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## Patterns of variation in bud-burst timing among populations in several *Pinus* species

By K. C. STEINER<sup>1)</sup>

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### Summary

Intraspecific variation in bud-burst timing was studied in range-wide provenance tests of eight north-temperate *Pinus* species: *P. banksiana* LAMB., the *P. flexilis* JAMES - *P. strobiformis* ENGELM. complex, *P. nigra* ARNOLD, *P. ponderosa* LAWS., *P. resinosa* AIT., *P. strobus* L., *P. sylvestris* L., and *P. virginiana* MILL. Only in *P. resinosa* were differences among populations statistically non significant. In all others, variation followed strong geographic patterns, as shown by the fact that regressions of population means in each species on polynomial functions of latitude and longitude of origin accounted for 69 to 88 percent of total variation.

Variation patterns were similar in all species when interpreted in general terms of the effects of latitude and proximity to oceans on climate. Populations from northern and continental regions were earlier to burst bud than populations from southern and coastal regions. The tendency for populations in the direction of coasts to burst bud late for their latitudes occurred farther inland on west sides of continents, where prevailing winds move from the ocean to the continent. Furthermore, this tendency was strongest in Europe, where prevailing winds are unimpeded by major north-south mountain ranges. Most of the pronounced departures from major trends were consistent with more local climatic anomalies caused by factors other than latitude or proximity to oceans.

There was a close correspondence between variation patterns in all species (except *P. resinosa*) and January mean temperature isotherms over the species' ranges. Similarly, consistently high correlations in all species were obtained between bud-burst timing and January through March mean temperatures measured near population origins, but not between bud-burst timing and spring and summer temperatures or variables related to spring frosts. Similarities among the species in their variation

patterns presumably indicate similarity in adaptive response to environmental gradients. Other species in other genera have variation patterns in budburst timing that differ from those observed here in minor or major respects. This is to be expected, since closely related species should adapt to environmental gradients in manners more similar than distantly related species.

**Key words:** phenology, adaptive variation, provenance testing trend surface analysis, *Pinus banksiana*, *P. flexilis*, *P. nigra*, *P. ponderosa*, *P. resinosa*, *P. strobus*, *P. strobiformis*, *P. sylvestris*, *P. virginiana*.

### Zusammenfassung

In weitgestreuten Provenienversuchen wurde an 8 Kiefernarten der nördlich gemäßigten Zone die intraspezifische Variation im zeitlichen Austriebsverhalten untersucht. Es handelte sich dabei um: *P. banksiana* LAMB., den *P. flexilis* JAMES-*P. strobiformis* ENGELM. Komplex, *P. nigra* ARNOLD, *P. ponderosa* LAWS., *P. resinosa* AIT., *P. strobus* L., *P. sylvestris* L., und *P. virginiana* MILL. Nur bei *P. resinosa* waren die Unterschiede zwischen den Populationen statistisch nicht signifikant. Bei allen anderen Arten war eine große geographische Variation festzustellen, was durch die Tatsache belegt wird, daß in jeder Art die Regression auf polynome Funktionen von geographischer Länge und Breite der Herkunft mit 69–88% der Gesamtvariation zu erklären waren.

Durch den Einfluß von Breitengrad und Meeresnähe auf das Klima waren die Variationsmuster bei allen Arten ähnlich. Populationen aus nördlichen und kontinentalen Regionen trieben früher aus, als Populationen aus südlichen und Küstengebieten. Die Tendenz der küstennahen Populationen zum späten Knospenaufbruch setzt sich weiter ins Binnenland, bis in westliche Teile des Kontinents fort, da sich die vorherrschenden Winde vom Meer her auf den Kontinent zubewegen. Am deutlichsten wird diese Tendenz in Europa, wo die Winde durch keine größeren, in Nord-Süd-Richtung verlaufenden Gebirge aufgehalten werden. Die meisten der wichtigen Abweichungen von diesen Trends gehen mit lokalen klimatischen Anomalien einher, werden also durch andere Faktoren als geographische Breite oder Meeresnähe verursacht.

Bei allen Arten (außer bei *P. resinosa*) besteht eine enge Verbindung zwischen dem Variationsmuster und den Ja-

<sup>1)</sup> Assistant Professor, School of Forest Resources, The Pennsylvania State University, University Park, PA, 16802. Journal Paper No. 5564 of the Pennsylvania Agricultural Experiment Station. The research reported here was supported by a National Science Foundation Graduate Traineeship and was performed on experimental material provided through funds from the U. S. Department of Agriculture Regional Project NC-99. I am indebted to Dr. J. W. WRIGHT for guidance in performing this research and to Y. S. PARK for technical assistance with computer analyses.

nuar-Isothermen im Verbreitungsgebiet der Arten. Genauso ergab sich eine übereinstimmend hohe Korrelation zwischen dem zeitlichen Austriebsverhalten und den von Januar bis März in der Nähe der Herkunftsorte gemessenen Temperaturen. Es waren aber keine Beziehung zwischen dem Zeitpunkt des Austriebes und den Frühlings- und Sommertemperaturen oder Unterschiede im Zusammenhang mit Spätfrösten feststellbar. Ähnlichkeiten im Variationsmuster der Arten deuten möglicherweise auf eine ähnliche Anpassungsfähigkeit an Umweltfaktoren hin. Andere Arten in anderen Gattungen haben Variationsmuster, die sich von den hier beobachteten mehr oder weniger stark unterscheiden. Dies war auch zu erwarten, da miteinander verwandte Arten sich eher gleichartig an eine Umwelt anpassen, als entfernt oder nicht verwandte.

### Introduction

The primary objective in provenance research is usually to identify populations that yield well-adapted progenies with maximum productivity. To attain this objective, as suggested by CALLAHAM (1964), provenance research programs should include studies of adaptive variation and the relationships between this variation and environmental influences. Knowledge of the probable cause of existing genetic variation patterns is useful in understanding the consequences of manipulating variation to increase wood production. It is for this reason that much of what is known about adaptive variation in plants comes directly from provenance research in forestry.

Thorough comparisons of the geographic variation patterns of different species have been made only infrequently, but this approach to interpreting adaptive variation has potential utility. For example, WRIGHT (1972) was able to give a more plausible explanation for genetic divergence within five tree species occupying both peninsulas of Michigan than if the divergence had been noted in only one species. Similarly, KUNG and WRIGHT's (1972) interpretations of variation patterns in Rocky Mountain species were made much more credible by simultaneous consideration of four sympatric species. Precise methods of adaptation to environmental variations probably differ among species, but gross similarities in geographic variation patterns suggest that the adaptive strategies of some species must be very similar (McMILLAN 1965).

Among economically important traits, bud-burst timing is a good candidate for genecological research because it has obvious adaptive significance and is probably under at least moderately strong selective pressure from climatic factors. The study described here is a comparison of variation patterns in bud-burst timing among range-wide populations of several north-temperate species of pine.

The principal objective was to assess the degree of concordance between patterns of different species by simultaneously considering the relationships of all patterns to climatic factors of presumed significance in natural selection. Eight species were studied: jack pine (*Pinus banksiana* LAMB.), the limber pine (*P. flexilis* JAMES) - border pine (*P. strobiformis* ENGELM. = *P. flexilis* var. *reflexa* ENGELM.) complex, European black pine (*P. nigra* ARNOLD), ponderosa pine (*P. ponderosa* LAWS.), red pine (*P. resinosa* AIT.), eastern white pine (*P. strobus* L.) Scotch pine (*P. sylvestris* L.), and Virginia pine (*P. virginiana* MILL.).

### Materials and Methods

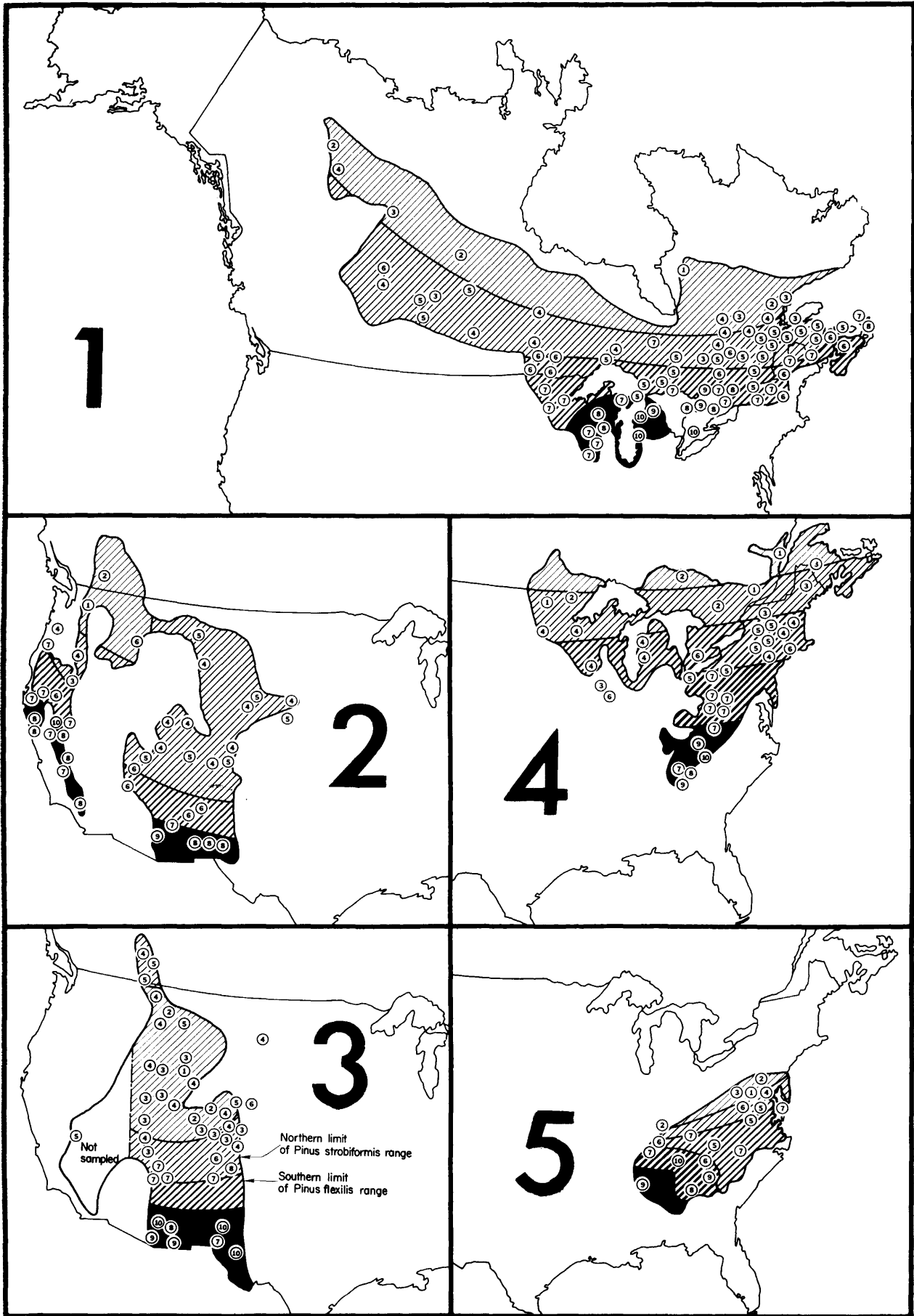
Data for this study came from provenance plantations located at W. K. Kellogg Experimental Forest near Battle Creek, Michigan. In general, each provenance in these plantings is represented by seed collected from five to ten average-sized trees within 1 km. of one another in a natural population of the species. All parts of the ranges of most species are well represented by population samples in these plantations. Most notable is a lack of Scotch pine populations from its Asian range. Table 1 gives some details regarding the plantations, all of which follow randomized complete block designs. Further information regarding the origin of some of these provenance tests may be found in the following articles: jack pine—CANAVERA and WRIGHT (1973), limber pine—WRIGHT *et al.* (1971), European black pine—WRIGHT and BULL (1962), ponderosa pine—WELLS (1964), red pine—WRIGHT *et al.* (1972), eastern white pine—GENYS *et al.* (1978), and Scotch pine—WRIGHT and BULL (1963).

Relative time of bud bursting was estimated spring 1973 by scoring trees shortly after growth initiation according to the degree their needles protruded beyond the fascicle sheaths. Each species' plantation was measured in one day (Table 1) at a time when new needles on some trees had not yet emerged from fascicle sheaths while those on others extended 2 cm. or more beyond fascicle sheaths. For a typical species, the scoring system was 1 = fascicle sheaths unbroken and 5 = needles 2.5 cm. longer than fascicle sheaths, with intermediate scores corresponding to appropriate degrees of development. Depending upon species, 4 to 6 bud-burst grades were distinguished. Since plot means were used as data elements, this gave effective measurement scales of 6 to 21 points for analyses of variance, depending upon original scale and number of trees per plot. After analyses of variance were performed, provenance means were linearly transformed for each species to a scale of 1 = early to 10 = late. This was done to simplify interpretations when considering many species in which different numerical scales had been used originally.

Table 1. — Details of the research plantations at Kellogg Experimental Forest in southern Michigan in which relative time of bud bursting was measured in 1973.

Species	Date of measurement	Age of trees (years)	Number of replicates	Number of trees per plot	Number of populations represented	Origin of experiment
<i>Pinus banksiana</i>	May 28	9	3	4	92	Canadian Forestry Service
<i>Pinus flexilis</i>	June 4	12	20	1	48	Michigan State University
<i>Pinus nigra</i>	June 5	14	10	4	27	Michigan State University
<i>Pinus ponderosa</i>	May 26	13	7	6	54	Michigan State University <sup>a</sup>
<i>Pinus resinosa</i>	June 1	13	5	4	63	Michigan State University
<i>Pinus strobus</i>	June 6	9	5	4	86	University of Maryland
<i>Pinus sylvestris</i>	June 2	14	6	4	108	Michigan State University
<i>Pinus virginiana</i>	June 3	16	10	4	19	University of Maryland

<sup>a</sup> In cooperation with the U. S. Forest Service.



Figures 1 - 5. — Relative times of bud bursting of natural populations of *Pinus* species measured in lower Michigan plantations. Shaded intervals represent trend surfaces that are least-squares fits to population means (circled numbers). Means plotted outside species' ranges indicate isolated but natural populations. More darkly shaded intervals and higher means represent later bud bursting. Figure 1. — *P. banksiana*, Figure 2. — *P. ponderosa*, Figure 3. — *P. flexilis*/*P. strobiformis*, Figure 4. — *P. strobus*, Figure 5. — *P. virginiana*.



Figure 6. — Relative times of bud bursting of natural populations of *Pinus sylvestris* measured in a lower Michigan plantation. See Figures 1-5 for explanation.

A common approach in the study of geographic variation patterns is to calculate correlations or simple linear regressions between observed values and latitudes or longitudes of origin. This approach was elaborated upon in the present study by regressing mean bud-burst values for all populations in a species on a polynomial function of X and Y, Cartesian coordinate analogues of longitude and latitude of origin, respectively. The resulting polynomial for each species described an imaginary, curved surface that is a least squares fit to observed population values plotted (on a third, vertical axis) at population origins on a two-dimensional range map of the species. Second-order or third-order equations were sufficiently complex to describe the variation in all species; higher order equations gave little improvement in fit.

To represent the trend surface of each species on a two-dimensional map, predicted values at all points within the range were divided into either 4 or 5 classes and the corresponding „contour intervals“ on the map were distinguished by different intensities of shading. Observed population means, rounded to the nearest unit, were then plotted at their respective geographic origins. Trend surface analyses thus provided a graphical representation of patterns underlying the observed variation. No trends were elucidated by the analysis that had not been previously identified through close inspection of the data. However,  $R^2$  values for the resulting prediction equations provided useful measures of the extent to which variation followed a geographic pattern, since geographically random variation would yield  $R^2$  values near zero. Differences between observed values and predicted values were presumably caused by adaptations to very local environmental conditions, sampling error in original seed collections (or genetic drift), or experimental error.

To relate order of bud bursting with variation among local habitat climates, 10 climatic variables were examined in three or more species each: normal mean monthly temperatures for January through July, mean date of the last spring frost, average length of the growing season (days

with a mean temperature of at least  $5.6^{\circ}\text{C}$ ), and average portion of the growing season (expressed in days) that occurs before the last frost. Data for these variables from stations within approximately 50 km. (depending on local climatic variability) of the population origins were extracted from A.E.S. (1973), HOLST (1963), various publications by the U.S. National Oceanic and Atmospheric Administration (Asheville, North Carolina), WERNSTEDT (1972), and several minor sources. Growing season data were not determined directly, but were estimated from the annual progression of monthly normals. European black pine was not considered in this part of the study because reliable climatic data were not available. Several populations of the other species also had to be eliminated from consideration because no climatic stations were located nearby.

In addition to the above variables, the standard deviation of the date of the last spring frost was estimated for provenances of jack pine. This was done by extracting from climatic records the range of observed dates and the number of years of observation, and then dividing the range by the corresponding value from a table of mean ranges of samples of varying sizes for the standard normal distribution. Temperature data were analyzed for their relationships with bud-burst timing by multiple regression, factor analysis, and simple correlation. A comparison of simple correlation coefficients ultimately proved to be the most useful technique for elucidating concordant patterns among species. Only those results are presented here.

## Results and Discussion

### Geographic Variation Patterns

Differences among populations were statistically significant in all species except red pine. This result with red pine is in accord with that of REHFELDT and LESTER (1966), who found no variation in time of growth initiation among 18 populations of that species. FOWLER (1964) and FOWLER

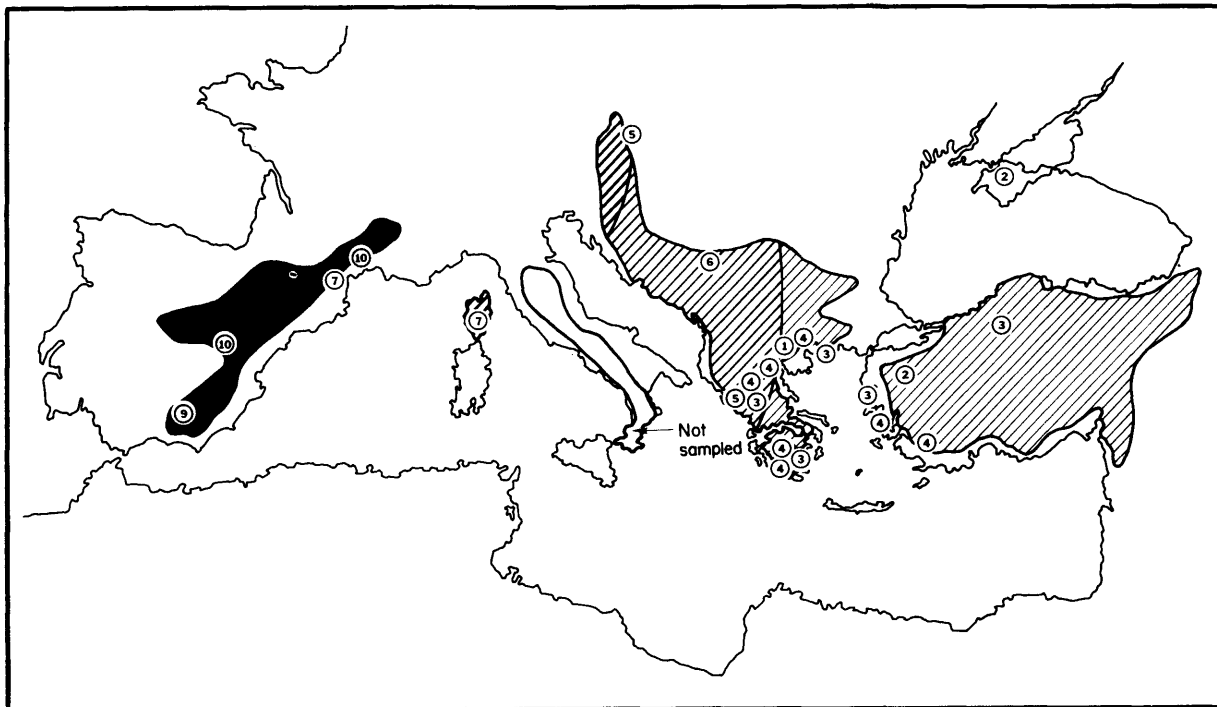


Figure 7. — Relative times of bud bursting of natural populations of *Pinus nigra* measured in a lower Michigan plantation. See Figures 1–5 for explanation.

Table 2. — Coefficients of correlation between relative bud-burst timing and climatic and geographic variables at population origins for several species of *Pinus*.<sup>a</sup>

Species	Trend surface <sup>b</sup>	Latitude	Longitude	Date of last frost	Growing season <sup>c</sup> Before last frost	Normal mean monthly temperature for:							
						Year	Jan	Feb	Mar	Apr	May	Jun	Jul
<i>P. banksiana</i>	.87	-.65	-.08 <sup>d</sup>	-.54	.01 <sup>d</sup>	.80	.75	.72	.76	.77	.74	.73	.75
<i>P. strobus</i>	.89	-.86	.12 <sup>d</sup>	-.47	.49	.78	.86	.87	.86	.85	.81	.71	.59
<i>P. virginiana</i>	.83	-.78	.47	-.70	.50	.79	.83	.87	.83	.83	.80	.78	.64
<i>P. ponderosa</i>	.86	-.64	.18 <sup>d</sup>	--	--	.49	.66	.60	.52	.35	.24 <sup>d</sup>	.21 <sup>d</sup>	.07 <sup>d</sup>
<i>P. flexilis</i> <sup>e</sup>	.87	-.65	-.05 <sup>d</sup>	--	--	--	.73	.72	.68	.64	.64	.67	.57
<i>P. sylvestris</i>	.94	-.62	-.69	--	--	--	.76	.77	.80	.73	.60	.28	.17 <sup>d</sup>
<i>P. nigra</i>	.92	.12 <sup>d</sup>	-.90			no climatic data available							

<sup>a</sup>For correlations with climatic variables, coefficients connected by a line are not significantly different from the highest at  $P \geq .85$ , a level chosen to compromise the probabilities of making Type I and Type II errors in discriminating among coefficients.

<sup>b</sup>R-values from the regression of population means on second- or third-order polynomial functions of latitude and longitude.

<sup>c</sup>Number of days with mean temperatures of 5.6° C or greater.

<sup>d</sup>Not significantly different from 0 at  $P \geq .95$ ; all other coefficients statistically significant

<sup>e</sup>Including *P. strobitiformis*.

and MORRIS (1977) commented on the unusually high genetic uniformity of red pine in other respects. The uniformity of red pine in time of bud bursting is probably not a function of its geographic range, as suggested by FLINT (1974)—populations of other species within this region differed significantly.

In the seven other species, measured differences represented a range in bud-burst timing among populations of a least one to two weeks in the year of study. In all these, there was a strong geographic component to variation among population means, as shown by Figures 1—7 and the fact that the trend surfaces are good fits to the data. Based on R<sup>2</sup> values for the various species, polynomial functions of latitude and longitude accounted for 69 to 88 percent of the total variation among population means in bud-burst timing.

In most cases, trend surfaces explained substantially more of the total variation in bud-burst timing than did simple correlations with either latitude or longitude (Table 2). Consequently, variation patterns were generally more complex than can be described with reference to either latitude or longitude alone. However, population means in all species except European black pine were significantly correlated with latitude of origin—northern populations burst bud earlier than southern populations. And there was a strong tendency for deviations from this trend to occur in regions whose climates are under the influence of oceans—continental populations burst bud earlier than coastal populations in the same latitude. Thus, it is possible to describe the general features of the patterns in terms of the two geographic factors that have the greatest influence on world climates: latitude and proximity to oceans.

This is most easily illustrated by the variation patterns of North American species (Figures 1—5). Variation in all five was predominantly latitudinal, but three of the species showed departures from this trend in the directions of coasts. Departures occurred farther inland in western than in eastern North America, as is particularly evident in the pattern for jack pine (Figure 1). Similarly, because

of the effect of prevailing westerly winds, the oceanic influence on climate extends much farther inland in western than in eastern North America. Indeed, the trend surfaces for jack pine (Figure 1) and ponderosa pine (Figure 2) closely parallel the isotherms of a number of temperature variables that are strongly influenced by Pacific air masses moving eastward (KENDREW 1961, VISHER 1954).

The trend surface in the western portion of the limber pine range (Figure 3) showed a pattern similar to that for ponderosa pine. However, the trend surface in this region was not mapped because it was based on only one population in California. That population was slightly later than others directly east, but little can be confidently said about variation in near-coastal vs. interior populations of this species. The data for limber pine and border pine were combined for convenience in computing the trend surface in Figure 3. Most of the latitudinal trend in the map was actually caused by differences between the two species. However, less pronounced latitudinal trends were evident in each species, as shown by the following tabulation:

Populations	Mean score
Limber pine (bulk of range)	3.5
Limber pine (sympatric zone with border pine)	6.5
Border pine (sympatric zone with limber pine)	7.3
Border pine (bulk of range)	9.1

Thus, differences between these species are paralleled by variation within each, as STEBBINS (1950) suggested should occur with closely related species.

Patterns of variation in eastern North America were more strictly north to south than in western North America. Tendencies for populations closer to the Atlantic to burst bud late for their latitudes occurred only when populations very near the coast were sampled. Several late populations of jack pine (Figure 1) from the Canadian maritime provinces, and one late and very coastal population of Virginia pine (Figure 5), tilted the trend surfaces for those species. However, the one near coastal population of eastern white pine (Figure 4) was somewhat late

for its latitude but had little effect on the overall variation pattern.

Like western North America, the climate of Europe is also under the influence of westerlies. However, an oceanic influence on climate is felt much farther inland (as far as Siberia with decreased effect) in Europe than in North America (BIEL 1944). Similarly, the tendency for populations in the direction of the coast to burst bud later occurred much farther east in Scotch pine (*Figure 6*) than in western American species. Asian populations of Scotch pine burst significantly earlier than European populations in the same latitudes. The earliest population in the plantation was native to Siberia, which is climatically the most continental region in Eurasia.

Scotch pine in the European part of its range south of Scandinavia showed very little variation among populations in time of bud bursting and virtually no latitudinal trend (except, as noted later, in southeastern Europe). This corresponds to the general character of the region's climate. Europe has no major north-south mountain ranges south of Scandinavia that can block the eastward movement of oceanic air masses. As a result, the climate of the region is mild for its latitude, and north-south temperature gradients are very gradual most of the year and even nonexistent in winter (KENDREW 1961). However, the British Isles have a distinctly more maritime climate than the continent (RUMNEY 1968), and Scottish populations were significantly later to burst bud than others in the same latitude.

European black pine (*Figure 7*) was unique among the species studied (except red pine) in showing no relationship between latitude of origin and time of bud bursting. There was, however, a strong tendency for eastern populations to burst bud earlier than western populations ( $r$  with longitude =  $-0.90$ ). Again, this deviation from a latitudinal trend is describable in terms of an oceanic effect on climate. Prevailing winds in the Mediterranean region are westerly or northwesterly and carry the ameliorating influence of the Atlantic eastward to approximately the longitude of Yugoslavia. East of this longitude, and corresponding with an increase in earliness of bud bursting, winds are primarily from the north or northeast, especially in winter, and carry air masses originating over the cold Balkan highlands and Russian steppes (BIEL 1944, KENDREW 1961).

Thus, there is a west-east gradient of increasing continentality of climate in the region, and it appears to correspond with the pattern of variation in European black pine. This climatic gradient is particularly true of winter temperatures. Mild, „mediterranean“ climate is found only on coasts and does not apply to the relatively high elevations from which the populations of European black pine originated. The higher mountains in Greece experience cold winters with much snow, and average winter temperatures in the interior Balkans are lower than those in most parts of Norway. This is also true of higher elevations in Turkey and the Caucasus. Similarly, north of the mountains on the Crimean Peninsula, where one of the earliest of the populations originated, the climate is typically Russian with little or no influence from the Atlantic Ocean (BIEL 1944, KENDREW 1961).

#### *Deviations from General Trends*

As the figures show, the means of individual populations often deviated from the general trends as they have

been described. However, surprisingly few deviations involved two or more populations and were otherwise strong enough to be attributable with confidence to more than just experimental error. Most of these anomalies appeared to follow climatic trends similar to those already discussed.

Several populations of Scotch pine in southern Europe burst bud significantly earlier than most or all of the numerous populations in central Europe, contradicting the usual north-south trend. This had a noticeable effect on the shape of the trend surface in the Balkan Peninsula and Asia Minor (*Figure 6*). As already discussed with respect to European black pine, relatively early bud bursting in the Balkan Peninsula, Turkey, and especially the Caucasus is reasonable because the higher elevations in these regions have temperatures substantially lower than those in most parts of central Europe. Two relatively early populations of Scotch pine also occurred in Spain and southern France. Both were native to the Pyrenees, the coldest part of the Iberian Peninsula and the coldest area in western Europe south of Scandinavia, other than the Alps (STEINHAUSER 1970). The earliest of the western populations of European black pine was also from the Pyrenees (*Figure 7*).

The pronounced curvature of the trend surface in the Lake States portion of the jack pine range (*Figure 1*) was caused by the fact that southern Michigan populations were significantly later ( $\bar{x} = 9.5$ ) than all Wisconsin populations ( $\bar{x} = 7.5$ ) in the same latitude. This corresponds with the climate of the region--winter temperatures (but not spring and summer temperatures) are lower in Wisconsin than in all but the northern tip of southern Michigan (VISHER 1954). Eastern white pine (*Figure 4*) should presumably have followed this pattern also, but it did not.

Both ponderosa pine (*Figure 2*) and limber pine (*Figure 3*) showed essentially random variation in the central and northern Rocky Mountains, with little relationship with latitude. This appears to be in agreement with the climate of the region, although generalizations about the climate are difficult to make because of the rough topography. From southern Colorado and Utah northward through the Rocky Mountains there is little or no relationship between latitude and mean temperatures (VISHER 1954). South of there, and corresponding to a gradient in bud-burst timing, isotherms run east and west as expected.

Despite the absence of a latitudinal trend in the bulk of the limber pine range, there were two minor features of the variation pattern that appeared significant. North of southern Colorado and Utah, among the latest populations were two in southeastern Wyoming and adjacent Nebraska (isolated from the main range in *Figure 3*) and two in the northern part of the range in Alberta. All four appeared to have an effect on the shape of the trend surface. The two isolated populations were from an unusually low elevation for the species at that latitude, and an area that is warmer than the mountains to the west in all months. This could perhaps account for their performance. However, it is difficult to correlate the lateness of the two northern populations with any characteristic of climate.

#### *Relationships with Habitat Climates*

Continentality and latitude appear to adequately describe the major features of the variation patterns ob-

served here. In addition, the patterns of all species except red pine are very similar when interpreted in terms of the combined effects of these factors on climate. This suggests a close relationship between genetic variation and climatic variation. Furthermore, similarities among variation patterns suggest similarities among the species in adaptive response to environmental gradients. If the patterns are indeed concordant, then specific climatic variables should exist that are correlated with genetic variation in all species, regardless of coincidental relationships of the patterns with latitude and longitude.

Climatic maps show that isotherms for January mean temperatures fit remarkably well with the variation patterns in all species. In contrast, July isotherms depart from the patterns, especially near coasts (Anonymous 1967, STEINHAUSER 1970, VISHER 1954). This result agrees well with the major trends in variation: north-early, south-late; interior-early, coastal-late. Coastal areas have climates resembling those of southern areas only in winter; in summer they are not warm for their latitudes and even tend to resemble northern areas in being rather cool. For example, Scotland is as warm or warmer than most parts of central Europe in January, but it's as cool as most parts of Norway in July. The parts of California where most of the late, western populations of ponderosa pine originated are as warm as Arizona and New Mexico in winter; but have temperatures very similar to those in the central and northern Rocky Mountains in summer.

Similarly, the highest, or nearly the highest, correlations between bud-burst timing and climatic variables in each species were obtained with normal monthly mean temperatures in winter (Table 2). Nearly all correlations with climatic variables were statistically significant, and most were larger than correlations with latitude or longitude in each species. However, there was a tendency in most species for correlations with spring and summer temperatures, and variables related to spring frost, to be either nonsignificant or significantly smaller ( $P \geq .85$ ) than correlations with January through March temperatures. Correlations with length of the growing season (calculated for four species only) were almost as large or (in jack pine) slightly larger than most correlations with winter temperatures. However, this was expected because growing season data were originally estimated from monthly normals.

Although climatic data were not available for European black pine populations, there is reason to believe that variation in this species also is more strongly associated with winter temperatures than summer temperatures. As discussed above, variation in European black pine paralleled a west-east increase in continentality over the Mediterranean region. This climatic gradient is pronounced in winter, when temperatures decrease eastward because of the increasing influence of Eurasian continental air masses. However, in summer there is little change in mean temperatures from west to east, and this is true both in continental Europe and along the Mediterranean coast (BIEL 1944). Elevations of origin were similar for all populations, so this generalization is probably true for the native habitats as well.

VEEN (1954), BURLEY (1966), and others have suggested that selection for late bud bursting occurs in maritime climates because they have a long and uncertain period of rise in spring temperatures above freezing. This expla-

nation does not adequately account for the variation patterns common to the species studied here. True maritime climates do not extend nearly as far inland as did the deviations from strictly latitudinal variation in jack pine, ponderosa pine, and Scotch pine. Furthermore, the data suggest that this interpretation of maritime climates may not be universally applicable.

Two variables that are measures of the rapidity of transition from frost-prone to frost-free growing conditions are (1) the portion of the growing season that occurs before the last frost (examined in three species, Table 2) and (2) the standard deviation of the date of the last frost (examined in jack pine only). None of the four correlations between bud-burst timing and these variables was very high, and correlations between both variables and bud bursting in jack pine were near zero ( $r = 0.01$  and  $0.03$ , respectively). In the jack pine data, which showed a strong tendency for maritime populations to burst bud late, I could find no evidence that maritime climates (Prince Edward Island and southwestern New Brunswick) actually do have a longer period of late frosts than continental climates (Manitoba and Saskatchewan). Although maritime habitats experience mild temperatures considerably before the danger of frost is past, very warm weather, permitting rapid heat accumulation and vegetative growth, frequently precedes the last frost in continental areas.

Correlations between bud-burst timing and date of the last spring frost were statistically significant in all three species in which they were calculated (Table 2). However, this variable did not account for more than half of the variation in bud-burst timing in any species. It is unlikely that spring frosts play more than a minor role in selection for bud-burst timing in the pines. In contrast to some other conifers, visible late-frost injury on pines is rare, even when they are planted outside their native habitats. Furthermore, at least some of the species are known to be resistant at the time of growth initiation to temperatures considerably below freezing (DEHAYES 1977, GLERUM 1973, MARONEK and FLINT 1974).

Bud bursting in the pines and most other woody plants is believed to be primarily a response to rising temperature (FLINT 1974, PERRY 1971). It is therefore reasonable to suppose that the response is adapted to the prevailing temperature regime at the time it occurs, as for example FRYER and LEDIG (1972) apparently found with photosynthesis in *Abies balsamea*. Thus populations native to habitats with cooler growing season temperatures are expected to have a lower temperature threshold for growth and begin growing earlier in the spring. YEATMAN (1966) found that this is true in jack pine. Observed variation in the present study generally fit this expectation, except that correspondence with winter temperatures was better than with temperatures at the time bud bursting actually occurs. However, since pines are photosynthetically active in winter, adaptive responses to temperatures during the cold months could be more important for the processes that culminate in bud bursting than responses in months when temperatures are generally favorable.

No measure of the apparent similarities among these species in adaptive response was as consistently good as monthly mean temperatures in winter. The patterns tend to be dissimilar in their relationships with latitude and longitude and in their relationships with other climatic



variables investigated, with the possible exception of growing season length. As discussed above, winter temperatures could have a direct role in natural selection for bud-burst timing. More likely, however, winter temperatures are merely good expressions, at least partly indirect, of a climatic *gestalt* to which all species except red pine responded similarly. Winter temperatures are correlated with many other variables, such as length of growing season, that could also have adaptive influence on bud-burst timing. The fact that climate is both spatially and temporally continuous and variable suggests that any evolutionary response to it must have an exceedingly complex cause. Furthermore, it is unlikely that all populations of all species have evolved modes of bud bursting in response to *exactly* the same climatic factors; and of course temperature may not be the only aspect of climate that is adaptively important.

#### Agreement with Other Studies

Results obtained at Kellogg Forest in 1973 are consistent with data taken from some of the same provenance experiments at other ages and locations (DeHAYES 1977, READ 1971, WELLS 1964, YEATMAN 1966). For at least Scotch pine, ponderosa pine, and jack pine, the major features of the variation patterns appear to be true regardless of the year of measurement, and regardless of whether time of bud bursting is measured directly or indirectly, by the method I used.

A north-early, south-late pattern of genetic variation in bud-burst timing is common to a number of north-temperate tree species (NIENSTAEDT 1974). Nevertheless, patterns of variation in species other than pines often differ in minor or major respects from those reported here. In *Betula alleghaniensis*, which has a range very similar to that of eastern white pine, STEINER (1975) found that southern populations burst bud later than northern populations, but all populations from maritime areas (Nova Scotia and southeastern Maine) burst bud *earlier* than interior populations from the same latitudes. In contrast, variation in time of bud bursting in *Picea sitchensis* showed no relation to latitude of origin, but populations nearer the Pacific Coast were later than those away from the coast (FALKENHAGEN 1977). KRIEBEL *et al.* (1976) found that variation in time of bud bursting in *Quercus rubra* was geographically complex and had no simple relationship with latitude or longitude. Populations of *Prunus serotina* collected throughout the eastern United States exhibited random variation in this trait (GENYS and CECH 1975). The pattern of variation in *Pseudotsuga menziesii* var. *glauca* was found by STEINER (1979) to be virtually the opposite of the patterns in ponderosa pine and limber pine, even though the three species are sympatric.

Thus, the similarities among the variation patterns in Figures 1—7 are emphasized by their differences with those of some other species. This is to be expected, of course, since closely related species should adapt to environmental gradients in manners more similar than distantly related species. It is likely that very similar environmental factors are important in selection for the same trait in species whose physiological responses to the environment are closely related.

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## Dry Matter Accumulation in Twenty Wind-Pollinated *Pinus pungens* Families from Southwest Virginia

By P. P. FERET, D. WM. SMITH and H. M. RAUSCHER<sup>2)</sup>

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### Summary

Twenty wind-pollinated families of *Pinus pungens* LAMB. were greenhouse grown under two soil types, a Muskingum fine sandy loam and a Groseclose silt loam. Seedling survival and growth were significantly different between soils and significant family effects on survival and growth were also observed. Genotype × environment interaction between families and soil type was also significant. The implications of these results were discussed.

**Key words:** Genotype-environment interaction, seedling survival, Muskingum, Groseclose.

### Zusammenfassung

Zwanzig frei abgeblühte Familien von *Pinus pungens* LAMB. wurden im Gewächshaus auf zwei verschiedenen Bodentypen angezogen: einem feinen sandigen Lehm der Muskingum-Serie und einem tonigen Lehm der Groseclose-Serie. Das Überleben und Wachstum der Sämlinge auf beiden Bodentypen waren signifikant verschieden, ebenso wurden signifikante Familieneffekte auf das Überleben und das Wachstum beobachtet. Die Genotyp × Umwelt-Interaktion zwischen Familien und Bodentypen war auch signifikant. Die Bedeutung dieser Ergebnisse wurde diskutiert.

### Introduction

Table-Mountain pine (*Pinus pungens* LAMB.) is an Appalachian endemic (LITTLE, 1971) usually found on extremely droughty sites of southwesterly exposure. It often occurs in relatively small and scattered populations; the genetic relationship among these populations is ambiguous (FERET, 1974).

In an attempt to understand more of the genetics of *P. pungens* a greenhouse experiment was established to test genotype-environment interaction of wind-pollinated families grown on different soil materials. It was envisioned the study results might provide insight into the adaptive genetic mechanisms that permit the species to regenerate and grow on extremely poor sites in the Appalachian mountains of Virginia.

### Material and Methods

Twenty wind-pollinated families were grown from seed collected and kept separate by mother-tree, from 20 trees growing on Brush Mountain in Montgomery and Craig

Counties, Virginia. The elevational range exhibited at parent tree sites was 580—915 meters. All parent trees were growing within a 3 km radius.

Seed was extracted from cones and germinated in replicate petri dishes on filter paper. When cotyledons were developed and primary needles just visible, seedlings were transplanted into plastic 13 cm pots.

Two soil materials were used as a growing medium. Soil one (1) was the A horizon from a *P. pungens* site on Brush Mountain, VA. The soil is representative of the Muskingum Soil Series and is classified as a fine-loamy, mixed, mesic, Typic Dystrachrept. It is derived from fine sandstone and siltstone and because of the steep slope position it is shallow and quite droughty. The natural fertility is low (Table 1) and the mixed pine-hardwood stands that dominate the area are of very poor quality. The second soil material was the surface horizon from a cultivated field in Blacksburg, Va. The soil is representative of the Groseclose series and is classified as a clayey, mixed, mesic, Typic Hapludult. It is a deep, well drained soil derived from residuum of dolomitic limestone and shale breccia. The soil is common on broad ridges and uplands. It is high in natural fertility (Table 1) and has been modified by agricultural activity. Where the soil has not been disturbed good forest stands of predominantly white oak are prevalent. These two series closely represent the extremes of soils that dominate in the natural range of *P. pungens* in Southwest Virginia. Both soils were inoculated 8 weeks after seedling transplanting with 8 gm of ground litter root mat from the *P. pungens* mother tree site.

Plants were grown for 8 months in a replicated design consisting of five blocks, each with three complete replications. Each replication contained forty pots; each pot

Table 1. — Soil analysis data for soil materials used to grow seedlings of *P. pungens*. Characteristics for Soil 1 (Muskingum) and Soil 2 (Groseclose).

	Soil 1	Soil 2
ph	5.5	6.4
Soluble Salts (ppm)	256	269
Elemental Avail (kg/ha)		
CaO	740	2100
MgO	151	336
P <sub>2</sub> O <sub>5</sub>	6	90
K <sub>2</sub> O	79	202
Nitrates (ppm)	5	25
Organic Matter (%)	1.5	1.9

<sup>1)</sup> Research supported in part by the Reynolds Homestead Research Center.

<sup>2)</sup> Authors are respectively: Associate Professor, Associate Professor and Graduate Assistant, Department of Forestry, VPI & SU, Blacksburg, VA, 24061.