FROM

TREE GROWTH

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Geographic Variability in Growth of Forest Trees

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Introduction

Tree growth, like all plant characters, is a product of the interaction of genes and environment; however, the genes, environment, and interaction are not the same for every individual of a species. Genes exert master control over the plant's growth mechanisms. They control mechanisms for responding to environment and for utilizing environment in growth. Usually many genes control growth, and their individual effects are thought to be additive. The contributions of the individual genes establish the genetically fixed range of tolerance of a tree. The environment supplies the raw material essential to the tree's manufacturing plant. All component parts of the environment—climate, soils, biota—must provide their share to the manufacturing process called growth. Deficiency or excess in any part can limit the process.

For growth to occur, the range of variation in environmental factors must fall within the range of tolerance of the genotype. Individual trees of a species grow in diverse environments, and to expect all individuals of a species to be genetically alike and to be adapted to all environments would be illogical. Rather, each tree should be expected to be peculiarly adapted to the extreme variations in its environment. Each tree arrives at its balance with its environment on its own genetic basis.

Populations of trees can be described in terms of average values, and these averages can be closely related to characteristics of local environment. Investigations of genetic variation within species show the relation between these characteristics of trees and their environments.

Much evidence is available to support the foregoing and following statements. The purpose of this paper is not to present a bibliography on one of the largest subjects in the field of forest genetics. Review and summaries of the world knowledge on this subject already abound. Only selected references will be cited in support of statements and viewpoints. Primarily, reference will be made to research on *Pinus ponderosa* Laws. in which the writer has participated.

Genetic Controls of Growth Demonstrated in Progeny Tests

Progeny tests are the main tool which scientists have employed to demonstrate genetic variation in growth. A progeny test exposes genetic differences by bringing different genotypes together under one set of environmental conditions. Replication under a variety of environments brings forth each tree's genetically-fixed range of tolerance for factors of its environment, and replication exposes interactions between genotype and environment in growth control.

Genetic control over growth differs extensively between widespread populations of trees. Even crude tests comparing progenies from remote areas make this genetic change most obvious. Whenever seeds from many widespread sources are planted in one or more localities, genetically controlled growth differences catch the eye. The observer is struck by genetic differences in seeds, in germination behavior, in morphology of foliage, stems, and roots, in the periodicity, rate, and amount of shoot and root growth, and in many other characters (Langlet, 1938; Critchfield, 1957).

The closer two populations are to one another, the more obscure differences between them generally become. The growth differences between local populations close to one another are quite subtle. To uncover these differences, critical tests must employ rigid statistical or physical controls over environmental variation. Ponderosa pine progeny tests at the Institute of Forest Genetics at Placerville, California, illustrate this point. The purpose of these tests was to determine genetic differences between individuals and populations along a 50-mile transect covering 7,000 feet elevational rise on the west face of the Sierra Nevada. Replication and randomization were incorporated into the design of the tests. Hence, the investigator could estimate closely the environmental variation and split out the genetic variance.

Genetic growth potential does not vary much between neighboring trees on this transect. Callaham and Hasel (1961) recently

completed analyses of a test of progenies of eighty-one individual ponderosa pines in California. Growth was analyzed after 15 years. Some populations and individuals exceeded expected growth considering both the elevation of their parents and their nursery performance. Other individuals and populations fell well below expectation (Fig. 20–1). The factors related to such significant departures from normality are not known, but site factors undoubt-

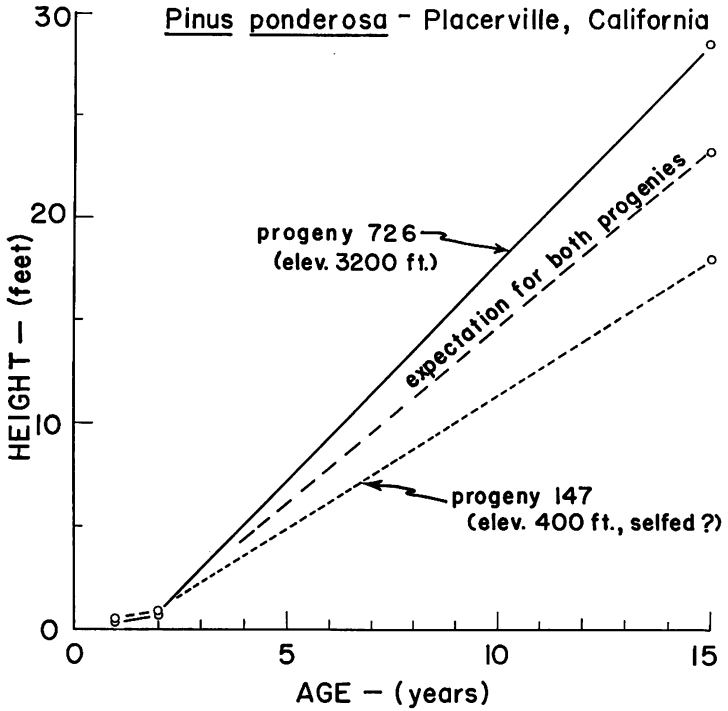

FIG. 20–1. Growth of the best and next to poorest of 81 progenies. The same 15-year heights were expected for both based on second-year height growth, elevation, and elevation [2].

edly have played a dominant role in evolution of local genetic growth variations (Squillace and Bingham, 1958a). In no case did the progeny of any seed tree differ significantly in height at fifteen years from the progenies of two to eight neighboring trees.

Of course, this does not mean that outstanding trees cannot be found. Many "elite" trees have been found which pass on to their progenies unusual genetic growth potentials. The quest for such super trees is world-wide, yet only rarely does the seeker find extraordinary germ plasm. Close neighbors in the forest usually

have evolved similar genetic growth controls. Two evolutionary forces both act to equalize individuals within populations. Cross-fertilization provides gene exchange, and environmental selection weeds out the nonadapted individuals.

In addition to the foregoing conclusions on growth, progeny tests have produced another item of basic information. Estimates of the heritability of height growth come from two ponderosa pine studies (Callaham and Hasel, 1961; Squillace and Silen, 1960). Heritabilities of height growth in the broad sense were 0.39 and 0.36. These values, although not high, indicate that a significant 36 to 39 per cent of the variations in height growth can be attributed to genetic differences.

Many genes contribute to genetic control over growth. Tests of progenies produced by controlled breeding show this through the pattern of inheritance of growth characters. The growth of offspring most often is intermediate between growth of parents. This is true whether crosses are analyzed between adjacent populations, or between races or subspecies, or between species themselves. Such intermediacy indicates multiple factor control of growth characters.

Crossing one tree with itself or a close relative, called selfing or inbreeding, further illustrates genetic control of growth. In progeny tests selfed or inbred lines are compared with their outcrossed parents; typically, vigor is depressed (Orr-Ewing, 1957; Squillace and Bingham, 1958b). The genetic interpretation is that deleterious genes become homozygous. One point of importance to growth discussions is that progenies from selfing do not give a true measure of the genetic worth of a seed tree. Seeds from isolated trees should be taken with caution; they are likely to be the fruits of self-pollination and to produce slow-growing seedlings (Callaham and Hasel, 1961) (Fig. 20–1). In stands of forest trees, self-pollination might be a general problem. However, evidence has accumulated that outcrossing is favored and that selfing is disfavored through a process called selective fertilization (Squillace and Bingham, 1958b).

Juvenile Growth: Preview to Mature Growth

Long-term progeny tests elucidate the link between juvenile and mature expressions of growth. From 49 to 72 per cent of the variation in height growth at 15 to 40 years can be related to height growth during 2 years in the seed bed (Callaham and Hasel, 1961; Squillace and Silen, 1960) (Fig. 20–1). Hence, early heritable

growth differences forecast later growth differences, and much can be learned from a progeny test in a few years.

Several non-genetic factors play a dominant role in early growth and can obscure heritable differences. Seed size partially determines germination time, and both strongly influence early growth (Callaham and Hasel, 1961; Squillace and Bingham, 1958b; Righter, 1945). The scientist has to account for environmental variation from these and other non-genetic causes when analyzing genetic variations in early height growth.

Climate Partly Determines Growth

Features of the climate are other non-genetic factors regulating all growth. Climate influences growth within a genetically fixed framework. Within this framework the plasticity of the phenotype can be seen as climatic factors vary.

Every introductory plant physiology textbook points out the partial control of growth by temperature, daylight, and moisture. Each has a strong influence on tree growth from the first division of the embryo to reproductive maturity. Temperature governs the rate of all growth processes, and extreme temperatures can determine survival. Growth generally occurs under a broad range of temperatures, but the best growth occurs at an optimum temperature between lethal high and low temperatures. Light varies in intensity, quality, and duration; in all its aspects light influences the growth process. Water is required for all plant life, of course. While a tree cannot exist without this trinity—heat, light, and water —research has demonstrated genetic differences within species in requirements for each of them. A few examples of genetic differences within ponderosa pine in requirements for these elements of climate will be examined.

Germination Rate. The rate of germination of tree seeds is governed primarily by temperature, given adequate moisture and light, of course. Germination proceeds most rapidly at some optimum temperature. This optimum differs from the optimum temperature for other growth characters. Furthermore, the genetically-fixed optimum temperature for germination is not the same for all trees or for all populations of a species (Critchfield, 1957; Olson *et al.*, 1959).

Studies of ponderosa pine illustrate this genetic variation in germination response to temperature (Callaham, 1959). Speed of germination was determined for lots of 10 seeds (Fig. 20–2). Each

lot represented up to five wind-pollinated progenies from each source. Incubation was at five constant temperatures—8°, 16°, 24°, 30°, and 36° C.

Broad geographic differences were noticeable immediately. Within one week, germination was under way at 24°, 30°, and 36° C. for progenies from sources east of the Rocky Mountains. The optimum temperature was somewhere between 24° and 30° C. Progenies from the Southwest behaved in the same manner except

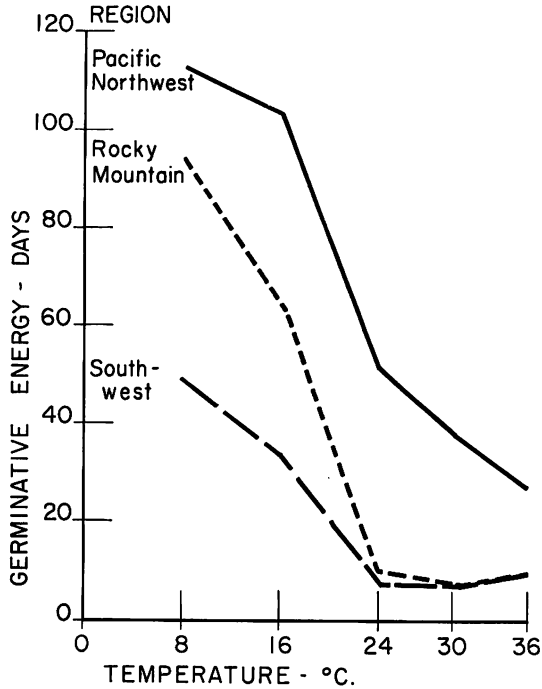

FIG. 20–2. Mean germinative energy at five incubation temperatures for ponderosa pine progenies from a number of field plots in three regions.

for one significant difference. Only a very few of the Southwest seeds germinated at 8°; yet, at 16° germinative capacity and energy were high. Progenies from the Pacific Northwest, including California, Oregon, and Washington, germinated three to six weeks later; their temperature optimum was at 36° C. or higher.

Variations among progenies within sources, although subtle, showed that optimum temperatures differed for individuals (Fig. 20–3). The cumulative germination for each of two trees growing near Corvallis, Oregon, shows a high temperature optimum for one tree (No. 5) and a low temperature optimum for the other tree

(No. 2). This one example suffices to illustrate the genetic diversity present within local populations.

Moisture relations during germination also illustrate genetic differences. Squillace and Bingham (1958a) found differences between progenies in their ability to take up water from a sugar solution during germination. Progenies from trees "as little as one-half mile apart in continuous *Pinus monticola* stands" showed dis-

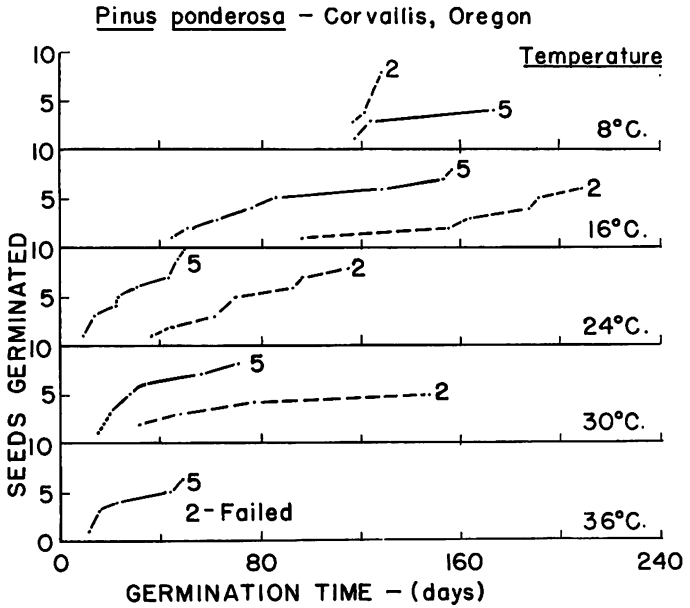

FIG. 20–3. Cumulative germination at five incubation temperatures for lots of ten seeds from each of two ponderosa pines near Corvallis, Oregon.

tinct genetic differences in this character. This was one of the first demonstrations of an inherent distinction between local populations on the basis of uptake of water needed for germinative growth.

SEEDLING GROWTH. Following germination, seedling development is dominated by temperature and light conditions, providing moisture is adequate. Their independent effects on growth can be ascertained by the use of controlled environment facilities. Such "growth chamber" studies are limited in the size of plants they can contain; hence, basic work on light and temperature effects has utilized seedlings in their first few seasons of growth. Tremendous inter- and intraspecific differences are found in seedling growth response to controlled change in lighting and heating.

Photoperiod can affect the inception and cessation of growth, establishing the duration of the growth period. This regulatory effect of daylength and, more important, nightlength has been demonstrated repeatedly. The onset and cessation of growth may be genetically fixed in relation to a particular photoperiod. Similarly, the length of the growth period may be fixed by some inherent "time clock." Such mechanisms probably have evolved in response to a particular length of growing season (Critchfield, 1957). Vaartaja (1959) and many others have shown that all individuals or

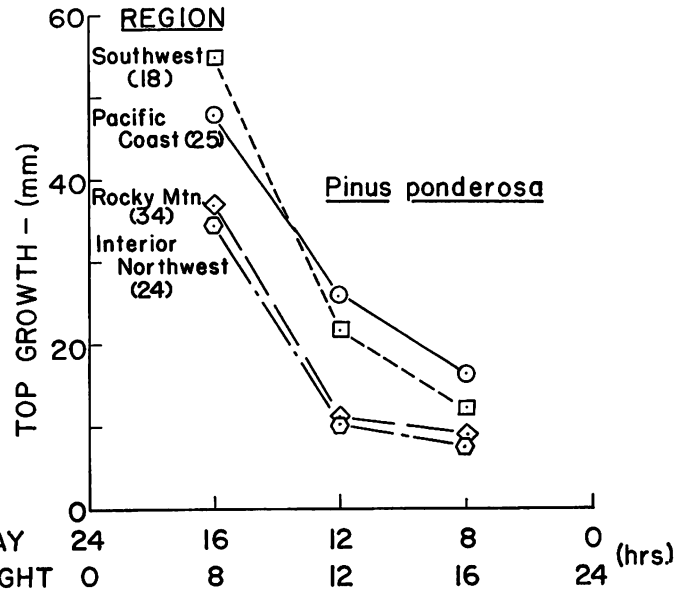

FIG. 20–4. Top growth of progenies of a number of ponderosa pines from four regions after 14 weeks of exposure to three daylengths.

populations of a species do not respond similarly to change in photoperiod. Evolution has led to a variety of genetic adaptations enabling plants to use the native photoperiod at their source as the clock by which to time their growth.

Studies of growth in relation to photoperiod for ponderosa pine from a variety of sources were conducted by Hellmers and Callaham in 1956. Progenies from 26 localities were grown under 16-, 12-, and 8-hour days at regulated optimum temperatures at the Earhart Plant Research Laboratories of the California Institute of Technology. During a 14-week period, average height growth increased with increasing day length for trees from all sources (Fig. 20–4). Progenies from trees growing in the Southwest—Arizona

and New Mexico—showed the greatest response to lengthening days. These Southwest trees are definitely different in their inherent growth controls from their neighbors to the north and east in the Rocky Mountains. Similar differences can be shown for other regions.

Temperatures primarily influence the rate of growth, although they sometimes influence growth period (Irgens-Möller, 1957; Kramer, 1957; Olson *et al.*, 1959). Kramer (1957) only recently made the first demonstration that trees have a thermoperiodic requirement for growth. Very little is known about the thermal requirements for growth of forest tree species, and even less is known of intra-specific variation in such requirements. Olson and his colleagues (1959) mention only briefly their tests of thermal requirements of *Tsuga canadensis* (L.) Carr. from fifteen sources.

Hellmers and the writer have unpublished data on thermal requirements for growth of ponderosa pine. Studies in 1956 of intraspecific variation in this species included progenies from 26 localities (in part different from the 26 referred to earlier). Growth was measured under nine combinations of three day temperatures, 30°, 23°, and 17° C. and of three night temperatures 22°, 14°, and 7° or 10° C.; daylength was an optimum 16 hours. The data (Fig. 20–5) lead to two conclusions. First, ponderosa pine grew best under relatively hot nights, 22° C. or higher, and under cool to warm days 17° to 23° C. Thus, ponderosa pine differs markedly from *P. taeda* L. which grows best under hot days and cool nights, according to Kramer (1957). Second, ponderosa pines from diverse parts of its range showed significantly different responses to variation in temperatures. Seedlings from east of the Rocky Mountains (Fig. 20–5 E, F) must have high night temperatures for good growth. The seedlings from the Southwest (Fig. 20–5 D) grew at a remarkable rate under cold days and hot nights. In contrast, Pacific Coast seedlings grew reasonably well at lower (14° C.) night temperatures (Fig. 20–5 A, B).

In the future, scientists will explore more of these inherent growth characters. As scientists discover what makes a tree "tick," they find that growth mechanisms of trees have evolved to be in harmony with the environment in which trees grow. Growth can be closely related to climate as many empirical studies have found. This reflects not a chance relationship but rather the product of an evolutionary process.

Tree Growth. According to the elementary texts, growth is related to temperature, light, and moisture. But how is growth related to climate? Only empirical studies of growth in a variety of climates

will give the answer. Such studies have been under way since the close of the nineteenth century. Langlet (1959, p. 16) reemphasizes this and points with just pride to his countrymen who were first to pursue their studies to fruition more than forty years ago. What is the relative importance of seasonal climate versus annual climate?

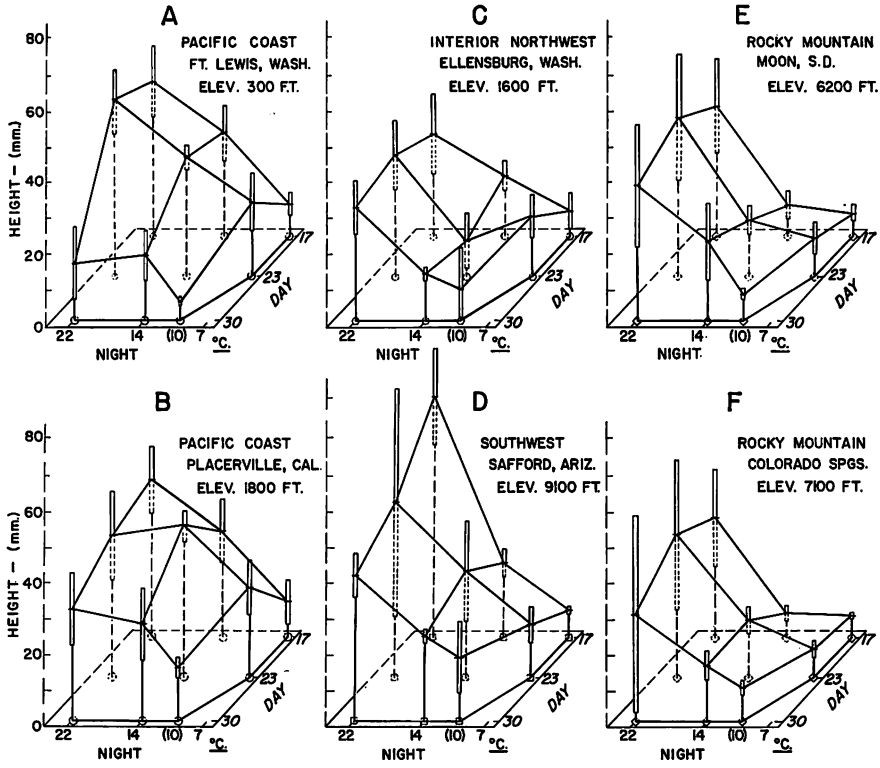

FIG. 20–5. Mean height growth of ponderosa pine progenies from six seed sources in four regions. Treatment included 16-hr. days and nine combinations of three day and three night temperatures. (Broad vertical bars show the range of the mean ±2 standard errors of the mean.)

When the plant is dormant during the winter, the day-to-day climate might be irrelevant. Yet, at the peak of production in the spring a slight climatic change, like an overnight temperature drop, could be crucial. Climate is an ever-changing combination of weather elements. Certain of these elements must be most critical for growth; Glock (1955) summarized what was known on this problem.

A very recent analysis of an old study illustrates the close correlation existing between inherent height growth and certain climatic factors (Squillace and Silen, 1960). Analysis of *Pinus ponderosa*

plantations in Idaho, Oregon, and Washington established significant correlations between height growth at the plantations and these features of climate at the source of the trees:

Precipitation	*Mean Temperature*
Annual	Annual
January through June	April–May
September through June	July minus January
$\frac{\text{September–June}}{\text{Annual}} \times 100$	

Areas which received most of their precipitation in fall, winter, and spring produced trees that usually grew faster; areas which received less moisture during those seasons produced slower growing trees. With respect to temperature, warmer areas produced trees that usually grew faster than trees from cooler areas. April–May temperature was more important in this regard than average annual temperature. In the multiple correlation, the proportion of rainfall occurring in the fall, winter, and spring plus the April–May temperature accounted for 33 to 76 per cent of the variation in progeny growth on the six plantings.

Recently, Langlet (1959) has correlated tree growth over a 17-year period to daylength. Inherent growth differences between trees from different sources were highly correlated with the length of day at the start of the "vegetation period," when average daily temperatures exceed +6° C. Further analysis of his data shows a significant correlation between height growth and duration of the "vegetation period" (Fig. 20–6). Daylength at the onset of the growing season and length of the growing season may be added to the list of critical climatic factors.

Many more factors probably can or will be added to this list, but this point stands out: tree growth is adapted inherently to climate. Probably a tie-up exists between growth and edaphic factors of the environment as well. However, little is known in this area. Until the significance of genetic adaptations to soils is appreciated, caution should be exercised in extrapolating from growth data obtained on one soil series to radically different soils.

Continuous Variation in Climate

The mass of climatic data can serve as a guide to better understanding of geographic variation in tree growth. Topographic variation in critical climatic factors may indicate topographic variation in inherent growth characters. A pattern for climate may be the pattern for growth.

Fortunately, available atlases of climate and detailed weather summaries simplify the chore of analyzing weather patterns. Scru-

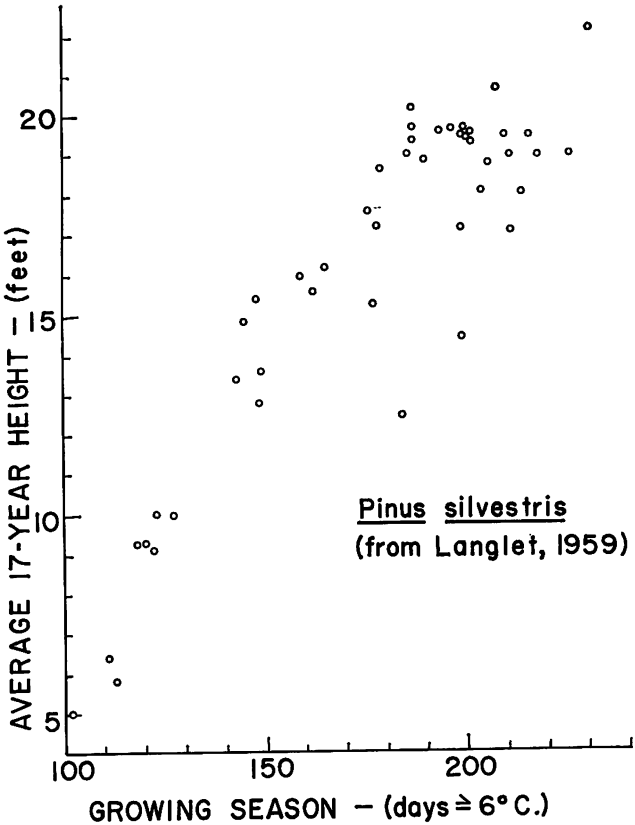

FIG. 20–6. Height of *Pinus silvestris* from forty-six sources, in relation to length of the "vegetation period" at the seed source. Data taken from Langlet (1959, Table 1).

tiny of these references brings forth regular relations between climate and topography. In ascending mountainsides, one encounters lower absolute temperatures, less diurnal and seasonal fluctuation in temperature, shorter growing seasons, and more precipitation. Going toward the earth's poles, one finds falling temperatures and increasing seasonal fluctuations in temperature and daylength, and progressively shorter growing seasons. Together, the facts add up to regular predictable change in a continuum of climate.

Clinal Variation in Tree Growth

Climate has a continuous and predictable variation, and tree growth is related to climate. The logical deduction follows: Tree growth varies continuously in predictable patterns. Individuals of

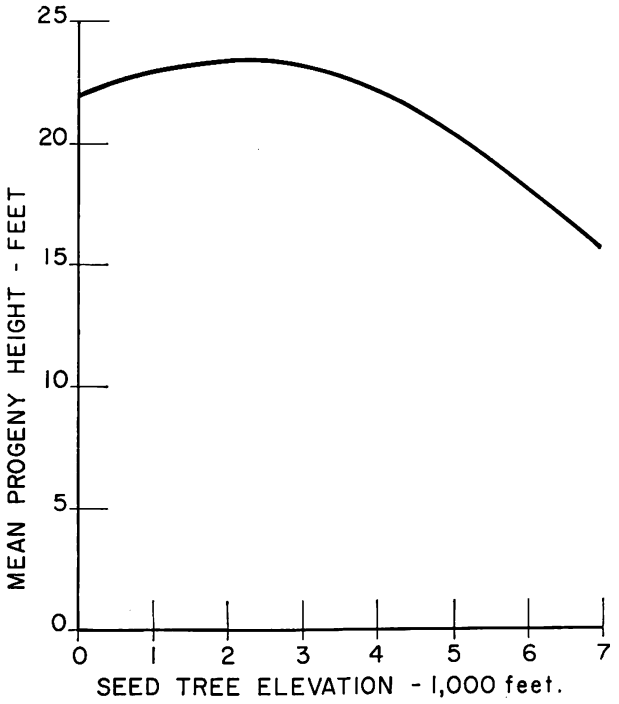

FIG. 20–7. Height of 15-year-old ponderosa pine progenies growing at 2,730 feet in the Sierra Nevada.

a widespread, uninterrupted species should show continuous variability (Langlet, 1934) or clines (Huxley, 1938) of inherent climatic adaptation. Interruptions in distribution of trees, as by water or mountains, might break such clines, of course. However, man should not come to the naïve conclusion that patterns of genetic variation are discontinuous because he has limited perception. He can neither study all populations of a species nor visualize inherent adaptation to the multidimensional interaction of all environmental variables. Discontinuities in factors of the environment, like abrupt change of soil type, may result in abrupt genetic change, producing ecotypes. Reasons for such changes usually are quite apparent. As Langlet (1959, p. 16) stated, "Discontinuities may thus very well occur—where the conditional ecological factors vary discontinuously." However, discontinuities or abrupt changes do not negate the basic premise of continuous variation.

Irregularities in the clinal pattern of variation certainly will occur. To forbid their occurrence would be to forbid evolution. These irregularities represent fluctuations in the rate of genetic change.

The California progeny test cited earlier illustrates this point well (Callaham and Hasel, 1961). Genetic variation in height growth takes the form of an ecocline (Gregor, 1939), related to elevational change in climate (Fig. 20–7). Certain progenies at lower elevation, possibly self-pollinated, showed significant reduction in growth from the ecocline. Nine progenies of another low-elevation population grew exceptionally well. They may be on the road to improved genetic adaptation. The important point is this: All individuals or populations need not fit an ideal statistical model of a cline. Certainly, statistics can be used to generalize on patterns of genetic change, but a waving free-hand curve or plane will fit data better and will be more meaningful in a biological sense.

Finally, the evidence for continuous genetic variation in tree growth mounts ever higher. Starting from the nineteenth century, to Langlet's (1934) presentation of overwhelming experimental evidence, to recent studies (Irgens-Möller, 1958; Olson *et al.*, 1959), the record leaves little doubt.

LITERATURE CITED

Callaham, R. Z. 1959. *Pinus ponderosa*: Geographic variation in germination response to temperature. Proc. 9th Internatl. Bot. Cong. 2: 57–58.

Callaham, R. Z., and A. A. Hasel. 1961. *Pinus ponderosa:* Height growth of wind pollinated progenies. Silvae Genetica 10: 33–42.

Critchfield, W. B. 1957. Geographic variation in *Pinus contorta.* Harvard University, Maria Moors Cabot Found. Pub. 3. 118 pp.

Glock, W. S. 1955. Tree growth. II. Growth rings and climate. Bot. Rev. 21: 73–188.

Gregor, J. W. 1939. Experimental taxonomy. IV. Population differentiation in North American and European sea plantains allied to *Plantago maritime* L. New Phytol. 38: 293–322.

Huxley, J. 1938. Clines: An auxiliary taxonomic principle. Nature 142: 219–220.

Irgens-Möller, H. 1957. Ecotypic response to temperature and photoperiod in Douglas-fir. Forest Sci. 3: 79–83.

———. 1958. Genotypic variation in the time of cessation of height growth in Douglas-fir. Forest Sci. 4: 325–330.

Kramer, P. J. 1957. Some effects of various combinations of day and night temperatures and photoperiod on the height growth of loblolly pine seedlings. Forest Sci. 3: 45–55.

Langlet, O. 1934. Om variationen hos tallen (*Pinus silvestris* L.) och des samband med Klimatet. Skogsvårdsför. Tidskr. 32: 87–110.

———. 1938. Proveniensforsok med olika Tradslag. Skogsvårdsför. Tidskr. 36: 55–278.

———. 1959. A cline or not a cline: A question of Scots pine. Silvae Genetica 8: 13–22.

Olson, J. S., F. W. Stearns, and H. Nienstaedt. 1959. Eastern hemlock seeds and seedlings: Response to photoperiod and temperature. Conn. Agr. Expt. Sta. Bull. 620. 70 pp.

Orr-Ewing, A. L. 1957. Further inbreeding studies with Douglas-fir. Forestry Chron. 33: 318–332.

RIGHTER, F. I. 1945. *Pinus:* The relationship of seed size and seedling size to inherent vigor. Jour. Forestry 43: 131–137.

SQUILLACE, A. E., and R. T. BINGHAM. 1958a. Localized ecotypic variation in western white pine. Forest Sci. 4: 20–33.

——— and ———. 1958b. Selective fertilization in *Pinus monticola* Dougl. I. Preliminary results. Silvae Genetica 7: 188–196.

SQUILLACE, A. E., and R. R. SILEN. 1960. Racial variation in ponderosa pine. Forest Sci. In press.

VAARTAJA, O. 1959. Evidence of photoperiodic ecotypes in trees. Ecol. Monog. 29: 91–111.