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A COMPARISON OF SEASON OF CAMBIAL GROWTH IN DIFFERENT GEOGRAPHIC RACES OF *PINUS PONDEROSA*

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Introduction

Ecotypic specialization in different parts of the ranges of widely distributed species is a phenomenon that has commanded the attention of botanists for several decades. Experience has usually shown that when plants are moved from their native habitat into a different environment they become subject to injuries from factors associated with the new environment, although occasionally they may prove more successful. The slow genetic fitting of plant populations to the peculiarities of the area which they have occupied for a long time is especially important in the artificial establishment of forests, for usually there are available for use in plantations seed lots representing the same species but from populations attuned to widely different environments. The long life-cycle of the tree makes it possible to invest much time

and money in reforestation before genetic weakness becomes apparent; moreover, the unsuccessful planting may be expensive to remove, and by cross pollination it may seriously contaminate near-by native trees. In recognition of this problem the United States Forest Service established an experimental plantation of *Pinus ponderosa* Laws. in northern Idaho, with the purpose of determining the relative value of seeds from different parts of its area for use in reforestation in northern Idaho.

Between 1911 and 1917 seeds or seedlings from twenty-two localities were planted in contiguous plots at the Priest River Experimental Forest in Bonner County, Idaho. The habitat is an upper river terrace mantled with sandy loam. Climate and soil in this region permit *P. ponderosa* to grow well under open conditions, but the environment is too cool for

satisfactory natural germination or satisfactory growth after the forest approaches maturity. This choice of location for the experiment has considerable bearing upon the practical application of the findings¹ but is of little consequence from the purely scientific standpoint; for, although the climate here may generally be unsuited for the commercial planting of this species, it is at least conducive to the growth of the trees in young plantations and therefore may be considered adequate for a comparative test of racial differences under uniform environment.

Twenty-two to 26 years after the seeds germinated the results were described by WEIDMAN (6). His report described the origin of the populations, climates of those regions, arrangement of the plantation, native vegetation and soils, and the following attributes of the populations: number of needles in the fascicle, length and persistence of needles, anatomy of needles, general appearance of foliage, and heights and diameters at ages of 22 or 23 years. In summarizing all the observations, WEIDMAN tentatively grouped the populations into four geographic races.

Some of the populations planted at the Priest River Experimental Forest have suffered very high mortality, and one (Shasta) was completely exterminated by a sudden drop of temperature from 7° to -25° C. within 20 hours in December, 1924. Appraisal of injury that may be attributed specifically to this sudden drop in temperature showed that the Siskiyou, Santa Fe, and Coconino races also suffered heavily, although devastation was not complete as with the Shasta race (4).

¹ Another study of ten populations of *P. ponderosa* from different regions, in which each population was distributed among six widely different habitats, showed that relative rates of height growth cannot be predicted for one habitat on the basis of comparisons made on another (5).

The hypothesis has been advanced that trees suffer from autumnal frost as a result of continuing some phase of growth activity too late in the season (3, 7), and WEIDMAN suggested this as a possible explanation for heavy mortality in some races: "Presumably the long period of growth activity characteristic of . . . Siskiyou progeny, has been one of the causes of the frost damage suffered by the latter in northern Idaho" (6:879). One of the objects of the present study was to determine if the races experiencing high mortality terminate radial growth of their stems relatively late in the season.

Studies by the writer of a number of species of trees growing some 177 km. (110 miles) south of the Priest River Experimental Forest indicated that day-length exerts a marked control over the date of commencement of cambial growth in some species, although this was not true of the specimens of *P. ponderosa* of unknown and possibly different geographic origin which were included in that study (2). It was evident that the collection of races of known origins at the Priest River Experimental Forest representing nearly 14° of latitude could provide conclusive information on this problem, and, consequently, this question represents a second object of the present study.

Since WEIDMAN's report did not include records of the season of cambial activity, permission was requested to study the trees from this standpoint. The writer is grateful to the United States Forest Service for making the experimental plots available and for assistance in reading dendrometers which the writer installed. Further support was given the project by funds provided for biological and medical research by the State of Washington Initiative Measure N. 171.

Figure 1 shows the total geographic area of *P. ponderosa* (incl. var. *scopulorum* Engelm. which the southernmost stations, at least, represent) and the points of origin of the populations selected for the present study. The populations are referred to by name of the National Forests in which they were collected.

Methods

Dial-gauge dendrometers of a type (1) which the writer has compared with similar instruments and found eminently more successful were used in this investigation. Instruments were installed in the autumn of 1947 and records maintained throughout 1948. During the period



FIG. 1.—Origins of populations considered in this study, as related to total range of *Pinus ponderosa*, including var. *scopulorum*.

when growth was expected to begin, readings were made at intervals of usually less than 1 week, but at other seasons longer periods elapsed between observations, depending upon the state of cambial activity.

For most trees of temperate latitudes, day-to-day diameter increase is a regular phenomenon only during the main period of growth. During the dormant season trunks commonly exhibit periods of shrinkage which are associated with series of dry days in the latter half of the summer, or subfreezing weather in winter. They may also swell intermittently. It is consequently very difficult to establish a precise date for the beginning and end of growth, but the date for completion of 5% and 95% of the season's increment may be approximated by interpolation, with very little probability of error owing to the smoothness of the curve once the cambium becomes active. Radii as measured on December 30, 1947, and on November 12, 1948, seemed least affected by frost shrinkage, and the differences between these readings were used in calculating growth on a percentage basis.

Results and discussion

A striking feature of the results was the variation exhibited by different trees from the same point of origin. In other studies by the writer three vigorous trees selected to represent a population have always showed reasonably close similarity in behavior, but at the Experimental Forest there was so much divergence among individuals which averages would obscure that, in presenting the results, the data for each tree are kept separate. It is obvious that statistical significance cannot be claimed for any of the results, but since they, for the most part, reveal little differences among the populations,

the main question which prompted the study can be answered with reasonable assurance of accuracy. The conclusions which may be drawn from the data represented by figure 2 are as follows.

Nearly all populations began growth after mid-May and completed growth in late August. Median dates for the 5%, 50%, and 95% levels were May 23, June 21, and August 22. The Coconino population was an exception in that its cambial growth began about 2 weeks later² than the average for all groups. The mid-point in its growth was proportionately late as well. The Harney population, represented by only two trees, also began growth distinctly later than average for all groups. Here, however, the rate of growth was exceptionally rapid once the cambium became active, so that its mid-point was not delayed and, in fact, was reached earlier than in certain of the other groups.

The Helena, Bitterroot 2200 m. (7200 ft.), and possibly Ashley populations all terminated their growth a little in advance of the others, although they had not begun to grow earlier in spring than most of the others. Except for one tree, the growing season of the Coconino population was shorter than average as a result of postponement of inception in spring, whereas the Helena, Ashley, and Bitterroot 2200 m. races exhibited slightly shortened growing seasons owing to earlier cessation of growth in late summer.

The Bitterroot populations representing different altitudes (1200 [4000 ft.] and 2200 m.) differed only in that the race from the higher altitude ceased growing earlier. In view of this evidence of racial differentiation in *P. ponderosa* according

² Lateness also characterizes the beginning of apical growth in this population (6).

to altitude, all results from the comparative plantation may be strongly conditioned by the elevation from which the populations originated. However, the physical data of altitude that are available (6) cannot be interpreted closely because the character of biologic environment in mountains depends upon the direction of slope exposure as much as upon elevation above the seas. The environment of the plantation at the Priest River Experimental Forest is close to the upper zonal (not altitudinal) limits of *P. ponderosa* in the Southern Selkirks, whereas the original habitats of the pop-

ulations may have been from the upper, middle, or lower parts of the total elevational ranges in the other mountain systems. Therefore, the change in zonal status in some cases may have reduced and in others augmented the temperature difference involved in latitudinal displacement.

WEIDMAN (6) suspected that the heavy mortality suffered by the Siskiyou population subsequent to planting might have resulted from too late an extension of the growing season in the autumn, for this population originated from a very mild climate. The present study, how-

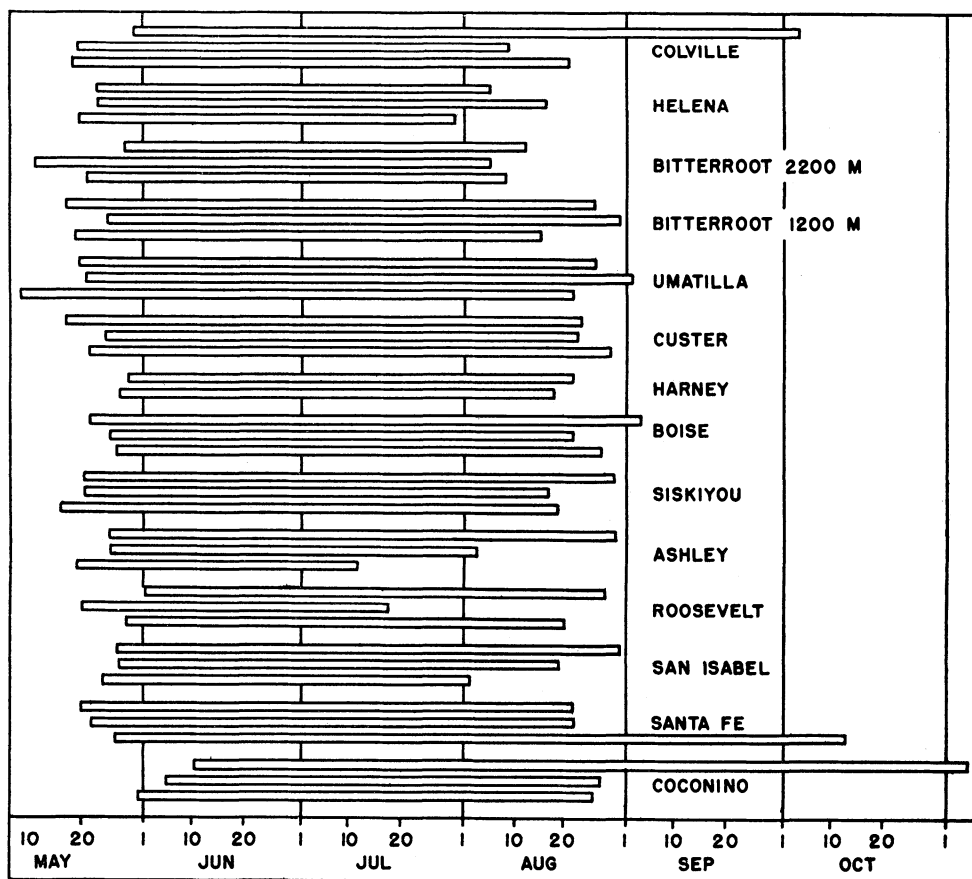


FIG. 2.—Principal period of cambial activity of each tree studied, based on period starting when 5% of total annual increment was recorded and ending when increment was 95% completed.

ever, does not substantiate this hypothesis. Among the Siskiyou, Bitterroot high altitude, Santa Fe, and Coconino populations, all of which have suffered high mortality, it might be suspected that climatic selection has eliminated biotypes that continued growth relatively late. But the fact that three of the forty-one trees studied continued cambial growth a full month later than all others without exhibiting ill effects therefrom indicates that the others do not exploit the potential growing season to the extent of its possibilities. If selection had operated upon this character, one would expect the survivors of the decimated populations to include a high percentage of individuals that continue growth rather late. But this is definitely not true. If the deceased trees were ones that continued growth late, they must have differed to a very great extent from the survivors. The conclusion therefore seems warranted that the termination of cambial activity is strongly determined by autogenous forces and occurs well in advance of the onset of critically low temperatures. Climatic selection must have operated on physiologic characters other than lateness of cambial activity.

Although there is considerable difference among individuals within one population, there is a striking similarity in periods of radial growth among populations originating in widely different climatic types and latitudes. This contrasts sharply with the relatively uniform appearance of trees within each population but distinct difference in appearance among the populations (6).

Deviations of particular populations

from the growth pattern of the species as a whole exhibit no geographic trends. Daylength either does not determine the beginning of cambial activity or on this habitat other conditions masked the influence of daylength. Since the results of earlier studies (2) of a population of unknown origin growing in a grassland climate also furnish negative evidence of photoperiodic control over inception of cambial activity, the former of the two possibilities mentioned above appears to be correct.

Summary

1. Radial growth was studied in forty-one trees including *Pinus ponderosa* Laws. and its var. *scopulorum* Engelm., during the calendar year 1948. These trees represented populations obtained from known sources over a wide area in the western United States and had been growing on the same habitat at Priest River Experimental Forest in northern Idaho since 1911-1917.

2. Median dates for completion of 5%, 50%, and 95% of total radial growth were May 23, June 21, and August 22. Although there was considerable variation in growing seasons within populations, there was but little difference among the populations. Susceptibility to frost damage does not appear to be correlated with radial growth that continues late in the season. In these fourteen populations representing nearly 14° of latitude, daylength appears to exert no influence upon the growing season. Duration of cambial activity is not related to grouping of the populations into races on the basis of morphology and anatomy.

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EFFECT OF 2,4-D ON CARBOHYDRATE AND NUTRIENT-ELEMENT CONTENT AND ON RAPIDITY OF KILL OF SOYBEAN PLANTS GROWING AT DIFFERENT NITROGEN LEVELS¹

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Introduction

The physiological response of plants to the selective herbicide 2,4-dichlorophenoxyacetic acid (2,4-D) is for the most part an unexplained phenomenon. Some species are readily affected, whereas others are more or less resistant. Most of the grasses are particularly resistant to injury from the usual applications of 2,4-D. Occasional informal reports have indicated that rapidly growing plants are more easily destroyed by 2,4-D than are those growing slowly. Some investigators (4, 5, 8) have suggested that the herbicidal properties of 2,4-D are related to the carbohydrate storage and nitrogen metabolism of plants.

In an experiment to determine the relative effectiveness of 2,4-D on soybean plants growing at different nitrogen levels, a pilot experiment was conducted by the senior author in 1947. Duplicate pots of Chief soybeans were grown in the

greenhouse in sand culture at three nitrogen levels—high (336 p.p.m.), medium (56 p.p.m.), and low (14 p.p.m.)—and then a drip aqueous solution of 20 p.p.m. 2,4-D (the sodium salt of 2,4-D was used) was added to the cultures. Plants growing on high nitrogen were affected much more rapidly than were those growing at low and medium levels. Plants growing on low nitrogen were least affected, and the plants on medium nitrogen were between the low- and high-nitrogen plants in response to 2,4-D.

The results of this test were of sufficient interest to warrant further study of the effect of applications of 2,4-D on plants growing at different nitrogen levels. Therefore, an attempt has been made to relate growth status with the speed and intensity of plant response to 2,4-D applications and to determine certain associated physiological changes.

Material and methods

Three plants of the Lincoln variety of soybeans were grown in sand culture in the greenhouse in each of twelve glazed 2-gallon pots from February 27 to April 23, 1948. Until the plants reached the six-leaf stage, a uniform nitrogen level was maintained by flushing the sand

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