschutes regions. Variation was partitioned by ANOVA into the sources mentioned above plus a random effect due to regions. The mean square (MS) for regions was tested over the MS for locations within regions.

Simple linear relations between tree MEANs and geographic variables were investigated by Pearson correlation coefficients. Correlations were estimated over the entire sample area ($N = 296$) and separately within the Malheur, Ochoco, and Deschutes regions ($N = 10, 94$, and 63 , respectively).

Results

Although germination speed is highly heritable in pines and is controlled, in particular, by the maternal diploid genotype (Bramlet and others 1983, Hoff 1987, McLemore and Barnett 1966, Stone 1957), it also is affected by environmental conditions (Bewley and Black 1985). In this study, trees were not grown in a common environment and were not sampled in the same year, so variation in germination speed potentially included nongenetic effects from maternal environment, collection year, and period of seed storage, among other things. Given the genetic control of germination speed, we assumed that variation patterns largely reflected genetic differences among trees, but variation patterns reported in this study are phenotypic by definition.

Nearly all seeds from the 296 trees germinated by 50 days of incubation. Total percentage of germination was 99.4 percent in the WARM and 98 percent in the COLD environment. All seeds germinated in 79 percent of the trees (families) in the WARM and in 57 percent of the trees in the COLD environment. The average number of germinated seeds per petri dish was 33 in the WARM and 32 in the COLD environment, with a minimum of 11 in both environments.

Mean rates differed greatly among petri dishes (table 1). On the reciprocal scale, mean days to 50-percent germination ranged from 2.3 to 20.0 days in the WARM (average 4.3 days) and from 2.6 to 30.9 days in the COLD environment (average 6.8 days).

Locations and trees within locations accounted for nearly all the variation in mean rates over the entire sample area (table 2). Both sources of family-related variation were statistically significant, but trees within locations accounted for more variation than did locations. The percentage of total variation due to locations and due to families (locations plus trees within locations) was slightly higher in WARMMEAN than COLDMEAN. Differences in relative variation levels between test environments were not due to scale effects; the same relative differences were observed if MEANs were analyzed on the same scale.

Locations accounted for relatively more variation in mean rates in the Deschutes than in the Malheur or Ochoco regions (table 2). Variation due to locations was statistically significant for only WARMMEAN in the Malheur region, for neither MEAN in the Ochoco region, and for both MEANs in the Deschutes region. The percentage of total variation due to locations was higher in the Deschutes than in the other two regions. Variation due to trees within locations was statistically significant in all three regions.

Differences in location-related variation between test environments were not consistent among the three regions (table 2). The percentage of total variation due to locations was higher in WARMMEAN than COLDMEAN in the Malheur region, but higher in COLDMEAN than WARMMEAN in the Ochoco and especially in the Deschutes. The percentage of total variation due to families (locations plus trees within locations) was slightly higher in WARMMEAN than COLDMEAN in all regions.

Mean rates did not differ significantly among the three regions ($P > 0.05$) but were lowest, on average, in the Deschutes. Average WARMMEAN and COLDMEAN, respectively, were 0.2338 and 0.1523 in the Malheur region, 0.2343 and 0.1476 in the Ochoco, 0.2241 and 0.1399 in the Deschutes.

Mean rates in the two environments were positively correlated at the family level (Pearson $r = 0.82$, $N = 296$ trees, $P < 0.001$). The correlation did not differ significantly among the three regions (chi-square, $df = 2$, $P > 0.05$).

Correlations between mean rates and geographic variables were generally low; the only statistically significant correlations involved latitude and longitude (table 3). Over the entire sample area, WARMMEAN and COLDMEAN rates increased from north to south, and COLDMEAN rate increased from west to east. Latitudinal trends in mean rates (in at least one test environment) were statistically significant in all three regions, but longitudinal trends were significant only in the Deschutes. The latitudinal trend was stronger in the WARM than in the COLD environment in the Malheur region, but stronger in the COLD than in the WARM environment in the Ochoco and Deschutes regions. The longitudinal trend was relatively strong in both environments in the Deschutes region.

Table 1—Descriptive statistics of germination mean rates (MEANs) in two test environments (WARM, COLD)^a

Germination	Mean rate (1/days to 50 percent germination)				Standard deviation
	Mean	Median	Minimum	Maximum	
WARMMEAN	0.2315	0.2311	0.0504	0.4344	0.0577
COLDMEAN	.1468	.1434	.0324	.3792	.0462

^a WARM was 30.5 days stratification, 16 °C incubation; COLD was 61.5 days, 11.3 °C. Sample size was 592 (2 MEANs per 296 trees).

Table 2—Analysis of variance of germination mean rates over the entire sample area and within the Malheur, Ochoco, and Deschutes regions^a

Germination	Mean square					Percent of total variance due to variance component			
	Locations	Trees within locations	Blocks	Residual	Total	Locations	Trees within locations	Blocks	Residual
Entire sample area:									
WARMMEAN	72.77067***	38.11463***	90.51963***	2.18744	33.22947	38.9	53.7	0.9	6.5
COLDMEAN	.04373**	.02381***	.34390***	.00133	.02058	35.3	53.0	5.4	6.3
Malheur region:									
WARMMEAN	72.57342*	37.17660***	65.58088***	1.91931	33.00263	39.9	52.7	1.7	5.7
COLDMEAN	.04148	.02596***	.14726***	.00128	.02004	28.2	59.3	6.4	6.1
Ochoco region:									
WARMMEAN	51.85671	43.87114***	31.15341***	1.96413	25.78011	10.9	80.4	1.2	7.5
COLDMEAN	.03418	.02557***	.10861***	.00155	.01711	17.3	67.6	6.4	8.7
Deschutes region:									
WARMMEAN	97.42381*	34.23360***	0.06907	2.94950	43.71945	57.9	35.4	0.0	6.7
COLDMEAN	.05722***	.00928***	.06732***	.00101	.02481	75.9	16.1	4.1	3.9

^a Scale of analysis: WARMMEAN rate $\times 10^2$, COLDMEAN $\log_{10}(\text{rate} \times 10^4)$. Asterisks indicate significance of F-ratios (not shown): *** $P \leq 0.001$, ** $P \leq 0.01$, * $P \leq 0.05$, no asterisk $P > 0.05$. Degrees of freedom for Locations, Trees within locations, Blocks, Residual, and Total, respectively: 221, 74, 1, 295, and 591 for entire sample area; 82, 27, 1, 109, and 219 for Malheur region; 66, 27, 1, 93, and 187 for Ochoco region; 50, 12, 1, 62, and 125 for Deschutes region. Expected mean squares (EMS) for Locations, Trees within locations, Blocks, and Residual, respectively: $\sigma_R^2 + b\sigma_T^2 + c\sigma_L^2$; $\sigma_R^2 + b\sigma_T^2$; $\sigma_R^2 + a\sigma_B^2$; σ_R^2 . Coefficients a, b, and c, respectively, of EMS: 296, 2, and 2.6652 for entire sample area; 110, 2, and 2.6466 for Malheur region; 94, 2, and 2.8008 for Ochoco region; 63, 2, and 2.4648 for Deschutes region.

Table 3—Pearson correlation coefficients (r) between germination speed and geographic variables over the entire sample area and within the Malheur, Ochoco, and Deschutes regions^a

Geographic variable	Germination							
	Entire sample area		Malheur region		Ochoco region		Deschutes region	
	WARMMEAN	COLDMEAN	WARMMEAN	COLDMEAN	WARMMEAN	COLDMEAN	WARMMEAN	COLDMEAN
Latitude	-0.133*	-0.155**	-0.299**	-0.198*	-0.073	-0.210*	-0.230	-0.402**
Longitude	-.093	-.143*	.169	.105	-.170	-.174	-.540***	-.444***
Elevation	.071	.080	.171	.064	.121	.070	-.068	.051

^a Asterisks indicate significance: ***P ≤ 0.001, **P ≤ 0.01, *P ≤ 0.05, no asterisk P > 0.05. Sample size: 296 for entire sample area, 110 for Malheur region, 94 for Ochoco region, 63 for Deschutes region.

Discussion

Severity of summer drought seemed to structure at least some of the geographic variation in seed germination speed (mean rates) in central Oregon ponderosa pine. We hypothesized that germination speed is greater in locations with short, drought-limited growing seasons, referred to below as the summer-drought hypothesis. Variation patterns generally were consistent with this hypothesis, but the geographic trends were weak and our evidence is inferential. In making our inferences about the relation between germination speed and precipitation, we relied mainly on an isohyetal map (USDA Soil Conservation Service 1964). Isohyets were derived by correlations between mean annual precipitation and physiographic features. The map is rough for central Oregon, because weather stations are sparse and almost nonexistent in the forested regions. But subjective comparisons of germination speed with mean annual precipitation, read from the isohyetal map, nevertheless were consistent with the summer-drought hypothesis.

Relatively greater geographic variation in germination speed was found in regions with greater ranges in mean annual precipitation. The proportion of location-related variation in mean rates was largest in the Deschutes region, intermediate in the Malheur, and smallest in the Ochoco (table 2). The range in mean annual precipitation, based on isohyets, decreased in the same regional order: 500 to 1250+ millimeters in the Deschutes, 500 to 875+ millimeters in the Malheur, and 500 to 625+ millimeters in the Ochoco (+ indicates that some sample locations occur above the given isohyet, but the next isohyet, 125 millimeters higher, is either above the sample location or not shown on the map). In theory (Endler 1977), we would expect this regional trend in geographic variation if the severity of summer drought were selectively important.

Correlations between germination speed and latitude were strongest in the region having the steepest latitudinal precipitation gradient. Mean annual precipitation, based on isohyets, decreases from north to south in the Malheur, Ochoco, and Deschutes regions. The latitudinal precipitation gradient is steepest in the Deschutes region, intermediate in the Malheur, and flattest in the Ochoco. The strength of correlations between latitude and germination speed, averaged over both test environments, decreased in the same regional order: -0.32 in the Deschutes, -0.25 in the Malheur, and -0.14 in the Ochoco (table 3). Although average correlations were weak, the regional contrast was consistent with the hypothesis. The steep precipitation decrease from north to south in the Deschutes largely reflects the northwest to southeast configuration of this region: the region extends eastward into an arid, high-elevation plateau between latitudes 43°30' N. and 44° N. (fig. 1).

Correlations between longitude and germination speed also conformed with precipitation gradients within regions. The Cascade Range casts a rain shadow over central Oregon, but the effect decreases with distance east of the Cascades. From the isohyetal map, mean annual precipitation decreases steeply from west to east in the Deschutes region; decreases slightly from west to east in the Ochoco, with the decrease occurring mainly in the eastern part of the region; and increases slightly from west to east in the Malheur, with the increase occurring mainly in the higher elevation, eastern part of the region. Correlations between longitude and germination speed, averaged over both test environments, were consistent in sign and strength with these precipitation gradients: -0.49 in the Deschutes region, -0.17 in the Ochoco, and 0.14 in the Malheur (table 3). The positive correlation in the Malheur reflects, in part, the northeast to southwest configuration of this region (fig. 1) and the decrease in precipitation from north to south.

Because precipitation generally increases with increasing elevation, one might expect negative correlations between elevation and germination speed, according to our hypothesis, but the correlations were not statistically significant and were generally positive in sign. It is likely that the expected correlations were not observed because elevation is confounded with latitude and longitude. Elevation increases in general from north to south and especially from west to east in central Oregon, and precipitation decreases from north to south and from west to east. In other words, expected negative correlations between elevation and germination speed were probably cancelled out by these latitudinal and longitudinal trends in precipitation.

Evidence was present that chilling requirements for germination showed broad geographic variation, although this was not measured directly. Germination speed was higher and germination was more complete in the WARM environment (30.5 days moist chilling, 16 °C incubation) than in the COLD environment (61.5 days, 11.3 °C). This contrast implied that, on average, chilling requirements for the given incubation temperature were satisfied for more seedlots in the WARM than in the COLD environment. One might, therefore, have expected greater location-related variation in the COLD than in the WARM environment in all regions. This was not observed in the Malheur region but was observed in the Ochoco and was particularly apparent in the Deschutes (table 2). This regional contrast suggested that average chilling requirements of seedlots were more variable among locations in the Deschutes than in the eastern part of central Oregon. Further research is necessary to specifically investigate variation in chilling requirements. A suggested pattern is that ponderosa pine seeds from more xeric sites not only germinate faster than seeds from more mesic sites, as reported here, but also have lower average chilling requirements for germination.

This study was designed to investigate geographic variation, but most variation in germination speed actually occurred within locations in central Oregon, especially in the Ochoco region. This local variation may reflect variable natural selection (Ager and Stettler 1983, Kalisz 1986) because seedbed microclimates can be extremely variable in space and time within a forest (Lee 1978). For example, natural selection may favor rapid germination in dry seedbeds and years but favor slow germination when and where late-spring frost occurs. Because ponderosa pine is a pioneer species that disperses its seeds into variable environments, extensive local variation provides a genetic buffer allowing the population to maintain adaptability in the face of environmental heterogeneity (Stern and Roche 1974).

Patterns of variation in germination speed, both local and geographic, are undoubtedly affected by numerous present and historical factors in addition to the growing season. These factors include, among others, mutation, migration, founder effects, and random genetic drift (Stern and Roche 1974); disturbance in the forest community (Sousa 1984); seed predators (Smith and Balda 1979); fungi (Rosochacka and Grzywacz 1980); allelopathic germination inhibitors (Rietveld 1975); and slope, aspect, soil characteristics, and plant community type (Weber 1988). Given these factors, the variable seedbed microenvironment, and the size of a seed, it is perhaps surprising that we observed an interpretable relation (albeit weak) at the geographic level between germination speed and the inferred severity of summer drought. This observation underscores the overwhelming general effect of the growing season in structuring phenological variation in forest-tree species (Flint 1974) and the effect of summer drought in particular in central Oregon.

This is one of several studies intended to supply information for establishing provisional seed transfer guidelines for central Oregon ponderosa pine. Only germination speed is considered here, so any guidelines are preliminary. Regional differences in location-related variation (table 2), nevertheless, suggest that of the three largest regions, seed transfer rules will be most restrictive in the Deschutes and least restrictive in the Ochoco. The relatively strong correlations between longitude and germination speed in the Deschutes (table 3) also suggest that longitudinal seed transfer will be highly restrictive in the Deschutes. Because variation in germination speed seems to be related to variation in moisture regime, it is probable that seedling growth traits will show a similar contrast among regions (Griffith 1960).

Nursery managers who handle seedlots from a broad range of environments must be aware of potential differences in chilling requirements and germination speed. The results of this study imply that if spring incubation temperatures are marginal for germination of central Oregon ponderosa pine seed, germination speed will differ more among locations in the Deschutes region than further east in central Oregon. Longer stratification will reduce this variation (Weber and Sorensen 1990) and help minimize the loss of genetic diversity in the nursery phase of a tree improvement program (Campbell and Sorensen 1984).

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Variation in speed of seed germination was investigated among ponderosa pine trees representing 225 locations in central Oregon. Results suggested that at least some of the geographic variation is related to the severity of summer drought. In general, germination speed was greater in locations with short, drought-limited growing seasons. Levels of geographic variation were highest in the region having the steepest precipitation gradients. Most of the variation occurred, however, within locations.

Keywords: Geographic variation, seed germination, ponderosa pine, adaptation, drought, central Oregon.

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