PATTERNS OF GENETIC VARIATION WITHIN FIFTEEN TREE SPECIES IN TIMES OF BUD BURST AND FLOWERING

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ABSTRACT

PATTERNS OF GENETIC VARIATION WITHIN FIFTEEN TREE SPECIES IN TIMES OF BUD BURST AND FLOWERING

By

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Genetic variation in time of bud burst was studied in replicated, Lower Michigan provenance tests of 15 tree species: *Abies balsamea*, *Betula alleghaniensis*, *Larix laricina*, *Picea glauca*, *Pinus banksiana*, *P. flexilis*, *P. strobiformis*, *P. nigra*, *P. ponderosa*, *P. resinosa*, *P. strobus*, *P. sylvestris*, *P. virginiana*, *Prunus serotina*, and *Pseudotsuga menziesii*. Genetic variation in time of flowering was studied in eight species: *Betula alleghaniensis*, *Larix laricina*, *Pinus banksiana*, *P. nigra*, *P. resinosa*, *P. sylvestris*, *P. virginiana*, and *Prunus serotina*. With the exceptions of the *Abies balsamea*, *Larix laricina*, *Prunus serotina*, and *Pseudotsuga menziesii* experiments, plantations contained provenances from virtually all parts of the native ranges. The *Prunus serotina* experiment was the smallest with eight provenances represented.

In all species except *Pinus resinosa* there was significant variation among provenances in time of bud burst. In general, results were consistent with those observed in other years in the same plantations, other plantations of the same provenance tests, and other provenance tests of the same species. When other studies involved the same provenances, nearly all correlations between results were between r = +.76 and r = +.80.

Most species shared certain geographic trends in variation in time of bud burst. Northern, interior, and eastern Upper Peninsula (Michigan) provenances burst bud earlier than southern, near-coastal, and western Upper Peninsula provenances. There appeared to be no relationship between elevation of origin and time of bud burst (independent of latitude), but deviations from the latitudinal trend in *Pinus flexilis* and *P. ponderosa* can be explained by the effect of topography on climate. Variation among central and northern Rocky Mountain provenances of these species was small and essentially geographically random. There were few conspicuous instances in any species in which deviations from general trends could not be attributed to regional climatic anomalies or peculiarities of the species.

Multiple regression analyses in four species between time of bud burst and 12 climatic variables yielded highly significant prediction equations for time of bud burst in each species. But they failed to indicate which variables may have been important in the evolution of the common patterns of variation. Adaptation was probably a compromise involving many factors of the year-round climate. However, continentality -- sometimes expressed as the mean annual range in temperature -- corresponded generally well with the geographic patterns in genetic variation. Earliest provenances in most species were native to regions with the most continental climates (*e.g.*, central Canada, interior Alaska, and northeastern Siberia).

The geographic pattern of variation in time of bud burst in *Pseudotsuga menziesii* was the opposite of that in all other species: southern provenances were earlier than northern provenances and provenances closest to the Pacific Coast were early for their latitudes.

This could occur if this species bursts bud in response to photoperiod and the others burst bud in response to temperature, or if *P. menziesii* trees were not chilled sufficiently to completely remove winter dormancy.

Some provenances in four species were represented by several half-sib families each. None of eight provenances of *Pinus flexilis* and *P. strobiformis* contained significant variation among families in time of bud burst. However, significant genetic variation was found within two of six *Abies balsamea* provenances and one of five *Prunus serotina* provenances. Within these three provenances the magnitude of differences approached or equalled those observed in the respective entire plantations.

In all species studied except *Pinus resinosa* and *P. virginiana* there was significant variation among provenances or families in time of flowering. This trait was significantly correlated with time of bud burst among provenances or families in all species. The degree of correspondence between the traits was better in species in which flowers and shoot systems arise from the same buds.

Genetic variation in time of bud burst could be important in breeding for improved resistance to some insect and disease pests and to damage by late spring frosts. Frost damage in three Lower Michigan plantations of *Pseudotsuga menziesii* was correlated with relative time of bud burst of the provenances. Early provenances were most damaged.

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INTRODUCTION

"'When I shake my flowing ringlets,'
Said the young man, softly laughing,
'Showers of rain fall warm and welcome,
Plants lift up their heads rejoicing,
Back into their lakes and marshes
Come the wild goose and the heron,
Homeward shoots the arrowy swallow,
Sing the bluebird and the robin,
And where'er my footsteps wander,
All the meadows wave with blossoms,
All the woodlands ring with music,
All the trees are dark with foliage!'"

Longfellow, *The Song of Hiawatha*

The "young man" in the poem is, of course, the weather bringing a triumph of spring over "old man" winter. Longfellow very eloquently characterizes spring, but not by its weather. Instead, he lists some of the special biological events of spring, alluding to the fact that our most vivid impressions of seasonal change are derived not from the weather, but from changes in the moods of life -- changes in the occurrence, behavior, or appearance of plants and animals. The events he lists are those Hiawatha might have observed in primeval Minnesota, but each of us can recall certain other phenomena which we perennially associate with spring or other seasons.

Phenology (short for phenomenology) is the study of these phenomena, particularly their times of occurrence in different species and at different places. It is an old science. Huberman (1941) places its origin with Linnaeus in 1751, though he notes that even ancient Greeks

and Latin writers recorded times of flowering and bird migration. But even further back in time, to the beginnings of agriculture, farmers probably planted and harvested according to rules associated with phenological events. Today we still find that phenological information is important in agriculture and the related field of forestry. Among other things, the results of phenological research are useful in determining when to take cuttings of plants for propagation, when to harvest, and when to apply pest control measures to plants.

The above falls under the category of descriptive phenological research -- listing the times of periodic biological events and noting which occur together. Some people have attempted to look at phenological data analytically, usually hoping to find causes for the differences in the times of events at various places. The best known such attempt was that of Hopkins (1938) who proposed that any periodic event in plants and animals is advanced or retarded a certain number of days for every regular change in latitude, longitude, or elevation.

But according to Daubenmire (1959), Hopkins' laws of phenology are subject to so many local deviations that they have little practical value. There are two reasons for this. One, of course, is that local climates usually deviate from broadly-based geographic patterns. The other is that most species are not genetically uniform over large areas, and to ascribe differences in the timing of phenological events entirely to the weather ignores the possibility of genetic causes.

The different roles that genetics and the environment play in phenology may be illustrated by the principal springtime event which I chose to study for this dissertation -- the timing of bud burst in trees. Fifteen species were studied: balsam fir (Abies balsamea), yellow birch

(*Betula alleghaniensis*), tamarack (*Larix laricina*), white spruce (*Picea glauca*), jack pine (*Pinus banksiana*), limber pine (*P. flexilis*), European black pine (*P. nigra*), ponderosa pine (*P. ponderosa*), red pine (*P. resinosa*), border pine (*P. strobiformis*), eastern white pine (*P. strobus*), Scotch pine (*P. sylvestris*), Virginia pine (*P. virginiana*), black cherry (*Prunus serotina*), and Douglas-fir (*Pseudotsuga menziesii*).

My research concerned the genetic aspects of bud burst. However, like many plant growth responses, time of bud burst is most directly determined by the environment. Heredity probably determines only the quantity and quality of the environmental stimulus to which the tree will respond. Hence, it is necessary to understand the effect of the environment on dormancy and dormancy release in order to grasp the meaning of genetic variation in time of bud burst. The following discussion of this subject as it pertains to temperate and cold climate trees is taken largely from reviews by Doorenbos (1953) and Perry (1971).

Many trees cease growing and set buds well before temperatures turn cool. Usually they can resume growth during this time if certain conditions occur or are imposed, such as lengthening of the photoperiod or removal of the leaves. As summer passes into autumn, however, changes occur within the buds which make them unable to immediately resume growth, regardless of the state of the environment. When this occurs the buds are said to be in winter dormancy or true-rest.

The natural stimulus which triggers the internal changes necessary for the release from true-rest is exposure to cool temperatures. (In the laboratory long photoperiods will substitute for the chilling requirement in some species.) Temperatures just above freezing are most effective in breaking true-rest, but longer periods of exposure to higher or lower temperatures will have the same effect. Up to a point, increments of chilling cause increased rapidity of growth initiation after a return of warm temperatures. However, chilling requirements of native trees are usually met well before the end of winter.

After the chilling requirement is met, buds remain in a state of imposed dormancy or after-rest until they are exposed to other conditions which stimulate bursting. Apparently, most species require only a period of exposure to warm temperatures at this point to begin growing. However, there is some evidence that in addition to the heat requirement there may also be a photoperiodic (long-day) requirement in certain species. Among the species covered by my research, photoperiod has been found to have little or no effect on removing after-rest in eastern white pine and white spruce (Watt and McGregor, 1963), yellow birch (Wang and Perry, 1958), jack pine (Yeatman, 1967), and Scotch pine (Jensen and Gatherum, 1965). However, photoperiod may influence the time of bud burst in some Douglas-fir trees (Irgens-Möller, 1957).

Since environmental conditions can affect the timing of bud burst, it is obviously necessary to grow trees under nearly uniform conditions to determine if they are genetically different. If that is done, and the plants still burst bud at different times, then genetic variation must exist. In the majority of species this variation would probably reflect differences in heat requirements for growth after true-rest is removed. In some species genetic variation in time of bud burst may reflect an interaction between differences in requirements for heat and photoperiod.

Within a species genetic variation may occur at several levels. For example, differences may exist among families from the same

population or provenance, among provenances of the same geographic variety, and among varieties of the species. My research involved variation among provenances in all of the 15 species studied. In addition, some of the species contain two or more varieties or races which were compared for time of bud burst and in four species I studied variation among half-sib families. The results show that genetic variation in time of bud burst exists in most of the species. Furthermore, the geographic patterns of variation in different species are similar in many respects, and I discuss the climatic factors which may be the historical causes of the evolution of these common patterns.

Variation in time of flowering was measured in eight of the species and compared with variation in time of bud burst. Finally, genetic variation in damage caused by late spring frosts was measured in Douglas-fir; and I discuss the relationship between spring phenology and frost susceptibility and other traits of economic importance.

MATERIALS AND METHODS

THE PLANTATIONS

All measurements were made in replicated plantations of trees from different provenances. (The term "provenance" will be used here to indicate not only the original stand of trees, but also the trees grown from seed collected in that stand.) In general, the seed was collected from five to ten average-sized trees located in an area less than 0.5 miles in diameter. In some species, where seed had been kept separate according to mother tree, some provenances consisted of three to ten half-sib families. Otherwise, provenances were represented by trees of unknown relationship, except that they were from the same population. Each provenance or half-sib family was represented by one randomly located plot in each replicate. Table 1 gives details of the plantations.

With the exception of four species, the plantations contain trees from virtually all parts of the native ranges. Provenances from far-northern parts of the ranges are lacking in the tamarack and balsam fir experiments; provenances from the Pacific Coast are lacking in the Douglas-fir experiment; and the black cherry experiment contains just eight scattered provenances from Michigan, Pennsylvania, Virginia, Tennessee, and North Carolina.

Except for two plantations measured for frost damage, all are located at W. K. Kellogg Experimental Forest, 10 miles west of Battle

Table 1.--Details of the research plantations at Kellogg Forest in southwestern Michigan.

Species	Planta-tion	Size of stock	Age in 1973	Repli-cates	Trees per plot	Material[(a)]		Survival to 1973	Origin of experiment
						Proven.	Progen.		
	no.-yr.	yrs.	yrs.	no.	no.	no. of seedlots		%	(b)
Abies balsamea	3-70	2-4	9	3	4	42	42	84	U.Wis.
Betula alleghaniensis	1-68	1-2	8	11	4	36	none	64	I.F.G.
Larix laricina	5,6-66	2-0	9	6	4	28	none	76	U.Min.
L. laricina	6-69	2-1	6	10	4	25	none	93	U.Min.
Picea glauca	5,6-63	2-3	15	7	4	24	none	93	I.F.G.
Pinus banksiana	7,8-66	2-0	9	3	4	92	none	84	P.F.E.S.
P. flexilis-strobiformis	11-64	2-1	12	20	1	48	55	54	M.S.U.(c)
P. nigra	5-61	2-0	14	10	4	27	none	83	M.S.U.
P. ponderosa	1-62	2-0	13	7	6	54	none	64	M.S.U.(d)
P. resinosa	2-63	3-0	13	5	4	63	none	84	M.S.U.
P. strobus	3-66	2-1	9	5	4	86	none	73	U.Md.
P. sylvestris	2-61	2-0	14	6	4	108	none	88	M.S.U.
P. virginiana	1-60	1-1-1	16	10	4	19	none	69	U.Md.
Prunus serotina	9-67	1-0	7	4	10	8	33	74	T.V.A.
Pseudotsuga menziesii	16-65/67	1-2-(2)	11	10	4	64	none	90	M.S.U.

(a) Provenances = seed grouped by stand of origin; Progenies = seed grouped by female parent.

(b) University of Wisconsin; U.S.F.S. Institute of Forest Genetics, Rhinelander, Wisc.; University of Minnesota; Petawawa Forest Experiment Station, Chalk River, Ontario; Michigan State University; University of Maryland; Tennessee Valley Authority, Norris, Teen.

(c) In cooperation with the National Science Foundation.

(d) In cooperation with the U. S. Forest Service.

Creek, Michigan. Kellogg Forest occupies 600 acres of rolling land formerly devoted to agriculture. Other plantations of the same experiments exist elsewhere, but those at Kellogg Forest are among the best in terms of growth and survival. In addition, there are few other places which contain provenance tests of so large a number of species. Thus, Kellogg Forest offered probably the best opportunity available for a study such as the one reported here.

Chemical weed control in the first 2 to 4 years following establishment boosted survival in all plantations. However, in some of them mortality was still higher than expected. The cause of this can be easily identified in the three plantations where mortality was particularly high: yellow birch, ponderosa pine, and limber and border pines (both included in the same plantation).

Mortality in the first two was largely due to edaphic factors. Part of the yellow birch plantation had been graded 3 years before planting as part of a highway project. Workers attempted to replace the top soil, but nearly all trees in this portion of the plantation died during a prolonged hot spell in 1969. In the ponderosa pine plantation mortality has apparently been due to a high water table. With its deep root system this species grows best in well-drained soil, and many of the larger trees were still dying 11 years after planting. In contrast, mortality in the limber-border pine plantation has been mostly confined to the slow-growing limber pines which failed to succeed in competition with herbs in spite of weed control efforts.

Further details of some of these experiments can be found in the following articles: balsam fir -- Lester (1970), tamarack -- Pauley (1965), white spruce -- Nienstaedt (1968), jack pine -- Canavera and

Wright (1973), limber and border pines -- Wright et al. (1971), European black pine -- Wright and Bull (1962), ponderosa pine -- Wells (1964a), red pine -- Wright et al. (1972), Scotch pine -- Wright and Bull (1963), and Douglas-fir -- Wright et al. (1971).

VARIETIES AND RACES

Some of the species are so genetically diverse that taxonomists and geneticists have recognized that they contain two or more varieties or races. I include these infraspecific units in the discussion of my results because their existence has a genetic basis and they are useful in describing geographic variation patterns.

The varieties I use are entities initially recognized by taxonomists on the basis of morphological variation, so their existence implies comparatively large genetic differences. On the other hand, the races were recognized by geneticists from analyses of data (gathered in provenance tests) on genetic variation in many major and minor traits. Usually they are difficult or impossible to identify in the field and may overlap genetically. However, when many traits are considered, races are real entities which differ more from each other than they do within themselves. Often races reflect adaptation to different environments.

Ponderosa Pine

Taxonomists have recognized two widely distributed varieties of this species in the United States: *Pinus ponderosa* var. *ponderosa* in California and the Pacific Northwest west of the crest of the Rocky

Mountains, and P. ponderosa var. scopulorum east of the crest of the northern Rocky Mountains and throughout the central and southern Rockies (Figure 10). Both are represented in the Kellogg Forest provenance test of this species. (A third variety, P. ponderosa var. arizonica, in southern Arizona and New Mexico and northern Mexico is not represented.)

Wells (1964a), from measurements on the nursery phase of this provenance test in East Lansing, Michigan, found sufficient evidence to recommend maintaining the distinction between the two varieties. The greatest genetic differences in seedling traits occurred between the varieties, but there were also smaller discontinuities in genetic variation within them. Since these tended to coincide with geographic barriers and climatic differences, he proposed the recognition of several races within each variety.

Wright et al. (1969) subsequently modified Wells' races slightly and split two of them into four others on the basis of measurements through age 8. In all, nine races were recognized, arranged approximately latitudinally within each variety: Northern Plateau (northeastern California and parts of Oregon, Washington, and British Columbia), Coastal Oregon, Western Nevada, Northern California, and Southern California in variety ponderosa; and Northern Interior (Montana, Black Hills, and Nebraska), Northern Colorado and Utah, Southern Utah and Northern New Mexico and Arizona, and Southern New Mexico and Arizona in variety scopulorum.

Douglas-fir

This species consists of two fairly distinct taxonomic varieties, *Pseudotsuga menziesii* var. *menziesii* (coastal) and *P. menziesii* var. *glauca* (interior). The boundary between them in the United States is the crest of the Cascade Range in Washington and Oregon. Only the interior variety is represented in the Kellogg Forest provenance test. On the basis of measurements of several traits in this provenance test at five plantations, Wright *et al*. (1971) divided the interior variety into the eight races shown in Figure 11.

Scotch Pine

Considering that this species has the largest natural distribution of any pine in the world, one should expect that it is also very variable. The Michigan State University provenance experiment of this species has been the source of considerable study on the nature of this variation. Measurements of many traits in the East Lansing, Michigan, nursery phase and the 30+ plantations (including Kellogg Forest) indicated that many of the varieties recognized by taxonomists are genetically valid (Wright and Bull, 1963 and Wright *et al*., 1966). Although some of the varieties overlapped, the genetic variation in most of them appeared geographically random and was only 10 to 20 percent as great as that within the species as a whole.

Ruby and Wright (in press) sorted out the nomenclature of those taxonomic varieties which had a genetic basis. The locations of these varieties are shown in Figures 12 and 13. Four are not represented in

the Kellogg Forest plantation: altaica, 'Krasnoyarsk', rossica, and romanica. Three are represented by only one provenance each and were included in three other similar varieties in the analysis of my data: 'NE Siberia' in lapponica, vindelica in hercynica, and pyreneica in aquitana.

Limber and Border Pines

The status of these taxa -- whether they are varieties of the same species or whether they are separate species -- has long been a subject of controversy among taxonomists (Steinhoff and Andresen, 1971). For this reason, provenances of both were included in this experiment with a view toward clarifying the degree to which they are genetically different. Steinhoff and Andresen (1971) and Wright et al. (1971) reported the early results of the experiment. They found that the nature of genetic variation in the complex generally supports the current view that limber pine and border pine are separate species.

However, as expected from the confusion of taxonomists, these species are closely related and tend to intergrade in the zone of overlap of their native ranges. The nature of genetic adaptation to environmental gradients must be similar in two such closely related species. According to Stebbins (1950), "The differences between closely related species are nearly all duplicated by or parallelled by differences between races or subspecies [varieties] of a single species." Thus, I considered both species together in analyzing geographic variation patterns of bud burst and treated them in the statistical analysis as I did varieties of other species.

DATA COLLECTION

Measuring Time of Bud Burst

Relative time of bud burst was determined by scoring each plot according to degree of leaf or shoot development shortly after growth initiation. Measurements were taken in Kellogg Forest plantations of all species in the spring of 1973 and again in one of the tamarack plantations in the spring of 1974. In addition, 1971 and 1973 data on bud burst in a Wisconsin plantation of the balsam fir provenance experiment were kindly furnished by Dr. Donald Lester of the University of Wisconsin. To minimize error, each plantation was measured in 1 day and at a time when most trees were growing but growth had not progressed so far that differences were not easily discernible. On their respective days of measurement the amount of variation in each plantation was as follows:

Balsam fir, white spruce, and Douglas-fir -- some trees in bud, others with 1- and 2-inch shoots.

Yellow birch and black cherry -- some trees in bud or just bursting buds, others with almost fully developed leaves.

Tamarack -- some trees in bud, others with 1/4-inch needles on short-shoots.

Pines -- new needles on some trees not yet grown beyond fascicle sheaths, those on others 1/2 inch long or more.

The scoring system varied for each species but scales of 9 to 20 bud burst grades were used in all but one Kellogg Forest plantation. In the limber-border pine plantation I used a scale of 6 degrees of

development. In the two sets of Wisconsin measurements scales of 4 and 5 were used. To simplify interpretation of the data, provenance means were converted to a scale of 1 to 10 after performing the analyses of variance. For each species the mean of the earliest provenance was set equivalent to 1.0 and that of the latest was set equivalent to 10.0. The other provenance means were then transformed accordingly.

Saatcioglu (1967) and McGee (1974), studying provenance tests of Scotch pine and Quercus rubra, respectively, found that differences in bud burst grades such as I used corresponded with differences in the actual times of bud burst. Likewise, I found that my results correlated with those of other studies of the same species in which the actual times of bud burst were measured. Thus, relative growth shortly after bud burst is an indicator of relative time of bud burst. Observing the actual times would have been more desirable in some respects, but this method requires frequent measurements on each tree during a short period in spring -- a task which would have prevented observations of all but a few species since nearly 14,000 trees were involved in the study. I was, however, able to judge within a few days the amount of time between the bud burst of the earliest and latest provenances by re-visiting each plantation once or twice after the date of measurement.

Measuring Time of Flowering

The time of flowering of each plot was recorded in all plantations in which most provenances were flowering by the spring of 1973: yellow birch, tamarack, jack pine, European black pine, red pine, Scotch pine,

Virginia pine, and black cherry. (While the term "flowering" is not strictly applicable to the conifers, it is used here for convenience.) In the wind-pollinated species the date of flowering was defined as the first date trees within a plot released appreciable amounts of pollen when the branches were shaken. Time of pollen release corresponds with time of female receptivity in the pines (Bingham and Squillace, 1957; Bramlett, 1973; Polk, 1967; and Wright, 1953); though it does not in yellow birch (Dancik and Barnes, 1972) and probably tamarack (Leven, 1951). In black cherry the date of flowering was defined as the first date on which at least 25 percent of the flower buds in a plot were open. Depending upon the rate that different provenances began flowering, each plantation was visited at regular intervals of 1 to 4 days.

Measuring Frost Damage in Douglas-fir

Late spring frosts have occasionally caused severe damage to young shoots in Lower Michigan plantations of the Douglas-fir provenance test. Such damage occurred in mid-May of 1973. To determine if there were any differences among the provenances in frost susceptibility and if they were related to differences in time of bud burst, I recorded the proportion of new shoots killed in each plot. In addition, similar data taken in previous years and on file at Michigan State University were obtained for comparisons.

In all, data were available for spring frost damage occurring in 3 years at three plantations: Kellogg Forest (1968, 1969, and 1973); Camp Kett (1969 and 1973); and Russ Forest (1968 and 1973). Camp Kett

is 11 miles south of Cadillac and Russ Forest is 5 miles east of Dowagiac. Sixty-eight provenances are represented in the three plantations.

PLANTATION DESIGN AND DATA ANALYSIS

All plantations are arranged in randomized complete block designs: there is one plot (usually of four trees) of each provenance or family randomly located within each of several replicates. Table 1 shows the plot size and number of replicates for each Kellogg Forest plantation. This design and the analysis of the data enables one to determine whether differences among provenances or families are greater than what would occur at least 95 percent of the time if the provenances or families were genetically alike. In species where the provenances are grouped into races or varieties the significance of variation among those groups can also be tested.

Measurements were recorded as plot sums or means. In plots where trees had died, the sum was computed from the mean of the remaining trees and recorded as if all trees in the plot were alive. If a few entire plots were missing, provenance (or family) means from the remaining plots were entered and the data analyzed as if the plantation was complete but with one less degree of freedom for the error and total sums of squares for each missing plot. If many plots were missing, though, the data were analyzed as if there were unequal sample sizes for each provenance, and replicate effects were ignored (included in error term). The effect of each of these irregularities is to make the error mean squares larger than they would be otherwise, but provenance

mean squares are not affected. As a result, significance levels for genetic effects were, if anything, underestimated.

A special problem arose with the eastern white pine data. This plantation is divided into three hillocks separated by two intersecting draws. The elevational difference is only 15 to 20 feet, but the topography is such that cool air collects in the draws on spring nights. As a result, trees in the draws were almost invariably later to burst bud. Unfortunately, this environmental effect ran across replicate boundaries. However, it was possible to remove the effect from the data by calculating the deviation of each plot from the provenance mean and then using a running average of the deviations of adjacent plots in the plantation to adjust the plot sum. This adjustment did not change the significance level for genetic effects, but it decreased the error mean square considerably.

For most plantations the analyses were straightforward. The mean squares for provenance and replicate were tested over the error mean square to determine their significance. However, analyses were more complicated for plantations which contained half-sib families or in which the provenances may be grouped into races or varieties. In these cases, the analysis of variance was of the nested design. The procedure is illustrated in Table 2 by a hypothetical example.

A complication was present, however, in those experiments which contained unequal numbers of data elements in the subgroups (e.g., different numbers of provenances in each variety). When this occurs, the coefficients of the respective variance components are unequal in the numerator and denominator of the calculated F-value. Consequently, the calculated F-value is not the simple ratio of the appropriate mean

Table 2.--Hypothetical analysis of variance for a nested model with "r" replicates, "v" varieties, "p" provenances in each variety, and "f" half-sib families in each provenance.

Source of variation	Degrees of freedom	Expected mean squares	Calculated mean squares	F
Replicate	r-1	$\sigma^2 + \mathrm{vpf}\ \sigma^2_R$	MS_5	MS_5/MS_1
Variety	v-1	$\sigma^2 + r\ \sigma^2_{F(P)} + \mathrm{rf}\ \sigma^2_{P(V)} + \mathrm{rfp}\ \sigma^2_V$	MS_4	MS_4/MS_3
Provenance (Variety)	v(p-1)	$\sigma^2 + r\ \sigma^2_{F(P)} + \mathrm{rf}\ \sigma^2_{P(V)}$	MS_3	MS_3/MS_2
Family (Provenance)	vp(f-1)	$\sigma^2 + r\ \sigma^2_{F(P)}$	MS_2	MS_2/MS_1
Error	(vpf-1)(r-1)	σ^2	MS_1	
Total	vpfr-1			

squares as in Table 2. Instead, one must adjust the mean squares to determine the proper coefficients.

However, the effect of this irregularity depends upon the level of the subgroup in which the unequal sample sizes occur. Thus, as is shown in Table 3, the calculated F-values were not biased in balsam fir by unequal numbers of families per provenance. The same was true of the analyses for Scotch pine and black cherry.

However, in the other experiments which had nested models (limber and border pines, ponderosa pine, and Douglas-fir) replication was incomplete because of mortality. This caused some of the F-values to be incorrect when calculated with unadjusted mean squares. The affected F-values were so very large, though, that correcting the bias would not change the significance levels. Thus, the main effect of these irregularities was to prohibit the simple calculation of the contributions of different sources of variation to the total variance.

If the analysis of variance indicated significant genetic variation, I was interested to know which provenances, varieties, *etc*. were different from others. This was done using the Least Significant Difference (LSD) statistic for the 5 percent level of significance.

$$\mathrm{LSD}_{.05} = t_{.05(v)}\sqrt{\frac{2}{n}\,(\text{Error Mean Square})},$$

where "v" equals the degrees of freedom for the error mean square and "n" equals the number of data elements that went into each mean being compared. When the means were calculated from different numbers of observations, I used the harmonic mean of their respective "n's." The

Table 3.--Generalized analysis of variance for the Abies balsamea plantation. The F-value is correctly calculated as shown, even though provenances contain different numbers of families.

Source of variation	Degrees of Freedom	Expected mean squares	Calculated mean squares	F
Replicate	2	$\sigma^2 + 78\sigma_R^2$	MS_4	MS_4/MS_1
Provenance	41	$\sigma^2 + 3\,\sigma_{F(P)}^2 + \underline{?}\,\sigma_P^2$	MS_3	MS_3/MS_2
Family (Provenance)	36	$\sigma^2 + 3\,\sigma_{F(P)}^2$	MS_2	MS_2/MS_1
Error	152	σ^2	MS_1	
Total	231			

LSD was then multiplied by the appropriate multiplier, taken from statistical tables, for the difference in rank between the means being compared.

PATTERNS IN TIME OF BUD BURST

Table 4 shows the results of the statistical analyses for genetic variation in time of bud burst. In all but one species there were significant differences among provenances; and in most species with varieties, races, or half-sib families differences among them were also significant. The amount of variation among provenances in time of bud burst was quite large, especially in some species:

At least 1 week -- balsam fir, yellow birch, white spruce, black cherry, and jack, European black, ponderosa, eastern white, Scotch, and Virginia pines

At least 2 weeks -- limber and border pines (together)

At least 3 weeks -- tamarack and Douglas-fir

The only exception was red pine. After an hour's examination of this plantation on June 1, I could find no measurable differences among provenances in degree of needle development, indicating no or very little genetic variation in time of bud burst.

Results for most species are shown in figures on the following pages. Each figure depicts the natural range of the species, with circles placed at the locations of the provenances and containing symbols representing relative time of bud burst. Occasionally two or more provenances in virtually the same location were represented by one circle, so not every circle designates only one provenance. Each of the

Table 4.--Significance of genetic variation in time of bud burst in plantations of 15 species of trees.

	Significance of variation among:				
Species	Varieties	Races (within varieties)	Provenances (within races)	Families within provenances	Error mean square
			F-value(a)		
Abies balsamea	--	--	3.5***	2.7***	1.64
Betula alleghaniensis	--	--	6.7***	--	2.01
Larix laricina (5,6-66)	--	--	5.9***	--	2.73
L. laricina (6-69)	--	--	12.3***	--	2.01
Picea glauca	--	--	16.8***	--	0.99
Pinus banksiana	--	--	30.0***	--	0.48
P. flexilis-strobiformis	94.6***(b)	--	10.8***	1.2 n.s.	0.42
P. nigra	--	--	16.0***	--	3.12
P. ponderosa	< 1 n.s.	24.6***	4.9***	--	0.65
P. resinosa	--	--	(c)	--	--
P. strobus	--	--	7.5***	--	3.19
P. sylvestris	37.1***	--	2.1***	--	1.73
P. virginiana	--	--	5.4***	--	12.22
Prunus serotina	--	--	2.7*	9.2***	2.32
Pseudotsuga menziesii	--	39.0***	4.4***	--	1.29

(a) n.s. = not significant, * = significant at the 5% level, *** = significant at the 0.1% level.
(b) *P. flexilis vs. P. strobiformis.*
(c) There were no measurable differences among provenances.

Figure 1.--Pinus banksiana: natural range, provenance locations, and pattern of genetic variation in time of bud burst at Kellogg Forest in 1973. Empty circles = very early, filled circles = very late.

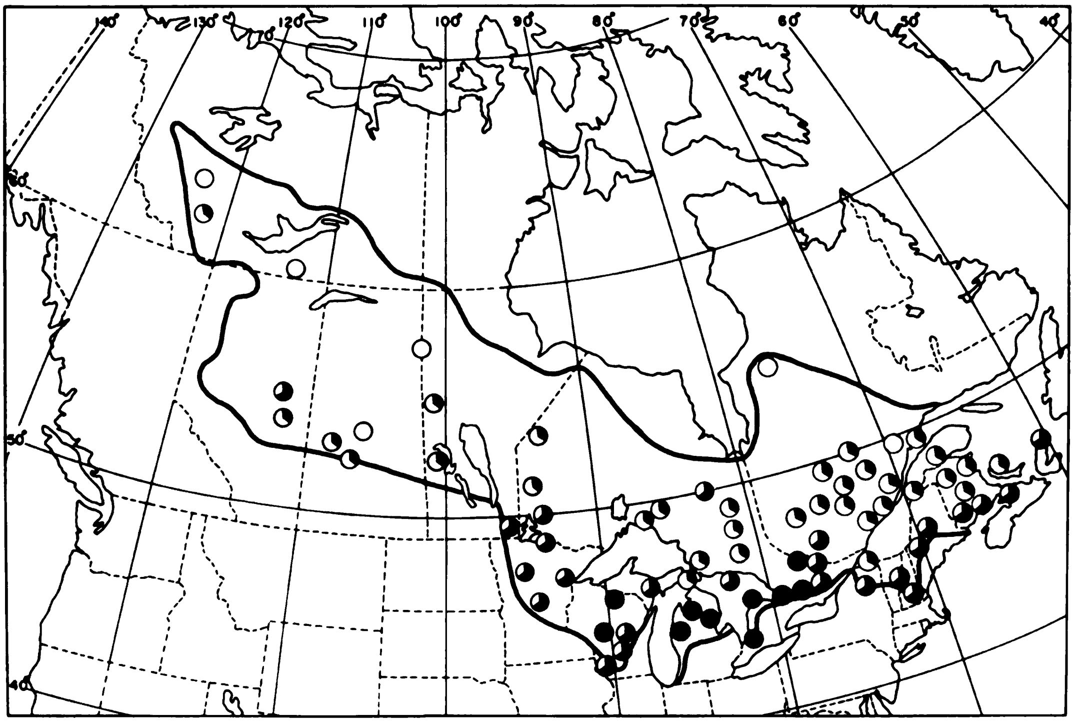

Figure 1.

Figure 2.--*Picea glauca*: natural range, provenance locations, and pattern of genetic variation in time of bud burst at Kellogg Forest in 1973. Montana and South Dakota provenances are isolated native stands. Empty circles = very early, filled circles = very late.

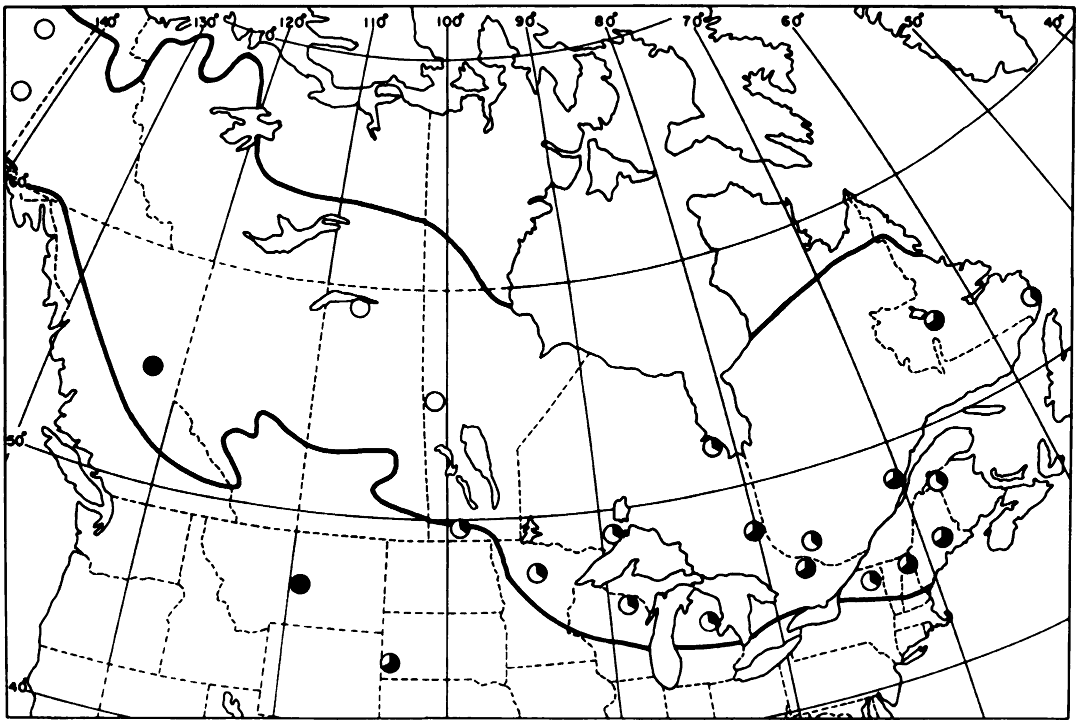

Figure 2.

Figure 3.--Larix laricina (plantation 6-69): natural range, provenance locations, and pattern of genetic variation in time of bud burst at Kellogg Forest in 1973. Maryland and Wisconsin provenances outside natural range are isolated native stands. Empty circles = very early, filled circles = very late.

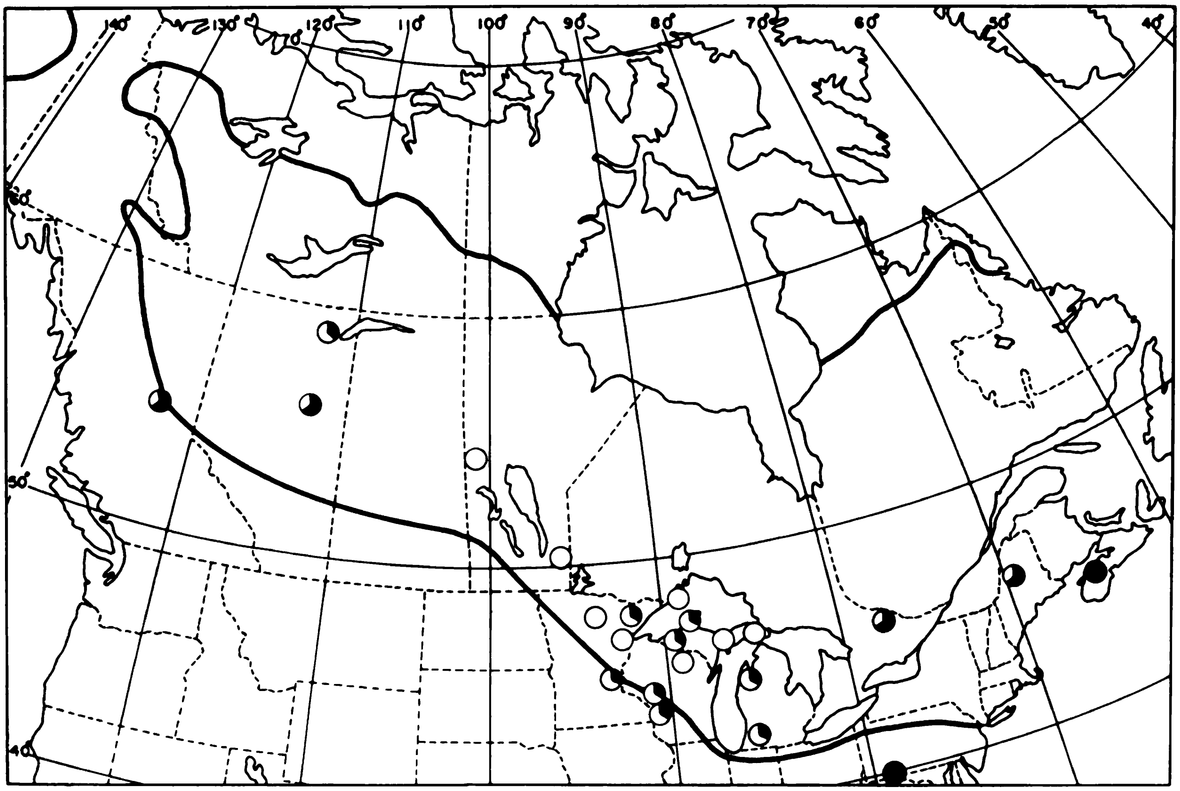

Figure 3.

Figure 4.--*Abies balsamea*: natural range, provenance locations, and average pattern of genetic variation in time of bud burst at Kellogg Forest in 1973 and Wisconsin in 1971 and 1973. Empty circles = very early, filled circles = very late.

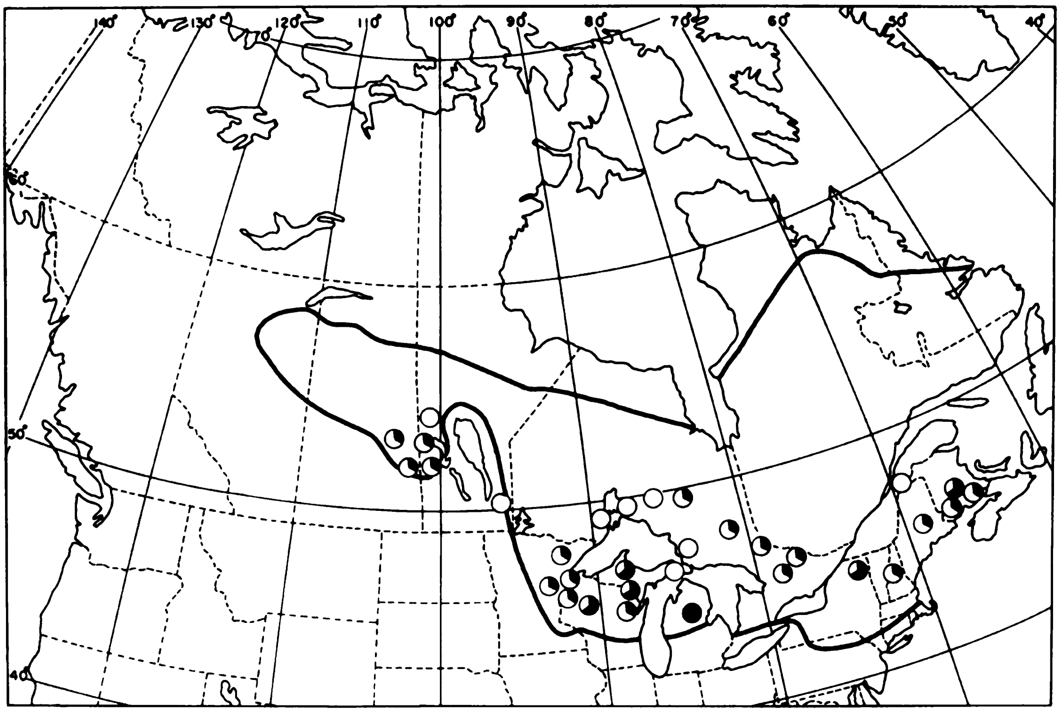

Figure 4.

Figure 5.--Pinus strobus: natural range, provenance locations, and pattern of genetic variation in time of bud burst at Kellogg Forest in 1973. Empty circles = very early, filled circles = very late.

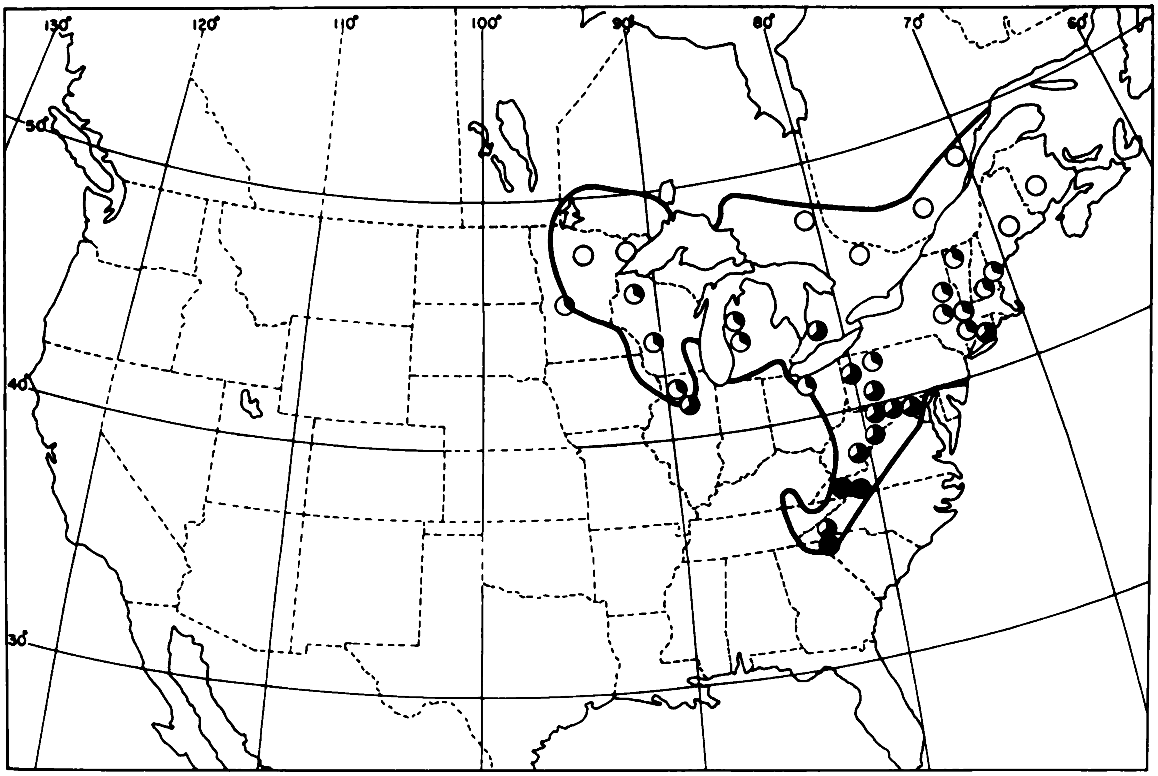

Figure 5.

Figure 6.--Betula alleghaniensis: natural range, provenance locations, and pattern of genetic variation in time of bud burst at Kellogg Forest in 1973. Indiana and Minnesota provenances outside natural range are isolated native stands. Empty circles = very early, filled circles = very late.

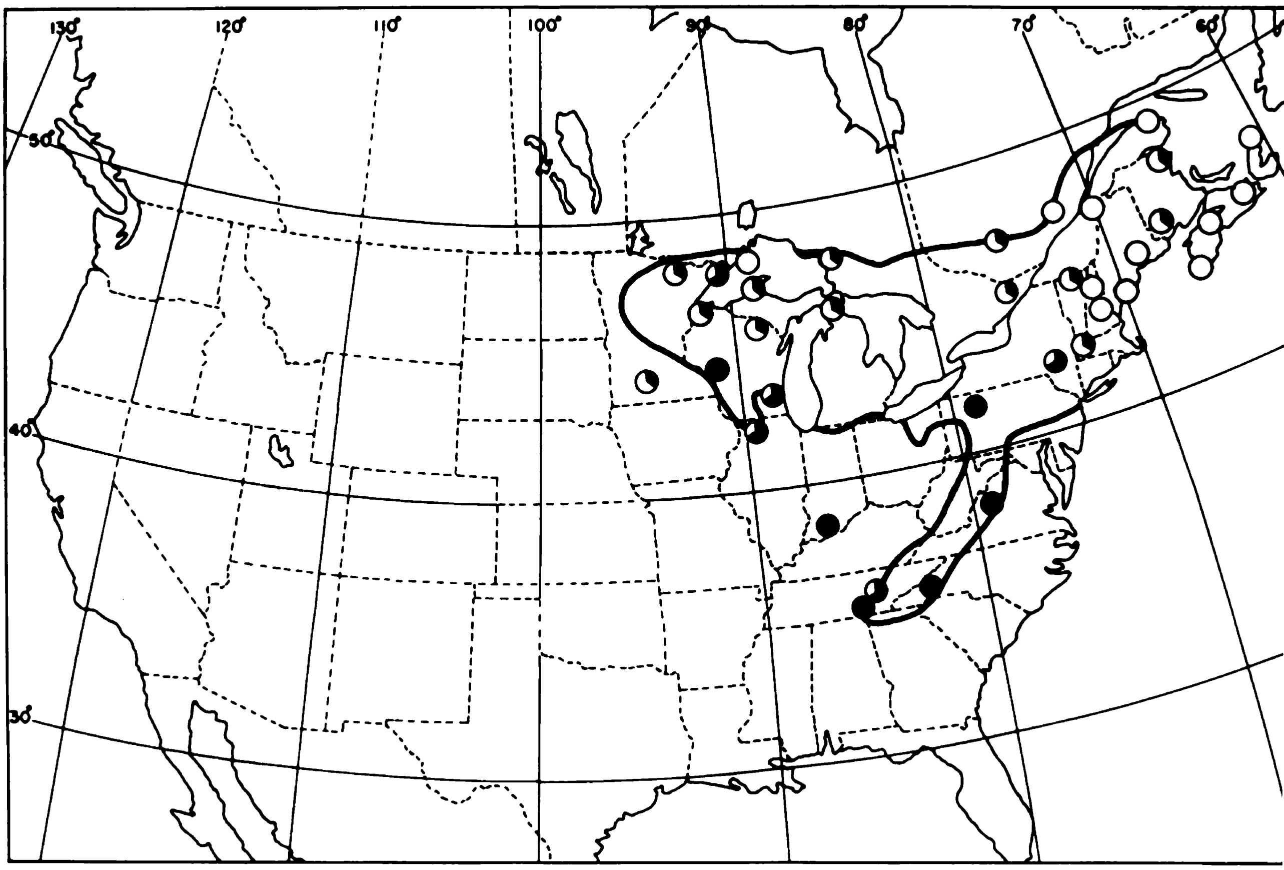

Figure 6.

Figure 7.--*Pinus virginiana*: natural range, provenance locations, and pattern of genetic variation in time of bud burst at Kellogg Forest in 1973. The Indiana provenance is an isolated native stand. Empty circles = very early, filled circles = very late.

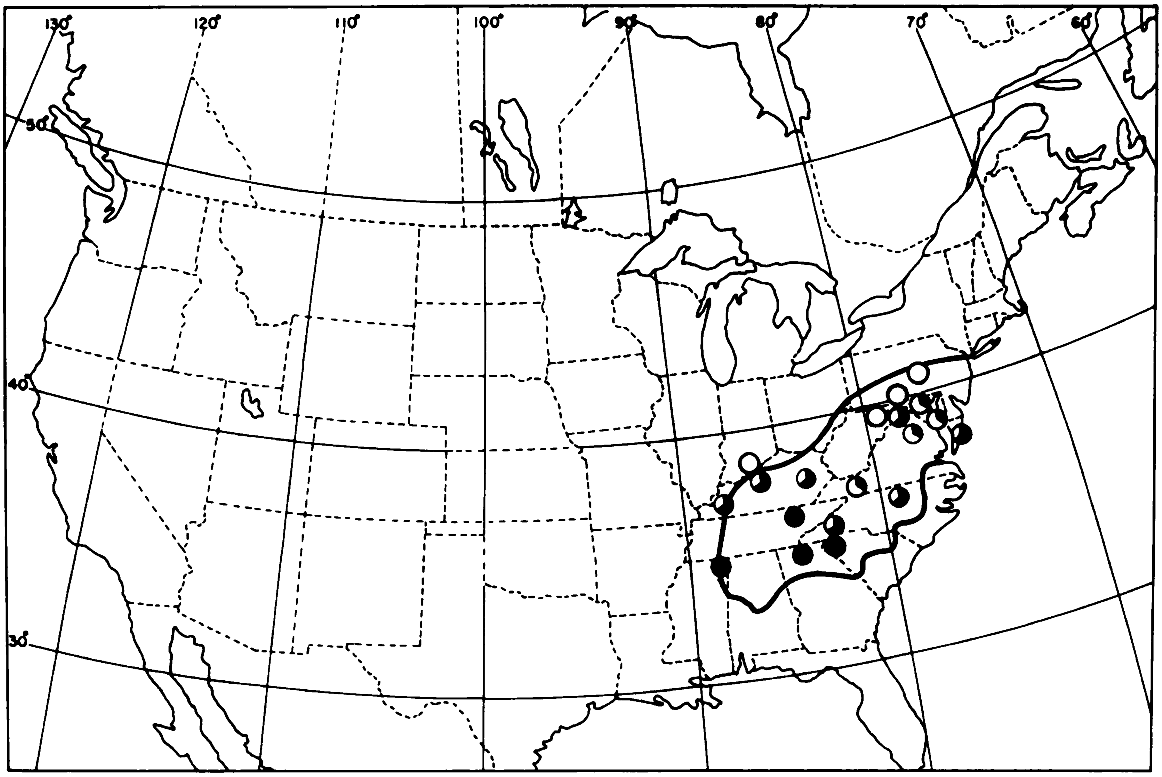

Figure 7.

Figure 8.--Pinus resinosa: natural range (bounded by dashed lines) and provenance locations (indicated by numbers). Provenances did not differ in time of bud burst. From Wright *et al*. (1972).

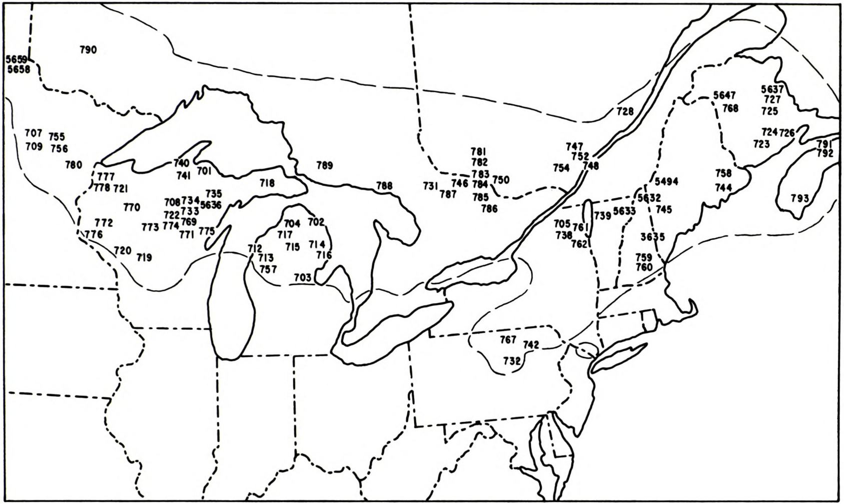
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Figure 8.

Figure 9.--Pinus flexilis and P. strobiformis: natural ranges, provenance locations, and patterns of genetic variation in time of bud burst at Kellogg Forest in 1973. North Dakota, Wyoming, and Nebraska provenances outside natural range are isolated native stands. Empty circles = very early, filled circles = very late.

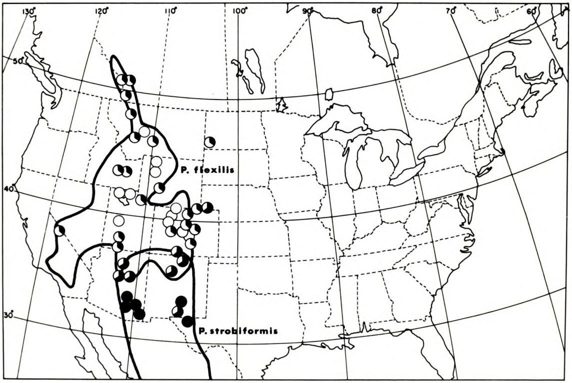
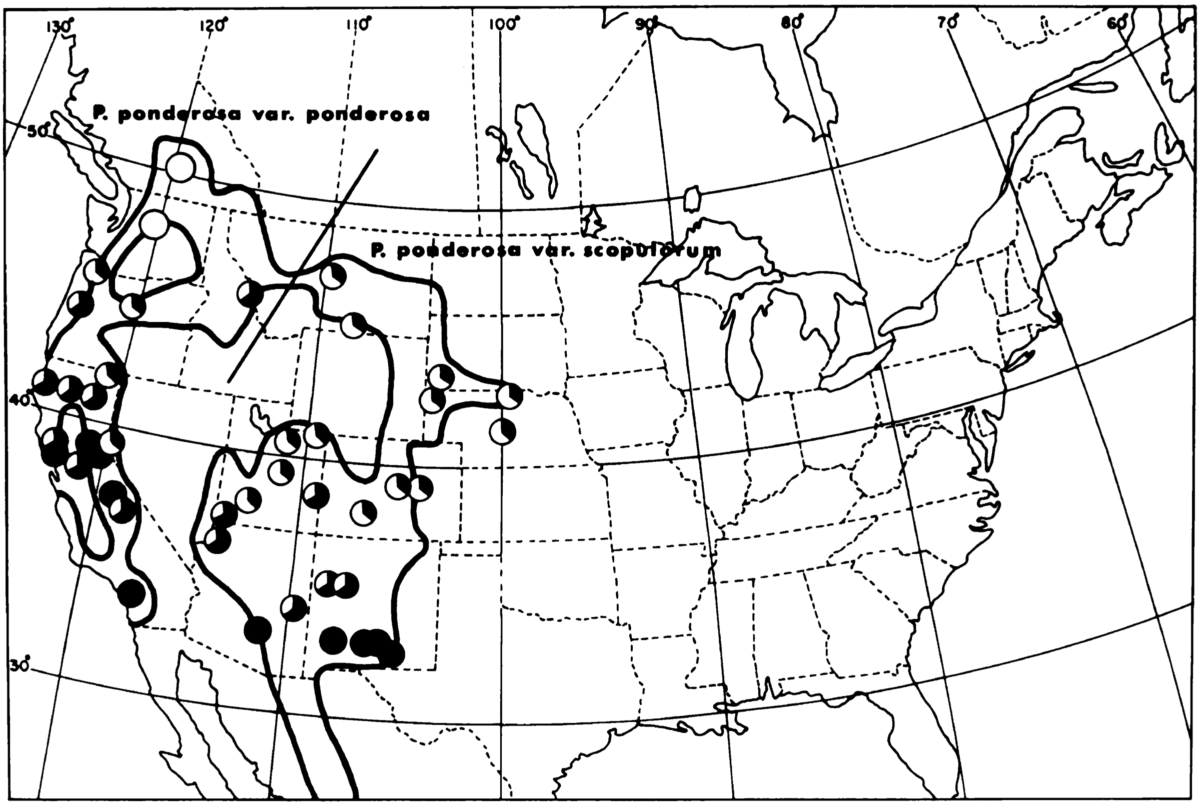


Figure 9.

Figure 10.--Pinus ponderosa; natural range, varietal boundaries, provenance locations, and pattern of genetic variation in time of bud burst at Kellogg Forest in 1973. The Nebraska provenance outside the natural range is an isolated native stand. Empty circles = very early, filled circles = very late.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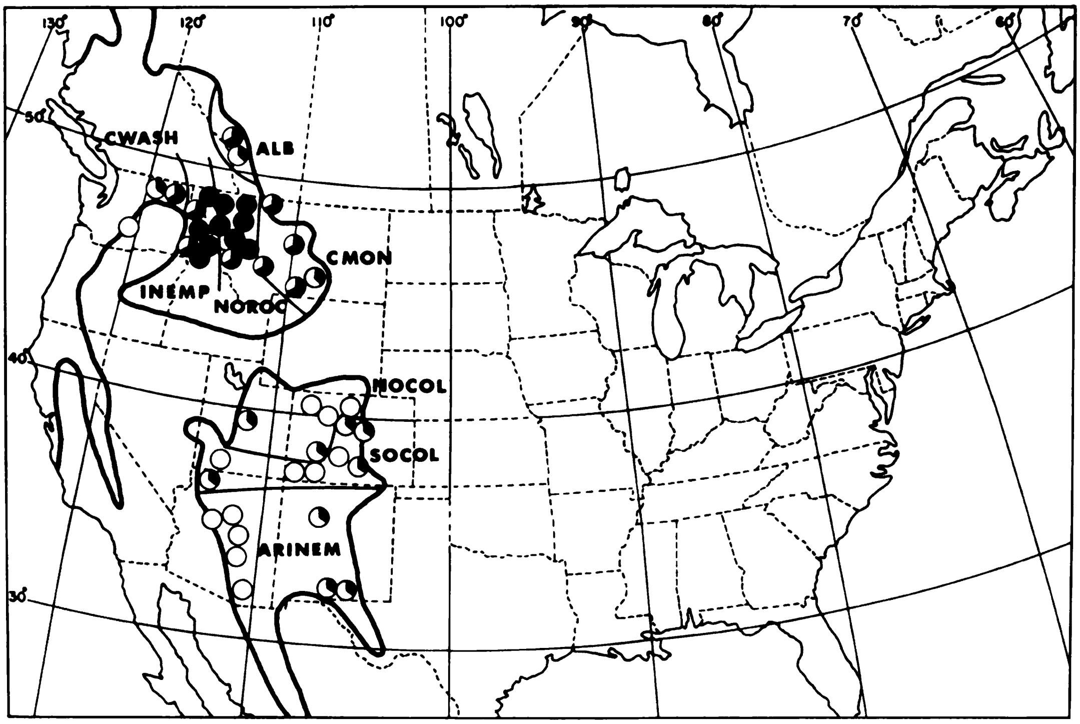
P. ponderosa var. ponderosa
P. ponderosa var. scopulorum

Figure 10.

Figure 11.--Pseudotsuga menziesii: natural range, racial boundaries, provenance locations, and pattern of genetic variation in time of bud burst at Kellogg Forest in 1973. Racial names are acronyms of their geographic origins: C WASH (Central Washington), ALB (Alberta), INEMP (Inland Empire), NOROC (Northern Rocky Mountains), C MON (Central Montana), NOCOL (Northern Colorado), SOCOL (Southern Colorado), and ARINEM (Arizona and New Mexico). Empty circles = very early, filled circles = very late.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ARINEM

Figure 11.

Figure 12.--*Pinus sylvestris*: natural range in Europe (shaded), approximate varietal boundaries, and provenance locations. Varieties are designated by the first 3 letters of their names: *aquitana*, *armena*, *carpatica*, *haguenensis*, *hercynica*, *iberica*, *illyrica*, *lapponica*, *pannonica*, *polonica*, *pyreneica*, *rhodopaea*, *rigensis*, *romanica*, *rossica*, *scotica*, *septentrionalis*, *subillyrica*, *uralensis*, and *vindelica*. Northern varieties burst bud earlier than the uniformly late central and southern varieties. From Wright *et al.* (in press).

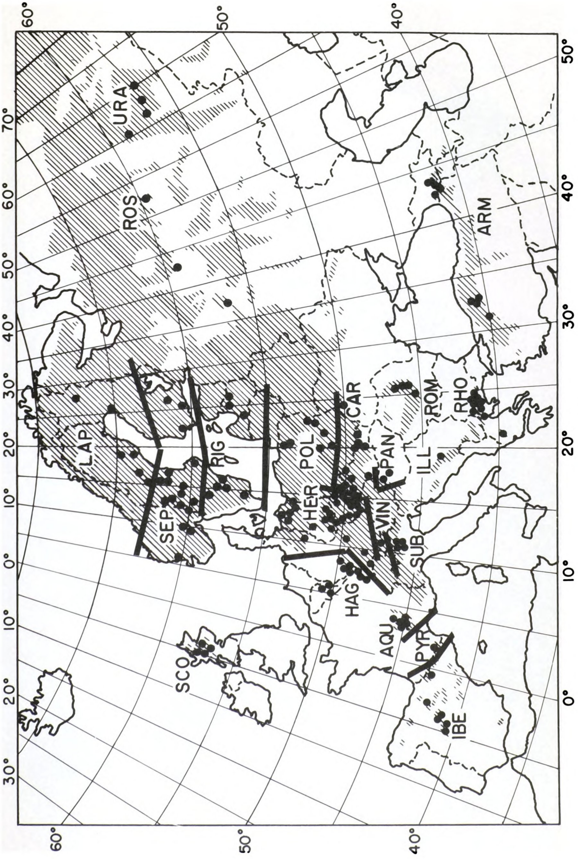
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Figure 12.

Figure 13.--*Pinus sylvestris*: natural range in Asia (shaded), varietal boundaries, and provenance locations. Varieties are designated by the first 3 letters of their names: *altaica*, 'Krasnoyarsk', *mongolica*, and 'NE Siberia'. All provenances burst bud very early. From Wright *et al*. (in press).

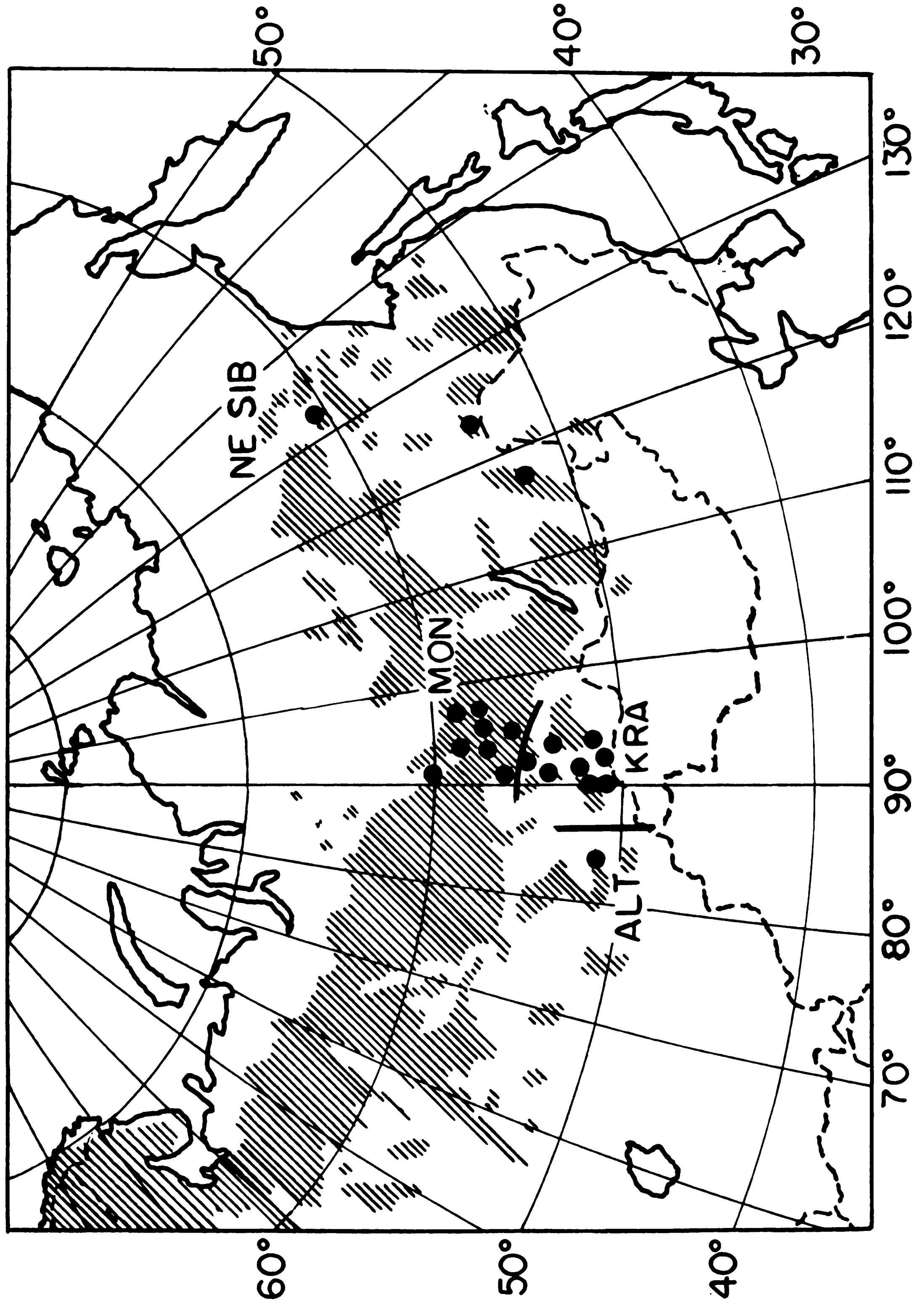

Figure 13.

Figure 14.--*Pinus nigra*: provenance locations (indicated by numbers and circles). Nearly all of the very broken range of this species is represented; only provenances from central and southern Italy and additional areas of Yugoslavia and Turkey are lacking. Time of bud burst was increasingly late from east to west. From Wright and Bull (1962).

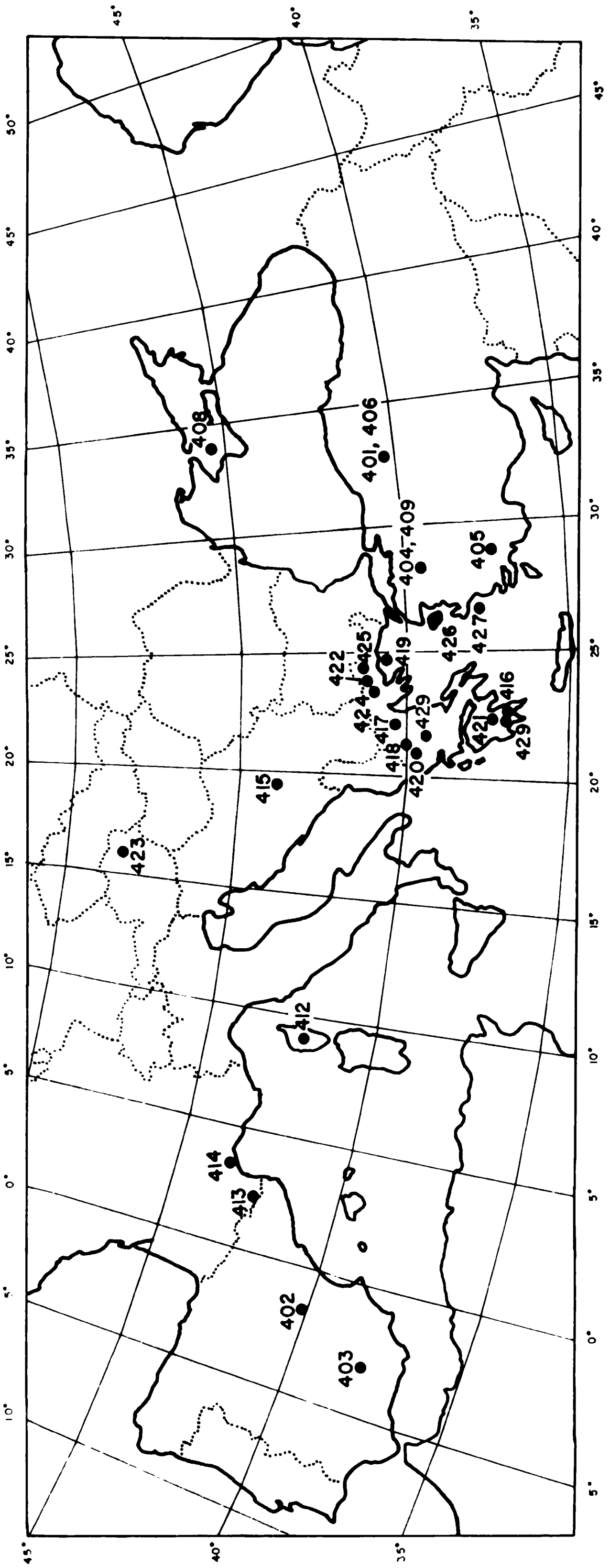
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Figure 14.

four symbols within the circles represents 1/4 of the range of bud burst grades within a species.

Only the natural ranges and provenance locations are shown on the red, Scotch, and European black pine maps (Figures 8, 12, 13, and 14). In contrast to other species, the geographic patterns of bud burst in these species are easily described. Of the two provenance tests of tamarack, only the results from plantation 6-69 are mapped (Figure 3). Plantation 5,6-66 contained slightly more provenances, but more of the species' range was represented in plantation 6-69. Patterns of genetic variation were the same for parts of the range represented in both experiments. Black cherry is the only species not mapped -- there were too few provenances to show any geographic pattern in genetic variation.

The figures reflect geographic patterns rather than actual details of the data. Some provenances with the same symbol were significantly different, and some with different symbols were not significantly different. Only statistically significant differences, however, are discussed in the test.

COMMON PATTERNS

The results for each species can best be described by comparing its variation pattern with that of other species. Most species shared certain geographic trends, and only one, Douglas-fir, had a distinctly different pattern of variation. These trends were undoubtedly shaped by climate (particularly temperature) as an instrument of natural selection, so they must be discussed and compared in light of how they correspond with climatic variation.

Northern vs. Southern Latitudes

The most important geographic factor affecting climate is latitude, so it is not surprising that time of bud burst was related to latitude of origin in most species. In one, Douglas-fir (Figure 11), the correlation was positive ($r = +.73$, significant at the 1 percent level): southern provenances were earlier than northern provenances. However, in most other species northern provenances burst bud earlier ($r = -.62$ to $-.86$, all significant at the 1 percent level). Since this was the major geographic trend in variation in the entire study, all results may be described as conforming with or deviating from it.

Jack pine (Figure 1), eastern white pine (Figure 5), yellow birch (Figure 6), Virginia pine (Figure 7), and border pine (Figure 9) all had fairly regular patterns of variation from north to south. In white spruce (Figure 2), limber pine (Figure 9), ponderosa pine (Figure 10), and Scotch pine (Figures 12, 13, and Table 5) there were regions where provenances were nearly uniform or the geographic pattern was mostly random, so the latitudinal trend was less regular. These regions were eastern North America in white spruce, northern Rocky Mountains in limber and ponderosa pines, and central and southern Europe in Scotch pine. In most cases (white spruce excepted) the areas of uniformity or randomness are explainable by other determinants of climate than latitude and these will be discussed later.

In only three species was the correlation between latitude and time of bud burst not significant. In tamarack (Figure 3) and balsam fir (Figure 4) this was probably due in part to a lack of provenances from the northernmost parts of the ranges. As expected, the latest

Table 5.--Relative time of bud burst of Pinus sylvestris varieties. The varieties are arranged from north to south and, within latitude, from east to west.

Variety	Countries or regions of origin	Time of bud burst
		1=early, 10=late
	Scandinavian and Siberian Varieties	
lapponica and 'NE Siberia'	Sweden, Finland, Siberia	2.7
mongolica	Siberia	2.1
uralensis	Ural Mountains	4.1
septentrionalis	Norway, Sweden, Finland	4.8
rigensis	Sweden, Latvian S.S.R.	6.3
	Central European Varieties	
scotica	Scotland	7.6
polonica	Poland	7.7
hercynica and vindelica	Germany, Austria, Czech.	8.3
carpatica	Czechoslovakia	8.1
haguenensis	France, Germany	8.2
pannonica	Hungary	7.8
	Southern European Varieties	
aquitana and pyreneica	France	8.3
subillyrica	Italy	7.4
illyrica	Yugoslavia	9.2
armena	Turkey, Georgian S.S.R.	6.8
rhodopaea	Greece	7.0
iberica	Spain	8.0

provenances in both species were the southernmost: Maryland in tamarack plantation 6-69, Pennsylvania and Indiana in tamarack plantation 5,6-66, and Lower Michigan in balsam fir. In addition, the earliest balsam fir provenance was the northernmost. But on the whole, the sampled parts of these species' ranges were rather narrow from north to south and rather broad in the other direction. Consequently, other factors influencing climate besides latitude probably shaped the variation patterns.

A similar situation existed in European black pine, though most of the range of this species was represented by provenances. European black pine is virtually confined to a narrow band of countries bordering the northern edge of the Mediterranean Sea (Figure 14). In that part of the world, as discussed later, climates tend to vary more from east to west than from north to south. The cause of this and some other deviations from the north-early, south-late trend is discussed in the next section.

Interior vs. Coastal

Next to latitude, proximity to oceans and their moderating influence on temperature is the second most important geographic factor affecting the world's climates. Both the Atlantic and the Pacific carry warm water northward with their clockwise currents, so mild climates extend farther north along their coasts. The importance of the oceans to climate is seen by the fact that in winter the North Atlantic Drift is a greater source of heat for Russia than direct insolation (Kendrew, 1961).

The extent to which this influence is felt in a particular region is determined by the direction of the prevailing winds. In the temperate regions of the northern hemisphere these winds are usually westerly, so the ocean's influence is felt more on west coats than east coasts. For example, at any given latitude from 35°N to 50+°N the Pacific Coast of North America is several degrees warmer than the Atlantic Coast in winter and several degrees cooler in summer (Gorczyński, 1945). Similarly, while Nova Scotia and parts of northern British Columbia and Sweden are all as warm in winter (at equal elevations) as Lower Michigan to the south, the two west coast regions lie much farther north than Nova Scotia (Espenshade, 1970).

Thus, the ocean's influence on climate could presumably have resulted in deviations from the latitudinal trend in time of bud burst. Because of the moderating effect of the ocean on temperature, one would expect provenances in coastal areas to be like those in southern latitudes in time of bud burst. Furthermore, deviations from the latitudinal trend should be more prominent on west coasts than east coasts.

This appeared to be true. In eastern North America there were few consistent deviations from the latitudinal trend. However, most provenances native very near the coast were significantly later than those farther inland in the same latitude. (For reasons discussed later, comparisons cannot be made as far west as the Great Lakes.) Of the species represented by near-coastal provenances, this pattern was found in jack pine (Figure 1), tamarack (Figure 3), balsam fir (Figure 4), and Virginia pine (Figure 7). It was particularly striking in tamarack where the Nova Scotia provenance was almost as late as the very southern Maryland provenance, explaining in part why there was no correlation with latitude in this species.

An exception to this trend (one of the most prominent inconsistencies in the study) occurred in yellow birch (Figure 6). In this species coastal provenances burst bud earlier than interior provenances. Somewhat different climatic variables have apparently been important in the evolution of variation in time of bud burst in this species than have been important in other species.

What at first appears to be another exception occurred in white spruce (Figure 2). Among the few significant differences among the eastern provenances of this species, one of the largest was between the two native to Labrador. The earlier one (and the earliest of all eastern provenances) was unexpectedly the one nearer the coast. However, along the coast of Labrador, as opposed to the coast farther south, ocean currents are from the north and carry cold water. In fact, the northern tree limit turns south along the coast of Labrador. So at least in some respects the coastal provenance is actually the colder one.

In contrast to eastern North America, deviations from the north-south trend occurred much farther inland in western North America. In the Canadian species provenances which were intermediate and late to burst bud were native to progressively higher latitudes west of Manitoba, parallelling northward shifts in the isotherms of a number of temperature variables in the Canadian West (Espenshade, 1970; Kendrew, 1961; and Money, 1972). For example, along the eastern slope of the Canadian Rocky Mountains, and as far as 300 miles east of there, winters are less severe than in the interior of the continent because of frequent warm westerly winds caused by Pacific air masses travelling over the

Continental Divide (Kendrew, 1961 and Rumney, 1968). Thus, Alberta, British Columbia, and Northwest Territories provenances tended to be late for their latitudes in jack pine (Figure 1), white spruce (Figure 2), and tamarack (Figure 3).

Like isotherms, vegetation zones also drift northward in western Canada. For example, the taiga according to Küchler's definition (Espenshade, 1970) does not occur south of latitude 60°N in western Canada, but in the east it reaches into northern Minnesota. In balsam fir (Figure 4) the earliest provenances of Manitoba and Saskatchewan are in the taiga, the latest are in the more temperate mixed coniferous-deciduous zone. Thus, while the sampled part of the range in this species does not extend very far west, the variation pattern still apparently reflects the influence of the Pacific Ocean.

A similar situation occurred in ponderosa pine in the western United States (Figure 10). The latitudinal variation in time of bud burst within both the coastal and interior varieties caused the relatively small differences between them to be non-significant in the statistical analysis (Table 4). However, when comparisons are made within the same latitudes there was a slight but statistically significant tendency for those provenances nearest the coast to burst bud later. This is even more evident in data taken by Wells (1964a) on bud burst of these provenances at age 1. Our data are compared in Table 6. Though his results indicate less latitudinal variation than mine, they do show a stronger tendency for coastal variety provenances to burst bud late.

The coastal variety of Douglas-fir was not represented in the provenance test. However, the race closest to the Pacific Coast, C WASH,

Table 6.--Relative time of bud burst of *Pinus ponderosa* varieties and races at age 1 (from Wells, 1964a) and age 13. The races are arranged from north to south within varieties.

Variety and race	Time of bud burst: Kellogg Forest (age 13)	Time of bud burst: Nursery (age 1)
	1=early, 10=late	day in May
Pacific Coast, var. *ponderosa*		
Northern Plateau	3.3	8
Coastal Oregon	5.9	16
Northern California	6.6	15
Southern California	8.0	16
Average (weighted)	6.4	14
Interior, var. *scopulorum*		
Northern Interior	4.4	2
Northern Colorado-Utah	4.2	5
S. Utah and N. New Mex.-Ariz.	5.7	12
S. New Mexico-Arizona	8.0	11
Average (weighted)	5.7	8

was significantly different from those farther east (Figure 11). In contrast to other species (except yellow birch), though, these provenances burst bud early for their latitude. The fact that Douglas-fir is an exception to the rule in this trend corresponds with its unusual latitudinal variation pattern.

The only areas of Europe represented in the Scotch pine experiment which have what Rumney (1968) termed distinctly oceanic climates are the British Isles and the southwestern coast of Norway. Significantly, variety scotica burst bud later than other varieties in the same latitudinal zone (rigensis, septentrionalis, uralensis, and mongolica), and the only provenance from coastal Norway was later than all provenances in the interior of the Scandinavian Peninsula (Figures 12, 13, and Table 5).

However, unlike North America, Europe has no major north-south mountain ranges and the warming effect of the North Atlantic Drift is felt as far as western Siberia (Biel, 1944). As a result, the climate of Europe is mild for its latitude and north-south temperature gradients are very gradual most of the year and even nonexistent in winter. Only in Scandinavia does a north-south mountain range present a small but real barrier to the influence of the Atlantic (Kendrew, 1961). Thus, it is not surprising that south of Scandinavia Scotch pine showed no latitudinal variation in time of bud burst and there were few significant differences among provenances.

The Asiatic provenances of Scotch pine were all early for their latitudes, corresponding to the decreasing influence of the ocean to the east. Thus, from east to west in approximately the same latitude, varieties mongolica, uralensis, and septentrionalis burst bud in that order. The earliest provenance in the plantation was the one in variety 'NE Siberia'. This is climatically the most continental region in the world (Rumney, 1968).

The major deviations from these patterns in Scotch pine occurred in several provenances in the Mediterranean region which were significantly earlier than other central and southern European provenances -- a surprising result considering their southerly position. These included one provenance each of varieties pyreneica and iberica, two of rhodopaea, and three of armena. The early provenances of the last variety were those located just east of the Black Sea and probably reflect the increasing continentality of the climate to the east. The other anomalies could be attributable to genetic drift, for this part of the Scotch pine range is very broken. However, they could also reflect climatic adaptation, and are best considered in terms of the pattern of variation found in European black pine, a species almost entirely confined to the Mediterranean region (Figure 14).

European black pine was unique in showing not even a hint of latitudinal variation in time of bud burst. However, there was a strong correlation between time of bud burst and east longitude of origin ($r = -.90$, significant at the 1 percent level). Eastern provenances were earlier than western provenances (Table 7). This longitudinal pattern of variation is probably due to the same factors which played a large part in molding the variation pattern in Scotch pine: the direction of the prevailing winds and the influence of the North Atlantic Drift. To approximately the longitude of the Yugoslavian provenance, prevailing winds are westerly or northwesterly and carry the ameliorating influence of the Atlantic inland with decreasing effect. East of

Table 7.--Relative time of bud burst of *Pinus nigra* provenances from different parts of the natural range. The regions are arranged from east to west.

Region of origin	Time of bud burst 1=early, 10=late
Crimean S.S.R.	1.6
Turkey	3.1
Greece	3.6
Yugoslavia	6.2
Austria	5.0
Corsica, France	6.7
Mainland France	8.5
Spain	9.7

this longitude, and corresponding to a sharp increase in earliness of bud burst, 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 and Kendrew, 1961).

Thus, there is a sharp increase in the continentality of the weather from west to east in this region. This is particularly true of winter conditions -- from west to east, winter temperature decreases and frost frequency increases (Biel, 1944; Gorczyński, 1945; and Money, 1972). Although Greece is usually thought of as having a mild Mediterranean climate and Crimea is famous for its mild winters, these popular conceptions do not reflect the climates of European black pine habitats. The resorts of Crimea are on the narrow coastal strip south of the Yaila Range. North of there, where European black pine occurs, the climate is typically Russian (Biel, 1944).

Similarly, in Greece and Turkey the true Mediterranean climate is found only on the coasts. This species occurs inland at relatively high elevations, and local climates in this region depend heavily on elevation. All shores of southern Europe record snow and frost more or less regularly and winter temperatures decrease inland. The interior of the Balkan Peninsula is very cold in winter and the higher mountains in Greece (even in the Peloponnesian Peninsula) have bleak winters with much snow. The mountains of southern Greece are free of frost only in July and August. Surprisingly, average winter temperatures in the interior Balkans are lower than those in northern Norway (Biel, 1944 and Kendrew, 1961). Thus, in terms of climate the variation pattern in time of bud burst in European black pine is very much like the patterns in other species.

Only two of the provenances of this species were significantly different from others in their respective regions. One was in northern Greece (number 424 in Figure 14). This provenance is shown by Critchfield and Little (1966) as being an isolated occurrence of the species, and it is possible that the population is small enough for genetic drift to have occurred. The other is in the French Pyrenees (number 413) and was earlier to burst bud than the other French provenance. Wright and Bull (1962) felt that this provenance might originally have come from Corsica, and it is similar to the known Corsican provenance in time of bud burst. Interestingly, however, one of the unusually early Scotch pine provenances is native only a few miles away.

Scotch pine was less variable within the Mediterranean region than European black pine, but there was a definite parallel between the patterns. In Scotch pine also, Spanish, French, and Yugoslavian provenances all burst bud later than Greek and Turkish provenances, which in turn were mostly alike. The main difference was that the one Yugoslavian provenance was later, not earlier as in European black pine, than most Spanish and French provenances.

Thus, the variation patterns in Scotch and European black pines in this region are similar and tend to correspond with those of other species when climate is considered. However, the correspondence is not perfect. As already noted, Scotch pine provenances in this region tended to be early for their latitude. Furthermore, there is no doubt that Austria is colder than Greece, but Greek provenances of European black pine were earlier to burst bud than the one from Austria. Perhaps this tendency to be early near the Mediterranean is due to some unknown effect of the sea on the climate. This effect is apparently one which does not parallel the effect of the ocean. However, it need not since Mediterranean currents do not carry warm tropical waters northward as do the Atlantic and Pacific.

Eastern vs. Western Halves of Michigan's Upper Peninsula

In some ways the counterpart of the Mediterranean Sea in North America is the Great Lakes. While the Great Lakes contain much colder water and, in fact, partially freeze over in winter, both bodies of water (Great Lakes and Mediterranean Sea) influence the climate of nearby land surfaces, and the influence of neither is quite like that of the great oceans (Kendrew, 1961).

Thus, in nearly all species native to the region there was at least some tendency for the latitudinal trend in variation to be confused in the vicinity of the Great Lakes. In some species there was tendency for provenances in eastern Ontario to be late for their latitudes. In others, provenances native to Isle Royale or the northeastern coast of Lake Superior were particularly early. In a few the patterns in Minnesota and Wisconsin were irregular. These patterns tend to coincide with climatic differences caused by the influence of the Great Lakes. This may be illustrated by one trend in variation which was particularly striking because it involved fairly large differences among provenances native to the same general vicinity.

In three of the four species with provenances in Michigan's Upper Peninsula, those in the eastern half were earlier than those in the western half (jack pine, Figure 1; tamarack, Figure 3; and balsam fir, Figure 4). All differences were significant except that in tamarack between the Keweenaw peninsula provenance and those to the east. In the fourth species, yellow birch (Figure 6), the two Upper Peninsula provenances were not significantly different, but the western provenance was on the Keweenaw peninsula, also. Thus, if Keweenaw is grouped with the eastern provenances, all four species had the same pattern of variation in the Upper Peninsula.

This grouping makes sense according to the climate of the region. Because of their position and the direction of the prevailing winds (south- to northwesterly), the climates of Keweenaw and the eastern half are much more affected by the Great Lakes than that of the interior western half of the Upper Peninsula (U.S.D.A., 1941 and Visher, 1954).

Spring temperatures furnish a good example because of their obvious importance to bud burst. Onshore winds in that season from the cold Great Lakes depress the average temperatures of Keweenaw and the eastern half of the Upper Peninsula several degrees, and they decrease diurnal fluctuations in temperature. Thus, in those areas to the lee of the lakes (where provenances were earlier to burst bud) there is the paradoxical springtime situation of cooler average temperatures but fewer late frosts. So genetic differences in the Upper Peninsula coincide with climatic differences, and (except for the frost pattern) the trend corresponds with the north-early, south-late trend.

High vs. Low Elevations

Topography has an important influence on local climate, and one would expect time of bud burst to vary among provenances native to different elevations and aspects. Such variation has been found in studies of several species: *Quercus rubra* (McGee, 1974); *Q. robur* (Pjatnickii, 1955); *Picea abies* (Holzer, 1969b and Langlet, 1960); *P. glauca*-*P. engelmannii*-*P. sitchensis* complex in British Columbia (Dietrichson, 1971 and Roche, 1969); and Douglas-fir (Hermann and Lavender, 1968 and Irgens-Möller, 1957). Most of these studies were designed specifically to test for genetic differences among trees from different elevations or aspects.

Elevations, but not aspects, are known for most provenances represented in the Kellogg Forest experiments. In about half of the species, correlations between time and bud burst and elevation of origin varied from r = -.29 and r = +.20, none significantly different from zero. In the remaining species, correlation coefficients were significant (at the 5 or 1 percent levels) and of the opposite sign of the respective correlations with latitude: Douglas-fir (r = -.73), yellow birch (r = +.58), tamarack plantation 6-69 (r = +.42), white spruce (r = +.63), eastern white pine (r = +.59), and Scotch pine (r = +.34).

It is doubtful, however, that these significant correlations reflect relationships between elevation and time of bud burst. In every case they appear to be due to the occurrence of provenances at higher elevations in the lower latitudes. In yellow birch and eastern white pine, for example, most of the high elevation provenances are native to the southern Appalachians, and their lateness is probably more directly related to their southerly positions.

To help eliminate the effect of latitude, I calculated correlations within subdivisions of the species' ranges: races, varieties, or regions (Southern Appalachians, Lake States, Northeast, etc.). Only one such correlation (in the ARINEM race of Douglas-fir) was significant at the 5 percent level and none were at the 1 percent level. (Correlations in other races of Douglas-fir varied from r = -.31 to r = +.19). Considering the large number of correlations calculated (over 30), this could easily have occurred by chance. Hence, the correlations furnish no evidence of a relationship between elevation or origin and time of bud burst.

However, the Kellogg Forest experiments were not designed to test the relationship between genetic variation and elevation, and the lack of significant correlations does not prove the lack of such a relationship. In fact, an association between time of bud burst and climatic factors arising from topographic influences would be consistent with the patterns of genetic variation in at least two species. The limber-border pine complex and ponderosa pine in the Rocky Mountains had similar patterns -- both deviated from the general latitudinal trend in the same manner and in the same region. (The only other Rocky Mountain species, Douglas-fir, had a slightly different distribution of provenances, and, as we have seen, a pattern of variation unique among all species. Thus, it is not considered in the following discussion.)

While limber pine and border pine differed considerably from one another when all provenances are considered, the two species rapidly intergraded where their ranges overlap in the southern Rocky Mountains (Figure 9, Table 8). Similarly, there was a rapid change in ponderosa pine from central Arizona and New Mexico to about the southern borders of Colorado and Utah, but provenances north and south of there were very different (Figure 10, Table 6). Kung and Wright (1972) observed this rapid change in other traits of these species and attributed the phenomenon to differences in climate.

North of southern Colorado and Utah there was essentially two groups of limber pine provenances -- those forming the bulk of the range and those native to an isolated population in southeastern Wyoming and southwestern Nebraska (Table 8). Those in the latter group were late for their latitude and similar to more southern provenances. Steinhoff and Andresen (1971) also found this to be true in other traits. These provenances occupy a much lower (ca. 3500 feet) average elevation than those to the west, so their climates are warmer and their performance is as expected.

Table 8.--Relative time of bud burst of *Pinus flexilis* and *P. strobiformis* provenances from different parts of the natural ranges. The regions are arranged approximately from north to south.

Species and region of origin	Time of bud burst
	1=early, 10=late
Pinus flexilis	
Bulk of range	3.4
SE Wyoming and SW Nebraska	5.6
Sympatric zone(a)	6.5
Average (weighted)	3.7
Pinus strobiformis	
Sympatric zone(a)	7.3
Bulk of range	9.1
Average (weighted)	8.3

(a) Area of overlap with the range of the other species.

The ponderosa pine experiment contained provenances from the plains in Nebraska, but, unlike limber pine, these were not later than provenances to the west in the mountains. However, ponderosa pine usually occupies the lower elevations in the Rockies (down to the plains), so these Nebraska provenances are typical in habitat for many parts of the species' range.

North of southern Colorado and Utah ponderosa pine provenances were more uniform than those of limber pine in the bulk of the range; but both species displayed essentially random variation with few significant differences in this large region. This is the most striking aspect of the variation patterns in these species because it is a major deviation from the latitudinal trend. Two factors may account for it: the locations of the provenances representing the species and the overall climate of the region.

The geographic randomness of the variation is typified by the variation which occurred in Colorado alone in the two species. The earliest and latest provenances of ponderosa pine in this region are located within a few miles of one another near Colorado Springs; and differences among Colorado provenances of limber pine were virtually as large as those among all provenances in the bulk of the range.

While these differences with Colorado do not necessarily correspond with the actual elevations of the provenances, it is still possible that they reflect the rugged topography of the Colorado Rockies compared with the mountains to the north. Mountains can cause great climatic diversity within short distances due to elevation, aspect, and air drainage patterns, and pollen transfer among populations could confuse any relationship between elevation and genetic variation.

The lack of latitudinal variation north of Colorado may be partly due to the elevations of the provenances sampled. In both species the average elevation of provenances in this region was much less than that of Colorado and Utah provenances (5600 _vs_. 9300 feet in limber pine and 3700 _vs_. 8000 feet in ponderosa pine). In limber pine this corresponds to a shift in habitat type to what, in the south, is the low elevation pinyon-juniper zone (Daubenmire, 1943). The shift in elevation in these species may more than compensate for climatic changes associated with the higher latitudes. The Alberta provenances in limber pine were particularly late for their latitude; their elevations were also particularly low (4200 to 5100 feet).

Climatic maps (Visher, 1954) are necessarily generalized in the Rocky Mountain region because of the complex topography. But isotherms reflect in a broad way the influence of topography and tend to conform with the variation patterns in these species. For example, the isotherm for a January mean temperature of 20°F loops south in the Rockies to extreme northern New Mexico. It encloses on its colder side (10 to 20°F) most of the region where genetic variation was small and geographically random. On the other hand, south of Colorado the isotherms run generally east-west and most of the late provenances in these species lie on the warmer side of the 30°F isotherm.

Thus, while it was impossible to detect a simple relationship between the results and elevation in these experiments, the variation patterns in these Rocky Mountain species indicate that the effect of topography on climate has influenced the evolution of genetic variation

in time of bud burst. If such an influence has occurred, it has been in the direction expected on the basis of the north-early, south-late trend.

Synthesis

In summary, there were several trends in genetic variation in time of bud burst which were common among species. The most predominant trend was latitudinal, but deviations occurred near the oceans. Southern and coastal provenances were late, northern and interior provenances were early. Other deviations occurred near the Great Lakes and in the Rocky Mountains. Patterns in the Great Lakes region were confusing, but one trend was quite striking and consistent. Provenances in the eastern half of Michigan's Upper Peninsula were earlier than those in the interior western half in species with provenances from those places. Deviations from the latitudinal trend in the Rockies are explainable by the effect of topography on climate, although correlations between time of bud burst and elevation of origin provided no firm evidence of such an effect in any species. Northern provenances in this region were not necessarily earlier than more southern provenances, but their elevations are much lower and this may have compensated for the latitudinal difference. Furthermore, genetic variation was greatest within Colorado where the topography is most rugged.

Variation patterns in different species were not identical in every respect. The results in red pine and Douglas-fir were quite different from those in other species. (These two species will be discussed in the following section.) Coastal *vs*. interior comparisons in yellow birch showed a trend which was the reverse of that in other species. White spruce was essentially uniform in eastern Canada, while other species varied in this region. Even when trends were consistent among species, they were not always exactly parallel. For example, in both tamarack and jack pine Nova Scotia provenances and the southernmost provenances were almost equally early, but the southernmost provenance of tamarack was much farther south than that of jack pine.

These and other inconsistencies, if they have a genetic basis, emphasize the individuality of evolution -- species adapt to their environments in different ways. However, the generality of certain trends indicates parallel adaptation to at least some climatic gradients. What aspects of climate have been involved in the evolution of these common patterns of variation in time of bud burst?

It is doubtful that the variation reflects adaptation to only one climatic variable. Spring frosts, for example, might be considered to have been of primary importance because they frequently damage trees which burst bud too early. This is particularly true of white spruce and balsam fir. Tamarack, on the other hand, frequently bursts bud long before the last frost with apparently no ill effects. Tamarack is physiologically adapted to spring frosts -- it still retains considerable winter cold hardiness by the time of bud burst, but white spruce does not (Glerum, 1973). Thus, adaptation to spring frosts need not involve time of bud burst, and this selection mechanism alone cannot have been responsible for the common patterns of variation which were observed.

Bud burst is the culmination of a gradual process of growth in the primordial shoot system. It probably begins with the first warm day following removal of true-rest and becomes more rapid as warm temperatures become more frequent. Therefore, time of bud burst (in species not responding to photoperiod) must be determined by the degree of warmth necessary for growth. Trees differing in this requirement will also differ in time of bud burst.

A number of studies have demonstrated intraspecific genetic variation in rate of growth and other physiological processes at different temperatures (*e.g.*, Bourdeau, 1963; Fryer and Ledig, 1972; Klikoff, 1966; Mergen, 1963; Mooney and Billings, 1961; and Perry, 1961). Usually, when genetic variation exists, plants from colder climates are adapted to function at lower temperatures. This corresponds with the observed patterns in time of bud burst. Provenances from colder areas probably burst bud earlier because the undeveloped shoot system can begin growing earlier in the spring when temperatures are lower.

Complete adaptation in time of bud burst to both low temperatures for growth and late spring frosts would be impossible in most areas -- growth initiation at cooler temperatures usually means greater exposure to frost damage. Furthermore, climate at other times of the year than spring may have been important. Winter cold hardiness, rate of shoot growth in summer, and even time of bud set in autumn could all be physiologically and adaptively realted to time of bud burst. Consequently, adaptation was probably a compromise involving many climatic factors. Some were undoubtedly more important in some species than in others, perhaps even more important in some parts of a species' range than in other parts. But the net effect of adaptation to all factors in each species has resulted in similar variation patterns.

To determine what climatic factors may have been involved, I attempted multiple regression analyses with time of bud burst as the dependent variable and the following climatic parameters as independent variables:

X(1), X(2), ..., X(6) = March, April, May, June, July, and yearly mean temperatures, respectively.

X(7) = Number of days per year with a normal mean temperature of at least 42°F.

X(8) = Number of days as in X(7) which occur before the average date of the last frost.

X(9) = Average length of the frost-free season.

X(10) = Average date of the last frost.

X(11) = Daylength on the first day with a normal mean temperature of at least 42°F.

X(12) = Daylength on the average date of the last frost.

Climatic data were obtained from summaries for weather stations nearest all provenances of tamarack (both experiments), white spruce, jack pine, and eastern white pine. Daylengths were derived from tables in Eckert and Clemence (1946).

All five sets of data yielded highly significant regression equations which accounted for most of the variation in time of bud burst (R = .75 to R = .87). Thus, variation in climate can be used to explain genetic variation in this trait. However, the analyses failed to furnish any clues as to which factors of the climate were most important in the evolution of common patterns of variation. Each

independent variable, except X(9) and X(10), occurred in at least one equation, and none of the equations were similar.

At least part of the problem with the analyses lies in the variables themselves. All are climatically related and all are strongly correlated with latitude. This is probably why a daylength variable was included in two of the equations (tamarack and eastern white pine) -- latitude would have served equally well. Furthermore, such chance factors as which provenances were included in each analysis probably had much to do with the forms of the regression equations. For example, the equations for the two tamarack experiments should have been similar, but only two of the four variables in each were the same and neither of the equations fit the data of the other plantation. Thus, while each equation appeared to have good predictive potential, it is doubtful that either could be used to accurately predict relative times of bud burst of many provenances not included in the original analyses.

No one variable used in the analyses was significantly correlated with time of bud burst in all four species; and the analyses indicated no composite variable which would work for all species. However, one composite expression of climate, embodying a number of temperature variables, which corresponds generally well with the common variation patterns is "continentality." Among the many ways to express continentality of climate, one of the most often used is mean annual range in temperature. The greatest ranges (most continental climates) in North America and Eurasia occur in central Canada, interior Alaska, and northeastern Siberia. The smallest ranges occur in coastal and southern North America, western and southern Europe, and southern Asia

(Money, 1972). The annual range in temperature in the Mediterranean region increases eastward (Biel, 1944).

These facts are in agreement with the major trends in variation in time of bud burst. Provenances from regions with the most continental climates were earliest to burst bud. (The relationship was not perfect -- _e.g._, the eastern half of the Upper Peninsula is not more continental than the western half.)

Regions with the greatest annual ranges in temperatures are characterized more by very low winter temperatures than by high summer temperatures. This is readily obvious when it is considered that they lie in northern latitudes (Canada and Siberia) and actually have fairly cool summers. (Temperature gradients in the northern hemisphere are much steeper in January than in July.) Furthermore, the major geographic trends (north-early, south-late and interior-early, coastal-late) have parallel climates only in winter. Coastal areas in winter are warm like southern latitudes, but in summer they are cool like northern latitudes. Consequently, variation patterns in time of bud burst correspond better with winter temperatures than summer temperatures.

An excellent illustration of this is the case of two provenances of Scotch pine near Riga, Latvian S.S.R. and Yakutsk, Siberia. They were very different in time of bud burst with a range two-thirds as great as that among all provenances of Scotch pine. The one near Yakutsk was the earliest in the plantation. Likewise, their January mean temperatures are very different (Yakutsk, -49°F and Riga, +24°F), but their July mean temperatures differ by only one degree (Kendrew, 1961).

Another example is that of the earliest (central Manitoba) and second-latest (Nova Scotia) provenances of tamarack. The January means of the nearest climatic stations differ by over 30°F, but the July means are within 2°F of one another. The efficacy of winter vs. summer temperatures in discriminating among provenances is illustrated by the fact that January means of the jack pine provenances differ by as much as 45°F while July means differ by a maximum of 14°F (Holst, 1963).

Probably, winter temperatures are simply related to other, more important, climatic variables. For example, places with equal summer temperatures but colder winters will also have cooler springs. However, this general correspondence with winter temperatures could also reflect a physiological or adaptive relationship between bud burst and cold hardiness.

TWO UNIQUE SPECIES

Red Pine

Even though the red pine provenance test sampled virtually the entire range of the species (Figure 8), red pine was the only species in which I found no genetic variation in time of bud burst. This, of course, does not prove that the species is not variable in this trait, but it is certainly true that the variation is much less than that in the other species studied.

The natural range of red pine is small compared with that of others in the same region, and I considered the possibility that the lack of variation may be associated with a relative uniformity in the climate. However, the other species all contain significant genetic variation within the natural range of red pine. The other species have apparently adapted to climatic variation to which red pine is either immune or not adapted.

Red pine is genetically variable in growth rate, but less so than most tree species which have been studied in detail (Fowler and Lester, 1970). The geographic pattern of variation in this trait is obscure and does not correlate well with climatic gradients. More so than other species in the Northeast, red pine is apparently homozygous for a large number of alleles, both as a species and as individual trees (Fowler, 1965a, 1965b, and 1965c). Thus, the small amount of variation in time of bud burst is not surprising in view of what is known about the species.

Douglas-fir

Douglas-fir (Figure 11) was the only species in which southern provenances burst bud earlier than northern provenances, and only yellow birch shared with it a tendency for provenances near the coast to be earlier than those farther inland. In all other species these trends were exactly or nearly the opposite.

It is possible that the pattern of variation in Douglas-fir is unusual only in a geographic sense, and not when the actual climates of its habitats are considered. However, limber pine, border pine, and ponderosa pine commonly occur with Douglas-fir where their ranges overlap, so all are often found in similar climates. Since the variation patterns in ponderosa pine and the limber-border pine complex conformed with those in other species, there is little doubt that the pattern in Douglas-fir is unusual from the climatic as well as the geographic standpoint.

Douglas-fir would not adapt to the same climatic factors by evolving in the opposite direction, but perhaps different aspects of the climate are important in this species. For example, of the three species Douglas-fir is most sensitive to spring frosts in its native range (Pearson, 1931). However, white spruce and balsam fir are also very frost sensitive and their patterns of variation conformed with those of other species.

Heiner and Lavender (1972) and Irgens-Möller (1967) proposed that early bud burst in Douglas-fir may be an adaptation to summer drought. Ponderosa and limber pines are less susceptible to drought than Douglas-fir (Bates, 1924). However, this explanation is inadequate for the overall pattern of variation evident in Figure 11. Not all parts of the species' range in the central and southern Rockies regularly experience growing season droughts (Baker, 1944). In fact, Pearson (1931) pointed out that growing season droughts in the Douglas-fir type are rare when soil moisture is considered.

An alternative explanation for the variation pattern is that the trigger mechanism for bud burst may be different in Douglas-fir. As explained in the introduction, most species require only warm temperatures to initiate growth after the removal of true-rest. However, lengthening photoperiod (probably in conjunction with temperature) may determine time of bud burst in some species (Wareing, 1969). Irgens-Möller (1957) found that this may be true with Douglas-fir. If so, it could explain the geographic pattern of variation in time of bud burst.

Two latitudinally extreme provenances will serve as illustrations. Three facts are important -- southern trees usually burst bud before northern trees in nature, days are lengthening in the spring, and days are shorter in more southern localities on any date after the spring equinox. Trees of the southern provenance would therefore burst bud in nature under shorter photoperiods. If the trees are adapted to the photoperiodic sequences of their native localities, in a common environment the southern provenance would burst bud before photoperiods lengthened enough to trigger growth in the northern trees, and the observed pattern of variation would result.

In support of this, Irgens-Möller (1957) found that long photoperiods hastened bud burst in seedlings of the coastal variety transplanted from high elevations to Corvallis, Oregon. Seedlings from low elevations nearby were not affected. However, Worrall and Mergen (1967) pointed out that the high elevation trees may have responded to photoperiod only because they were not chilled enough at Corvallis to completely overcome true-rest. Douglas-fir trees from the northern Rockies have a greater chilling requirement than trees from the southern Rockies (Irgens-Möller, 1968), and presumably the same could be true of trees from high _vs._ low elevations. Long photoperiods will stimulate bud burst in Douglas-fir if the trees are insufficiently chilled.

Therefore, perhaps incomplete chilling is a more likely explanation for the pattern of variation in Douglas-fir. If this normally occurs in nature, photoperiod could be of _de facto_ importance in triggering bud burst, and the above model could explain the pattern. Alternatively, it may occur only in trees growing in conditions similar to those at Kellogg Forest. If so, delayed bud burst in the northern provenances could be attributed to insufficient chilling and incomplete removal of true-rest. True-rest in southern provenances (which require less chilling) is more quickly overcome and they may have had a more normal development in the spring of 1973.

As these studies show, the north-early, south-late pattern of genetic variation in time of bud burst is the most common among species. However, several other species have the same latitudinal pattern as Douglas-fir. Nienstaedt (1974) listed five, although extensive phenological studies have not been perforemd on all of them -- *Juglans nigra*, *Liriodendron tulipifera*, *Liquidambar styraciflua*, *Platanus occidentalis*, and *Populus deltoides*. These and Douglas-fir could all have the same trigger mechanism for bud burst.

Farmer (1968) tested the effects of chilling and photoperiod on an Alabama and a Tennessee provenance of *Liquidambar styraciflua*. Dormant seedlings were chilled for various lengths of time and then exposed to warm temperatures and different photoperiods. Even after as much as 100 days of chilling at 37°F, long photoperiod still hastened bud burst. As in Douglas-fir, if such a situation occurred in nature it could explain the pattern of variation in time of bud burst.

VARIATION WITHIN PROVENANCES

Some of the provenances in three plantations were represented by several half-sib families: balsam fir (6 provenances), limber and border pines (8 provenances), and black cherry (5 provenances). Of these 19 provenances only three (in balsam fir and black cherry, Table 4) contained families which varied significantly in time of bud burst.

Within the three provenances, however, the magnitude of genetic differences approached those observed in the respective entire plantations. Only five of 42 balsam fir provenances averaged earlier or later (none significantly) than families of one Baraga County, Michigan provenance. One Cass County, Michigan provenance of black cherry contained both the earliest and latest of the 33 families in the experiment, and differences among provenance means were much smaller. Estimates of variance components indicated that provenance effects were predominant in balsam fir; but family effects were predominant in black cherry, mostly due to the families of the one Michigan provenance. Wright and Lemmien (unpublished manuscript) found no significant variation within this provenance in several other traits.

The principal factors which restrict genetic variation within populations are the intensity of natural selection and genetic drift (Briggs and Walters, 1969). Genetic drift probably has little significance in woody plants of temperate climates -- generations are long and very small, isolated populations of such species are rare (Stebbins, 1950). Thus, natural selection was probably responsible for most of the small, non-significant variation within the remaining 16 provenances of the four species. However, at least some of the eight limber and border pine provenances could be exceptions. The tendency of these species to occur in small, scattered groves (Sargent, 1961) could have permitted genetic drift to occur. If so, this would account for some of the geographically random variation in limber pine.

CONSISTENCY OF THE RESULTS

With few exceptions, the results obtained at Kellogg Forest in 1973 agree with data obtained there in other years and with the results of other studies of the same species. Furthermore, most investigations of other species have revealed patterns of variation in time of bud burst which are similar either to that of Douglas-fir or to those of other species studied at Kellogg Forest. Nienstaedt (1974) reviewed the results of most such studies on American species.

Where plantations at other locations have contained the same provenances it is possible to correlate the results with those at Kellogg Forest. As will be seen, most such correlations vary between r = +.76 and r = +.80. This degree of correlation may represent an upper limit constrained by the high error involved in measuring this trait and the different methods used to measure it. If so, correlations of this magnitude indicate little genotype X environment interaction.

Jack Pine

Teich and Holst (1969) studied growth of 27 of the Kellogg Forest provenances growing at Chalk River, Ontario. By plotting weekly shoot growth they extrapolated the date when 1 percent of the growth was completed. The correlation between this date and time of bud burst at Kellogg Forest is r = +.77 (significant at the 1 percent level).

Yeatman (1967) measured needle length shortly after bud burst on 14 Kellogg Forest provenances growing in controlled environments. The correlation with Kellogg Forest data is high (r = +.77, significant at the 1 percent level), and the agreement increases considerably when comparisons are made only within eastern and western provenances. Other results from Yeatman's experiments indicated that growth data for provenances east of Lake Superior fell on a response curve with a different slope than the one for provenances west of Lake Superior.

Thus, dividing the provenances in this manner is valid when comparing results from different experiments on jack pine.

In a study of 11 Ontario provenances, Holst and Yeatman (1961) and Holst (1964) found that those from milder areas started shoot growth later than those from more continental and more northern parts of Ontario.

White Spruce

Picea engelmannii and white spruce are similar enough that they hybridize fairly extensively where their ranges overlap in western Canada. Thus, one would expect the pattern of variation between the two species to parallel that within white spruce. The British Columbia provenance of white spruce burst bud later at Kellogg Forest than those to the east. Similarly, in other experiments, British Columbia Engelmann spruce was significantly later than British Columbia white spruce (Roche, 1969); and most provenances of both species (not distinguished) in western Canada were later than most white spruce provenances in eastern Canada (Dietrichson, 1971).

On the other hand, there was little variation among the eastern provenances of white spruce at Kellogg Forest. The same was true of 18 different eastern provenances growing in a Norwegian experiment (Dietrichson, 1971).

Within plot variation in time of bud burst in the Kellogg Forest plantation of this species was quite large in comparison with that in most other species. This indicates that genetic variation within provenances might be present, but the experiment was not designed to

test such variation. Nienstaedt and King (1970) found genetic differences in time of bud burst among clones selected from a Wisconsin plantation of white spruce of unknown provenance.

Among other spruce species, genetic variation in time of bud burst has been studied in Picea mariana, P. abies, and P. sitchensis. The variation patterns are similar to that observed in white spruce and other Kellogg Forest species.

Trees of 148 half-sib families from 24 provenances were included in one Picea mariana experiment (Morgenstern, 1969a and 1969b). All but three were eastern Ontario provenances. Measurements were taken at age 1 in a German plantation. As in white spruce, there was a strong correlation with latitude -- northern provenances were earliest to burst bud. Variation among half-sib families within provenances was also significant.

Khalil (1973) measured time of bud burst of 39 eastern Canadian provenances of Picea mariana from Newfoundland and the mainland. The trees were growing in three Newfoundland nurseries. Differences among provenances were significant, though only as large as 4 days. Newfoundland provenances were earlier than those from the mainland. This appears at first to contradict the interior-early, coastal-late trend, but the situation is similar to what occurred in Labrador in white spruce. Labrador and Newfoundland are under the influence of cold ocean currents from the north, rather than warm currents from the south, so provenances near the coast in these regions are likely to be late for their latitudes.

Genetic variation in time of bud burst in Picea abies is also similar to that in white spruce and other species. Trees from high latitudes and elevations burst bud earliest (Langlet, 1960 and 1967 and Worrall and Mergen, 1967). But in Picea sitchensis there was no clear relationship between this character and latitude in 47 provenances from California to Alaska (Burley, 1966a). However, this is to be expected in a species which rarely grows far from the Pacific Coast. Some of the trends, in fact, corresponded closely with general trends at Kellogg Forest. Early trees were from inland or northern limits of the species' range, and island provenances were among the latest to burst bud. Other results were contradictory -- both California (southern) and high elevation provenances tended to be late.

Tamarack

One of the tamarack experiments had been measured for time of bud burst several years previously in the nursery at age 2. The correlation between this and the 1973 data is r = +.78 (significant at the 1 percent level). Thus, the relative order in which the provenances burst bud did not change appreciably with age.

This fact was emphasized when plantation 6-69 was re-measured in 1974 using the same methods as in 1973. The correspondence between provenance means for the two years is very high (r = +.92, significant at the 1 percent level), and provenance X year interaction was not significant according to the combined analysis of variance.

Balsam Fir

Figure 4 was constructed using averages of Kellogg Forest data and Wisconsin data gathered in two different years by Dr. Donald Lester.

Correlations between the Michigan and Wisconsin means of common provenances are highly significant (r = +.73 and r = +.63). However, both combined analyses of variance showed significant provenance X plantation interaction.

I collected data somewhat late in this species, and differences in amount of growth were difficult to detect among all but the latest provenances. The significance of provenance X plantation interaction is probably due to failure of the Kellogg Forest data to show differences among early provenances when, in fact, they existed. There is no indication that order of bud burst among provenances was different in the two plantations. General patterns of variation are identical in all three sets of data -- the earliest and latest provenances were always the same.

Eastern White Pine

The predominantly latitudinal trend in variation in this species is supported by the results of Mergen (1963). He measured genetic variation among seedlings of eight provenances as far south as North Carolina and as far north as New Brunswick and Minnesota. Seedlings from northern regions burst bud earlier than those from southern regions.

In another study of seedlings of 21 range-wide provenances, Santamour (1960) measured shoot growth at various times during the growing season. By mid-May the northern provenances had completed a considerably larger proportion of their total shoot growth than southern provenances. If this reflects relative time of bud burst, then the results are similar to those obtained at Kellogg Forest. However, the variation in that character was at least partly caused by the fact that northern provenances had less total growth for the season.

Yellow Birch

Time of bud burst of the Kellogg Forest provenances had also been measured six years previous to this study when the trees were growing in the East Lansing, Michigan, nursery. Considering that the earlier data consisted of only one observation per provenance, differences among provenances were quite similar to those observed in 1973 ($r = +.76$, significant at the 1 percent level).

Clausen and Garrett (1969) measured time of bud burst at age 3 in a Wisconsin plantation of the same experiment. Again, the correlation between results is highly significant ($r = +.80$). Geographic patterns of variation were similar except that Nova Scotia provenances in the Wisconsin plantations were slightly later than New Brunswick provenances. That this was not true in the Kellogg Forest plantation of yellow birch was one of the major deviations from general trends in the present study.

Wang and Perry (1958) found that northern provenances were earliest to burst bud in a study involving seedlings subjected to various combinations of photoperiod and winter chilling. Sharik (1971) studied phenology in 30 widely separated stands of this species and in a 2-year-old provenance experiment containing trees of the same provenances. In the wild, bud burst progressed from low to high latitudes. In the provenance test, as expected, bud burst varied in the opposite direction -- northern provenances were earliest.

Clausen (1973a) found that time of bud burst was significantly correlated with elevation of origin in a nursery planting of the Kellogg Forest experiment near Rhinelander, Wisconsin. As with the Kellogg Forest data, the significance of the correlations may have been due to a confounding of latitudinal effects with elevational effects, though this cannot be determined from Clausen's published information. Sharik (1971) sampled yellow birch populations along five elevational gradients from North Carolina to New Hampshire and found that trees from all elevations at a given latitude burst bud at about the same time when growing in the provenance test.

The Kellogg Forest plantation did not include half-sib families. However, Clausen (1973b) reported variation in time of bud burst within ten provenances of yellow birch. There was considerable variation among half-sib families within provenances, but the differences were smaller than those among provenances and individual families were not consistently early or late from year to year. Sharik (1971) also found significant genetic variation within provenances in this trait.

Virginia Pine and Black Cherry

No other studies of genetic variation in time of bud burst have been reported for these species.

Red Pine

The lack of variation observed in this species agrees with the results Larson (1967) obtained in a study of 3-year-old seedlings of ten widely separated provenances. The seedlings were allowed to become dormant, chilled for 5 months, and subjected to various combinations of day and night temperatures. He found no differences among provenances in time of initiation of shoot growth. Similarly, Rehfeldt and Lester (1966) observed no genetic differences in time of bud burst among 18 Canadian provenances with a latitudinal range of 6° (most of the range). All began growing within a period of 2 days in May.

On the other hand, Rudolf (1954) reported differences in amount of shoot growth in June of the second year in a provenance test of 160 Lake States origins. But the differences were small, and they probably reflect differences in rate of elongation rather than in time of bud burst since the measurements were taken near the end of the period of height growth. (Though they found no differences in time of bud burst, Rehfeldt and Lester (1966) found variation among provenances in rate of shoot elongation.)

Limber and Border Pines

No other studies of genetic variation in time of bud burst have been reported for these species.

Ponderosa Pine

The north-south pattern of variation in this species tends to be confirmed by several separate observations in very early provenance tests (Daubenmire, 1950; Hanover, 1963; Larson, 1966; and Squillace and Silen, 1962). In each case, the southernmost provenance (Coconino County, Arizona) began shoot or cambial growth later than provenances of the central or northern Rocky Mountains. In the more detailed studies (Daubenmire, 1950 and Hanover, 1963) it was difficult to interpret variation among the other provenances, but both were of the same unreplicated plantation and their results were limited by the experimental design.

Wells (1964a and 1964b) measured date of growth initiation at age 1 in the nursery phase of the Kellogg Forest provenance test. The results correlated best with mean January temperature and mean annual range in temperature of ten climatic variables measured near locations of origin. The correlation between our results is r = +.64 (significant at the 1 percent level). Wells' data showed greater differences between coastal and interior provenances, and Kellogg Forest data showed a stronger latitudinal pattern of variation (Table 6). Thus, each study better supports a different one of the variation patterns common to several species. The lack of close agreement between results may be due to the different methods of measurement, or to provenances X year or provenance X site interaction.

Douglas-fir

The results of several other studies of bud burst in this species tend to confirm the genetic variation pattern observed at Kellogg Forest. Irgens-Möller (1968) studied time of bud burst of several provenances from both the coastal and interior varieties. Among those from the interior variety, trees native to Arizona, New Mexico, and eastern Washington burst bud several days to 2 weeks earlier than trees native to northern Idaho and Montana. The relative time of bud burst of the coastal variety was confused, however. One provenance was early and one was late compared with provenances of the interior variety.

Similarly, Ching and Bever (1960) found no clear-cut geographic pattern of variation among 14 provenances of the coastal variety. However, bud bursting was generally earliest in southern provenances and the northernmost provenance was one of the latest. High elevation sources were also late. In two other provenance studies of more limited geographic scope but with various elevations represented, trees from increasing higher elevations were progressively delayed in time of bud burst (Irgens-Möller, 1957 and Hermann and Lavender, 1968).

Munger and Morris (1936) reported that among 13 provenances of Oregon and Washington the earliest to burst bud were from localities with the warmest spring temperatures. The latest were from localities where cold spring nights were most frequent. The order of bud burst among the provenances was similar in different plantations of the experiment. Two decades later the rankings had changed little (Morris *et al*., 1957).

The above results support the strong tendency for provenances of warmer climates (southern and near-coastal) to burst bud earlier at Kellogg Forest. Others are contradictory. In the nursery phase (age 1) of the Kellogg Forest experiment, southern and coastal provenances were later than northern and interior provenances, respectively (Kung, 1968). Likewise, in an unreplicated experiment Irgens-Möller (1967) found that trees from western Washington and Oregon burst bud later than trees from eastern parts of those states. Schober (1963) noted that a similar pattern usually occurs in European plantations of Douglas-fir.

The conflicting results of different studies could be related to the mechanism of bud burst in this species. If both photoperiod and temperature are involved, the interaction of the two factors could easily cause different sequences of bud burst among provenances at different places. If photoperiod is not involved but northern provenances received insufficient chilling at Kellogg Forest, the pattern of genetic variation would be different where all trees were sufficiently chilled.

A study by Sweet (1965) indicates what may be the best approach to resolving genetic variation patterns in time of bud burst in this species. He distinguished between the times of bursting of the terminal and lateral buds of 23 provenances of the coastal variety. The terminal is usually later, presumably as a mechanism to maintain height growth when late, killing frosts may occur. Neither character correlated well with climate or geography, but the time lag between the two events did. The longest lag occurred in trees from mild climates where the date of the late frost is most unpredictable. (These results neither agree nor conflict with those obtained at Kellogg Forest.)

Nienstaedt (1974) listed five other species in which southern provenances burst bud earlier than northern provenances. All are native south of Canada in the eastern United States and are therefore more southern than most species studied at Kellogg Forest. Perhaps this may be related to their unusual variation pattern.

Of the five, Juglans nigra has been studied most intensively. Bey (1972) measured time of bud burst in five plantations containing a total of 25 provenances and 82 half-sib families. There was significant genetic variation among provenances and among families within provenances. Results were highly and significantly correlated with latitude in all plantations, and the results indicated little or no genotype X environment interaction. Bey hypothesized that photoperiod may be involved in triggering bud burst in this species.

Scotch Pine

Similar studies of genetic variation in phenology have been performed in other Scotch pine experiments. Langlet (1936) measured the proportion of mature needle length completed by June 3 on seedlings of 22 Swedish provenances from latitudes 56°N to 70°N. His data were summarized by Wright and Baldwin (1957). There was a strong tendency for northern provenances to have better developed needles than southern provenances, indicating that the former had burst bud earlier.

Hagner (1970) and Dietrichson (1964) measured shoot development at various times during the growing season in separate provenance experiments. The former contained 48 provenances from throughout Sweden and the latter was a Norwegian plantation of the 1938 IUFRO experiment containing provenances from central and northern Europe. In each case, shoot development on a certain date was highly correlated with latitude -- northern provenances had developed most, so they had probably burst bud earlier. Dietrichson also measured needle development. Variation in this character corresponded very closely with variation in shoot development.

Saatcioglu (1967) recorded actual time of bud burst in an unreplicated Scotch pine experiment containing provenances from northern Scandinavia to Turkey. The variation among provenances in time of growth initiation was as great as 3 weeks. Northern provenances were earlier than southern provenances. Variation in this character corresponded with variation in amount of needle development completed by June 5. Hence, the results of all the above studies may be compared, even though different methods were used to estimate relative time of bud burst.

Time of bud burst has also been studied in other plantations of the Kellogg Forest experiment. Wright and Bull (1963) measured the actual dates of growth initiation at age 1 in the East Lansing, Michigan, nursery. Though all provenances burst bud within 3 days, the northern ones were significantly earlier than many southern ones.

Read (1971) used grades of shoot development in early May to estimate relative time of bud burst of 8-year-old trees in a Nebraska plantation. The correlation between means of provenances in both the Kellogg Forest and Nebraska plantations is r = +.77 (significant at the 1 percent level). Means of the 17 varieties represented in both

plantations are even better correlated (r = +.89). Thus, the genetic variation pattern observed by Read is very similar to that at Kellogg Forest. Again, the pattern of variation in central Europe appeared geographically random, and the performance of northern varieties corresponded with latitude and distance from the ocean. The same provenances in varieties *rhodopaea* and *armena* which were early for their latitudes at Kellogg Forest were also early in Nebraska.

Khalil (1969a and 1969b) recorded actual dates of bud burst in six Minnesota plantations at age 7. In only two plantations, however, was time of bud burst significantly correlated with latitude. Two factors might have contributed to this inconsistency with other results: (1) representation of varieties in the plantations (one contained only three varieties, the northernmost variety was included in only one plantation, *etc.*) and (2) high measurement error (the scope of the study permitted visiting each plantation only once a week).

European Black Pine

Genetic variation in time of bud burst has not been previously studied in this species. However, it is interesting to compare the genetic variation pattern in this character with that in other characters. Relationships between genetic variation and latitude, longitude, *etc.* are common in most species, but previous genetic studies of European black pine have revealed no strong geographic variation patterns, even though the species is quite variable (Arbez and Millier, 1971; Lee, 1968; Röhrig, 1966 and 1969; Wheeler, 1974; and Wright and Bull, 1962).

Thus, variation in time of bud burst is the only character known to be clearly associated with geographic or environmental gradients. An exception might be susceptibility to winter cold damage. Western provenances (Spain, France, and Corsica) are most susceptible (Lee, 1968; Röhrig, 1966; and Wright and Bull, 1962). These provenances were also latest to burst bud. Otherwise, the characters are not well correlated, but this weak parallel in variation is reasonable based on what is known about variation in these characters in other species. Trees which burst bud late and trees which lack cold resistance are usually native to warmer parts of the range.

CORRESPONDENCE BETWEEN BUD BURST AND FLOWERING

Most species which were genetically variable in time of bud burst were also variable in time of flowering (Table 9). Surprisingly, amount of variation in each species did not necessarily correspond with size of the natural range. Provenances of jack pine, a fairly widely distributed species, all flowered within a period of 6 days; but provenances of European black pine, a species with a comparatively small range, flowered as much as 16 days apart. Furthermore, families of just one Michigan provenance of black cherry differed by as much as 11 days. This is the same provenance which was so variable in time of bud burst.

The amount of variation within Scotch pine approached that in European black pine. While the range among provenances within varieties was only 7 days, the range among all provenances in the plantation was 14 days. Karrfalt and Gerhold (1973) found a similar amount of variation in time of flowering in the same Kellogg Forest plantation in 1969 and 1970, but Polk (1967) observed a range of 3 weeks in a Missouri plantation of the same provenances. Geographic patterns of variation were similar in both studies and parallelled that in the present study.

As was true with time of bud burst, red pine provenances all flowered at about the same time (within 4 days) and differences were not significant. On the other hand, black cherry and Virginia pine

Table 9.--Variation in time of flowering among varieties, provenances, and families in plantations of eight species of trees.

Species	Number of provenances with flowers	Range among means of:		
		Varieties	Provenances (within varieties)	Families within provenances
			days(a)	
Betula alleghaniensis	15	--	9***	--
Larix laricina (6-69)	17	--	8***	--
Pinus banksiana	79	--	6***	--
P. nigra	24	--	16***	--
P. resinosa	58	--	n.s.	--
P. sylvestris	83(b)	11***	7**	--
P. virginiana	18	--	n.s.	--
Prunus serotina	3(c)	--	n.s.	11***

(a) n.s. = differences not significant, ** = differences significant at the 1% level, *** = differences significant at the 0.1% level.

(b) In 17 varieties.

(c) Containing a total of 19 families.

exhibited significant variation among provenances in time of bud burst, but not in time of flowering. The contradiction is only an apparent one in black cherry, however. Only three of the eight provenances were flowering, and the three did not differ significantly in time of bud burst.

In Virginia pine it is possible that the lack of significance does not reflect genetic uniformity in this trait. Instead, it may be due to the difficulty encountered in measuring the plantation with precision -- the trees were tall and closely spaced, and often only a few strobili on weak, shaded branches could be observed. The statistical analysis for this species had the largest error term of all species, and this may have masked small genetic differences.

There is good reason to expect genetic variation in time of flowering to resemble genetic variation in time of bud burst. In most temperate tree species flower primordia, like vegetative primordia, are formed in the year previous to the time of full development, and both undergo a cycle of dormancy before resuming growth (Hillman, 1962). As with the bursting of vegetative buds, temperature seems to be the primary environmental factor determining the time that flowers reach full development in spring (Boyer and Woods, 1973 and references therein; Sarvas, 1967; and Winton, 1964). Furthermore, in many species the flowers are borne on vegetative shoots of the current year, and both arise from the same bud.

Consequently, in all species which contained genetic variation in both characters, time of flowering was significantly correlated with time of bud burst among provenances or families. The degree of correspondence differed considerably from species to species. As expected,

the correspondence was better in species in which flowers and shoot systems arise from the same buds (jack pine, Scotch pine, European black pine, and black cherry). Figures 15 through 18 show the association between bud burst and flowering in these species. In all four the degree of correspondence was good considering the amount of random error involved in measuring the two events on very large numbers of trees. While times of flowering of Virginia pine provenances were not significantly different, the earliest provenances were significantly earlier to burst bud than the latest.

In tamarack and yellow birch, flowers and vegetative structures arise from different buds. Thus, there is less reason than in the other species to suppose that genetic variation patterns in the timing of the two events would be parallel. They were to some extent ($r = +.52$, significant at the 5 percent level, in tamarack and $r = +.64$, significant at the 1 percent level, in yellow birch). But in each species the significance of the correlation depended upon the southernmost provenance. Without these provenances, which were the latest to flower and burst bud in both species, the correlation coefficients were smaller and not significant ($r = +.14$ and $r = +.41$ in tamarack and yellow birch, respectively).

Time of flowering was not as good a measure of phenological variation as time of bud burst. Sparse flowering in many provenances and an apparently greater tendency for time of pollen shed to be affected by exposure to sunlight than time of bud burst both contributed to higher error mean squares in the flowering analyses. However, geographic patterns of variation were similar for the two characters.

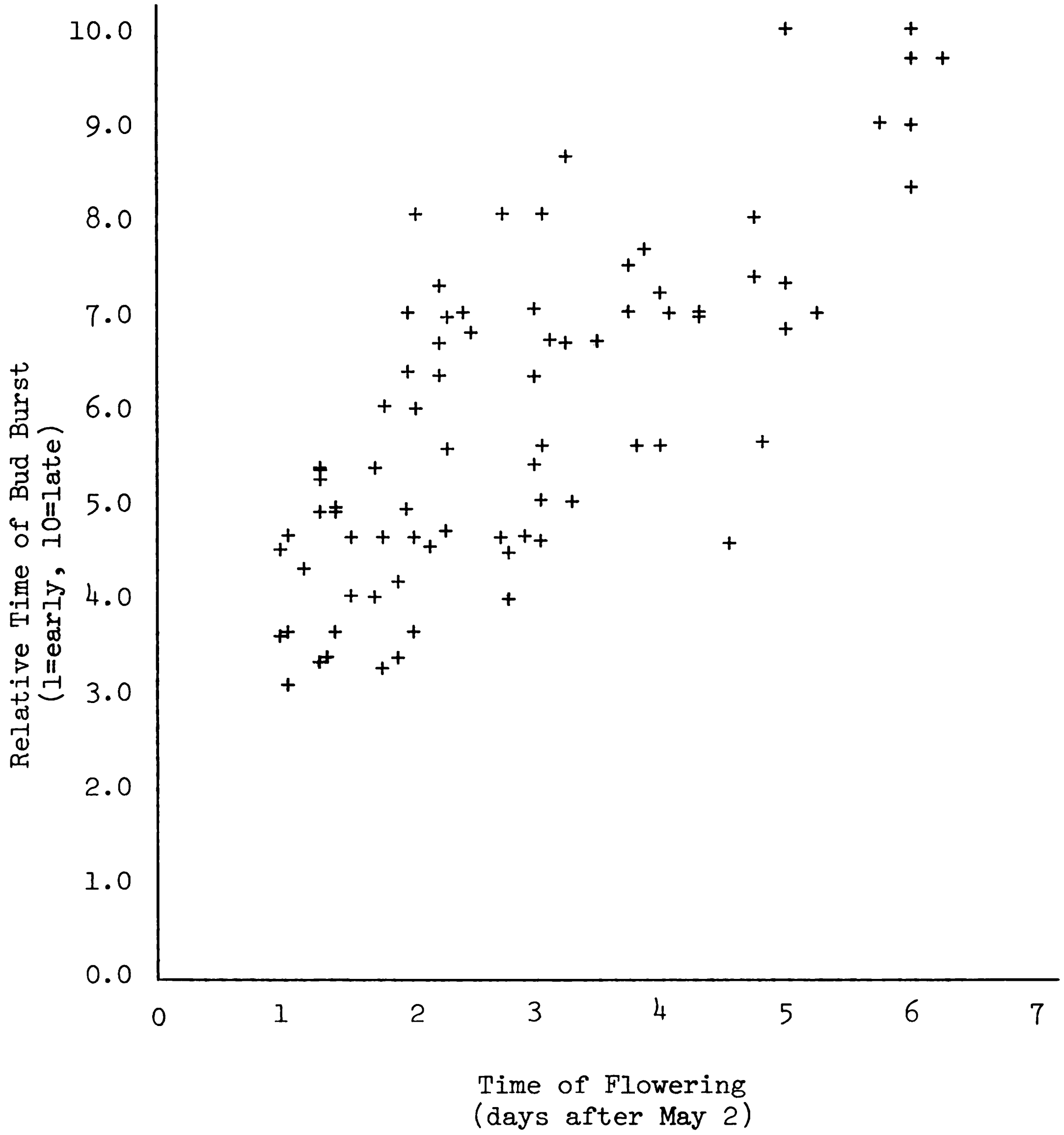

Figure 15.--Relation between time of flowering and time of bud burst in *Pinus banksiana* provenances (r = +.76, significant at the 1% level).

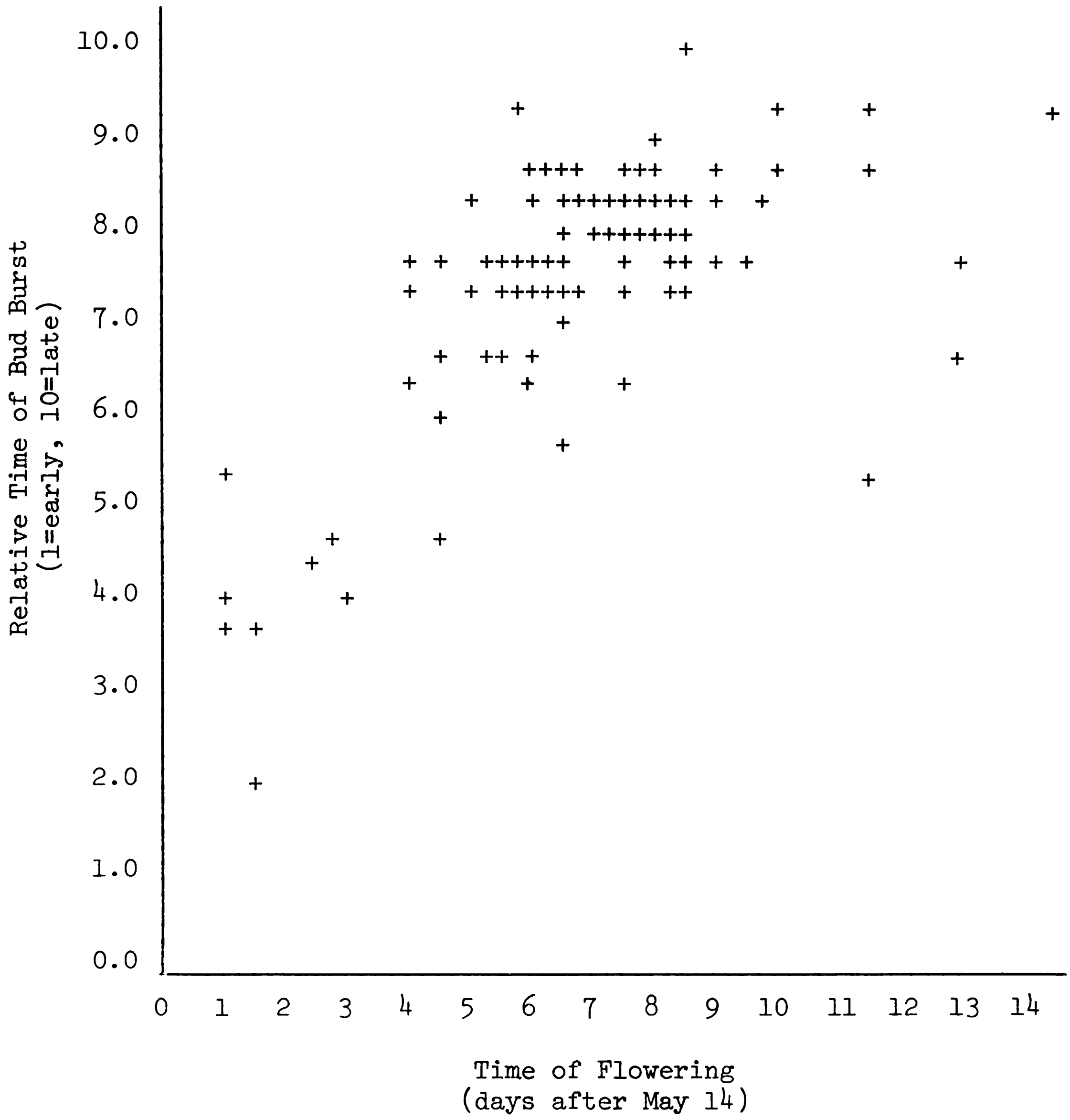

Figure 16.--Relation between time of flowering and time of bud burst in Pinus sylvestris provenances (r = +.63, significant at the 1% level).

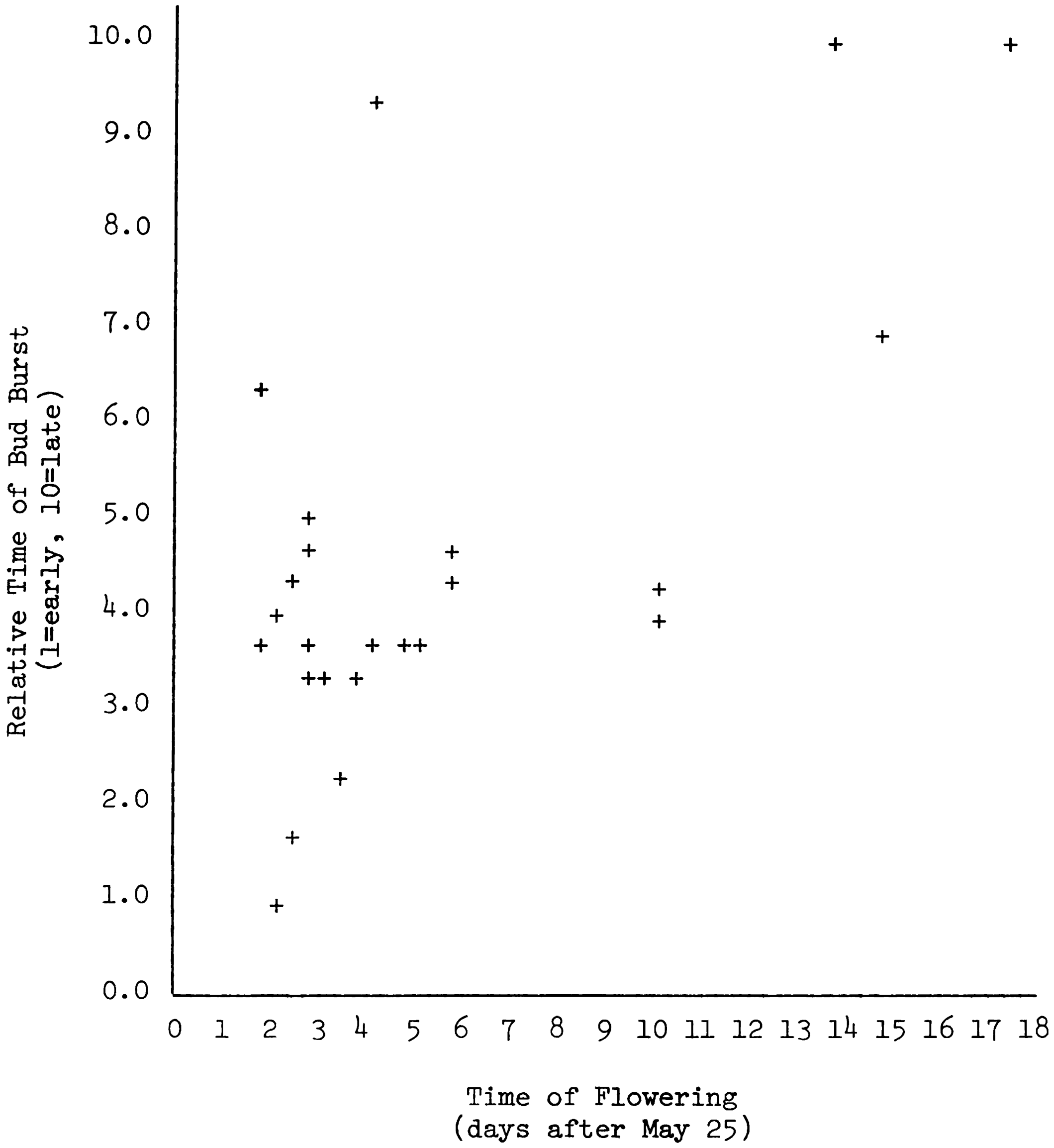

Figure 17.--Relation between time of flowering and time of bud burst in Pinus nigra provenances (r = +.67, significant at the 1% level).

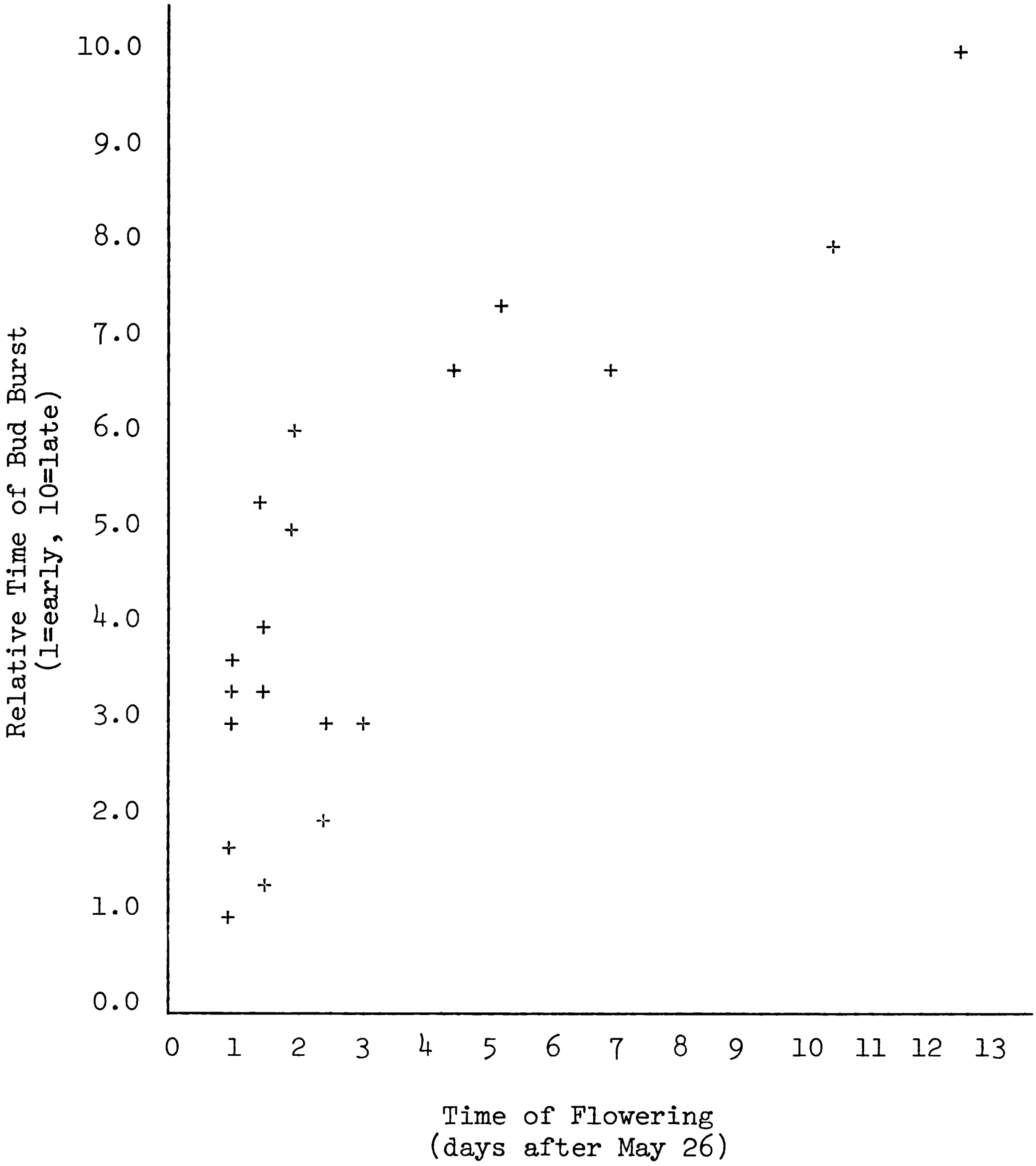

Figure 18.--Relation between time of flowering and time of bud burst in Prunus serotina families (r = +.82, significant at the 1% level).

In nearly all cases where time of bud burst was significantly correlated with latitude, longitude, or elevation, the same was true of time of flowering, although correlation coefficients were usually smaller. In all correlations the sign of the coefficient was the same for both characters. Thus, the discussions of geographic variation in time of bud burst probably apply in general to time of flowering, also.

UTILITY OF THE RESULTS

Genetic variation in time of flowering can determine the ease with which provenances may be cross-pollinated. While there are techniques to accelerate or delay time of pollen shed for artificial pollination, differences in this character of the magnitude observed in some species could affect crossing patterns in seed orchards. However, there is no direct measure of the significance to tree breeding practices and goals of genetic variation in time of bud burst. The value of this character lies in its relation to more economically important traits such as height growth, pest resistance, and susceptibility to damage by spring frosts.

HEIGHT GROWTH

Yearly growth in height is a function of the rate and duration of growth in each growing season. Since the latter is determined by the times of growth initiation and cessation, time of bud burst would appear to be one determinant of long-term growth rate. In support of this, several studies of different species have shown total growth to be correlated with duration of growth (Hellum, 1967; Holst and Yeatman, 1961; Perry *et al.*, 1966; and Rehfeldt and Lester, 1966). However, other studies have shown a small or no relationship between total growth and duration of growth (Bengston *et al.*, 1967; Boyer, 1970; Jensen and Gatherum, 1965; Lester, 1970; Reck, 1972; and Walters and

Soos, 1963). In these cases variation in rate of growth apparently predominates in determining variation in total growth.

Furthermore, even assuming that duration of growth is a major factor in height growth, genetic variation in duration appears to be more determined by time of growth cessation than by time of growth initiation. In most species studied, the magnitude of genetic variation in time growth cessation is greater than that in time of bud burst (Nienstaedt, 1974). Thus, several studies in different species have shown that variation in total growth is more related to time of growth cessation than to time of bud burst (Burley, 1966b; Rehfeldt and Lester, 1966; Roche, 1969; and Teich and Holst, 1969).

To illustrate the small effect that time of bud burst can have on genetic variation in overall rate of growth, the earliest varieties of Scotch pine to burst bud at Kellogg Forest in 1973 are also the slowest growing (Table 4 and Wright _et al_., 1966). The converse would be true if other determinants of growth were equal among varieties; so variation in time of bud burst must have a relatively small effect on variation in height growth. Similar examples could be drawn from many other species. Thus, it appears that genetic variation in time of bud burst will play a small part in initial improvement in growth rate, although it could conceivably be important if other components of growth were already maximized.

PEST RESISTANCE

The occurrence or success of an insect or disease attack upon a plant can depend upon the plant's stage of development when the attack

occurs. For example, Siggers (1955) associated greater susceptibility to fusiform rust (Cronartium fusiforme) with early bud burst in southern pines. Trees with early bud burst may be more in phase with the seasonal development of the pathogen. Higher incidence of infection by Rhabdocline pseudotsugae on Douglas-fir is associated with earlier bud burst (Haddock *et al.*, 1967 and Schober, 1963), presumably because late trees burst bud after the fungal spores have been disseminated (Liese, 1932). Similarly, spruce budworm (Choristoneura fumiferana) is a serious pest of balsam fir because the emergence of over-wintering larvae is synchronized with the expansion of balsam fir buds (Graham and Knight, 1965); but best survival of the larvae depends upon infestation at a certain stage of bud development (Eidt and Cameron, 1971). Gerhold (1966) cited other examples of relationships between insect resistance and time of bud burst.

Painter (1951) classified such "evasion" of attack as "pseudo-resistance" in contrast to mechanisms which may confer resistance in a wider range of environments. Nevertheless, if phenological events in the plant and pest are geared to the same environmental factor (*e.g.*, temperature), genetic variation in time of development in the host species could result in consistent variation in susceptibility. Thus, variation in time of bud burst could be used to improve resistance to certain insects and diseases if more information were available on such relationships. Simple correlations between time of bud burst and resistance cannot be relied upon to indicate the presence or (especially) absence of relationships. In some cases early and late trees can be equally resistant and intermediate ones most susceptible

(Eidt and Cameron, 1971) -- and the relationship would not be evident in the correlation coefficient.

RESISTANCE TO SPRING FROSTS

It is well established that variation in time of bud burst can strongly affect variation in damage by late spring frosts. Such a relationship has been found, for example, in *Picea abies* (Holzer, 1969b; Kiellander, 1970; Langlet, 1960; and Langner and Stern, 1964), Douglas-fir (Schober, 1963 and Schönbach, 1961), white spruce (Nienstaedt and King, 1970), and balsam fir (Lester, 1970). Selection for late bud burst may be the best means available for improving resistance to late spring frosts (Holzer, 1969a). Genetic variation has been found in the time at which cold hardening begins in the autumn (Smithberg and Weiser, 1968) and the ultimate degree of mid-winter cold hardiness (Maronek and Flint, 1974), but there is little evidence of genetic variation in physiological cold resistance at the time of bud burst.

Comparisons between phenological data and amount of frost damage are possible for four of the Kellogg Forest provenance tests: tamarack (plantation 6-69), balsam fir, white spruce, and Douglas-fir. The tamarack plantation furnished the only indication of a relationship between time of pollen shed and frost damage to male strobili. Bud burst and flowering in this species both occurred well before the last frost. While needles appeared to be resistant, however, many of the male strobili were apparently damaged by a severe frost which occurred in the middle of the period of flowering. Damaged strobili were arrested in development and eventually dried without shedding pollen. No data were collected, but one difference among provenances was very obvious -- on many provenances nearly all strobili were at least partially killed, but the very late-flowering Maryland trees sustained virtually no damage. Also, it appeared that early provenances completed pollen shed before damage occurred.

Lester (1970) measured time of bud burst and damage by spring frost in the nursery phase of the balsam fir provenance test. Amount of frost damage was associated with differences in time of bud burst; trees which burst bud late tended to be least damaged. The geographic pattern of variation in amount of frost damage (Lester, 1970) is similar to the pattern of variation in time of bud burst in later years at other locations (Figure 4).

Among 25 white spruce clones selected for early or late bud burst, late clones were significantly less damaged by frosts occurring in two different years (Nienstaedt and King, 1970). However, in the provenance test of this species planted at Kellogg Forest and two other Michigan locations, relative frost damage among the provenances has not been consistent (Wright _et al._, unpublished manuscript). This could occur if new growth in white spruce is most susceptible just after bud burst and rapidly becomes more resistant with maturity. Thus, the date of the frost could determine relative damage as much as time of bud burst. According to time of bud burst at Kellogg Forest in 1973, the least damaged provenances were early, intermediate, or late depending upon the year or location of damage.

Data taken in different years at three southern Michigan plantations furnished good evidence of a relationship between frost damage and time of bud burst in Douglas-fir (Steiner and Wright, 1974). Relative damage among races was consistent among environments, particularly within plantations, and corresponded with time of bud burst at Kellogg Forest in 1973 (Figure 19). In general, the earliest races sustained the most damage. However, the ARINEM race was less damaged than expected on the basis of its earliness of bud burst, particularly at Kellogg Forest. Height may play a role in frost susceptibility secondary to that of time of bud burst. The ARINEM race is the tallest (over twice the height of the NOCOL race), and the trees may have escaped damage by light frosts, which are most severe near ground level.

Figure 19.--Relative extent of frost damage on Pseudotsuga menziesii races at different plantations and years. Races with most damage (percent of new shoots killed) in each plantation and year, from left to right: NOCOL -- 37%, NOCOL -- 26%, NOCOL -- 62%, SOCOL -- 36%, ARINEM -- 29%, SOCOL -- 78%, ARINEM -- 95%. Races are arranged in opposite order of bud burst at Kellogg Forest in 1973: ARINEM was earliest and NOROC was latest. From Steiner and Wright (1974).

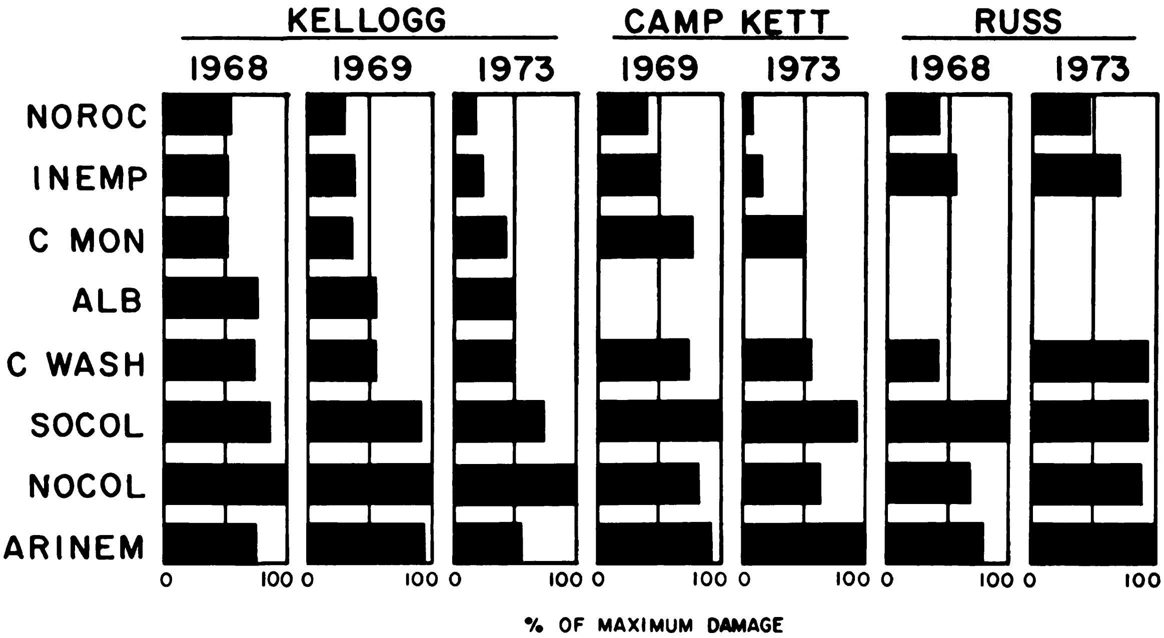
KELLOGG
CAMP KETT
RUSS
1968
1969
1973
1969
1973
1968
1973
NOROC
INEMP
C MON
ALB
C WASH
SOCOL
NOCOL
ARINEM
0
100
% OF MAXIMUM DAMAGE

Figure 19.

SUMMARY

Genetic variation in time of bud burst was studied in replicated, Lower Michigan provenance tests of 15 species: balsam fir, yellow birch, tamarack, white spruce, jack pine, limber pine, border pine, European black pine, ponderosa pine, red pine, eastern white pine, Scotch pine, Virginia pine, black cherry, and Douglas-fir. Genetic variation in time of flowering was studied in eight species: yellow birch, tamarack, jack pine, European black pine, red pine, Scotch pine, Virginia pine, and black cherry. With the exceptions of the balsam fir, tamarack, black cherry, and Douglas-fir experiments, plantations contained provenances from virtually all parts of the native ranges. The black cherry experiment was the smallest with eight provenances represented.

In all species except red pine there was significant variation among provenances in time of bud burst. In general, results were consistent with those observed in other years in the same plantations, other plantations of the same provenance tests, and other provenance tests of the same species. Most species shared certain geographic trends in variation. Northern, interior, and eastern Upper Peninsula (Michigan) provenances burst bud earlier than southern, near-coastal, and western Upper Peninsula provenances. There appeared to be no relationship between elevation of origin and time of bud burst (independent of latitude), but deviations from the latitudinal trend in limber and ponderosa pines can be explained by the effect of topography on climate.

Variation among central and northern Rocky Mountain provenances of these species was small and essentially geographically random. There were few conspicuous instances in any species in which deviations from general trends could not be attributed to regional climatic anomalies or peculiarities of the species.

Multiple regression analyses in four species between time and bud burst and 12 climatic variables yielded highly significant prediction equations for time of bud burst in each species. But they failed to indicate which variables may have been important in the evolution of the common patterns of variation. Adaptation was probably a compromise involving many factors of the year-round climate. However, continentality -- sometimes expressed as the mean annual range in temperature -- corresponded generally well with the geographic patterns in genetic variation. Earliest provenances in most species were native to regions with the most continental climates (*e.g.*, central Canada, interior Alaska, and northeastern Siberia).

The geographic pattern of variation in time of bud burst in Douglas-fir was the opposite of that in all other species: southern provenances were earlier than northern provenances and provenances closest to the Pacific Coast were early for their latitudes. This could occur if this species bursts bud in response to photoperiod and the others burst bud in response to temperature, or if Douglas-fir trees were not chilled sufficiently to completely remove winter dormancy.

Some provenances in four species were represented by several half-sib families each. None of eight provenances of limber and border pines contained significant variation among families in time of bud burst. However, significant genetic variation was found within two of six balsam fir provenances and one of five black cherry provenances. Within these three provenances the magnitude of differences approached or equalled those observed in the respective entire plantations.

In all species studied except red and Virginia pines there was significant variation among provenances or families in time of flowering. This trait was significantly correlated with time of bud burst among provenances or families in all species. The degree of correspondence between the traits was better in species in which flowers and shoot systems arise from the same buds.

Genetic variation in time of bud burst could be important in breeding for improved resistance to some insect and disease pests and to damage by late spring frosts. Frost damage in three Lower Michigan plantations of Douglas-fir was correlated with relative time of bud burst of the provenances. Early provenances were most damaged.

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