Ecotypic variation in Pinus contorta Dougl. var. latifolia Engelm. (lodgepole pine)
by David Anthony Perry

A thesis submitted in partial fulfillment of the requirements for the degree of DOCTOR OF PHILOSOPHY in Botany-
Montana State University

Abstract:
Seed was collected from ten lodgepole pine trees in each of five stands located in Utah, Montana, Idaho, Washington, and British Columbia. Seed was planted and seedlings grown in four daylength regimes--14, 15-1/2, 16-1/2, and 22 hours—in each of two temperature regimes—warm and cool. Other seedlings were grown at three levels of moisture stress--0, 3, and 5 bars. Mass, height, and dates of budset and budburst were recorded. Significance of variations among and within stands was determined by analysis of variance.

Stands tended to be uniform in their mass values and dates of budset and budburst. There was significant variation in height, with tallest seedlings coming from parent stands with the longest growing season. There were no significant differences which were latitudinally correlated in the way stands reacted to daylength, however, seedlings from high-elevation sources appeared to be favored in cool temperatures and short daylengths. Seedlings from parent trees in summer drought areas resisted moisture stress somewhat better than other seedlings.

Within-stand variation was of two types: (a) that among parent trees and (b) that among progeny from a single parent tree. With the exception of the Montana source, stands formed a north-south dine of decreasing type (b) and increasing type (a) variation.

ECOTYPIC VARIATION IN *PINUS CONTORTA* DOUGL. VAR. *LATIFOLIA* ENGELM. (LODGEPOLE PINE)

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ABSTRACT

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INTRODUCTION

Pinus contorta, lodgepole pine, is one of the most widespread of North American pines. Its geographic range extends from the divide between the Klondike and McQuesten Rivers at about 64° N. latitude to the Sierra San Pedro Martin in Baja California at about 31° N. latitude, and from the Pacific coast to the Black Hills (Tackle, 1959).

Along the Pacific coast lodgepole pine is a small tree, 7 to 9 meters in height, which is often characterized by a contorted bole and dense, irregular crown. In contrast, the inland form is a medium-sized tree with a clear, cylindrical bole and small crown (Harlow and Harrar, 1958). Some taxonomists distinguish two varieties of lodgepole pine, *Pinus contorta* var. *contorta*, the coastal form, and *Pinus contorta* var. *latifolia*, the inland form (Tackle, 1959).

In an extensive study of morphological characteristics, Critchfield (1957) suggested that the species be divided into four subspecies, *contorta* (coastal region), *bolanderi* (Mendocino white plains), *latifolia* (Rocky Mountains), and *murrayana* (Sierra Nevada). Critchfield also noted that within the inland subspecies low and high elevation populations formed groups with distinct morphological characteristics.

The environmental conditions under which the various regional forms of lodgepole pine grow vary widely. The Sierra Nevada and coastal populations grow in zones of high precipitation, while in the Rocky

Mountains and other areas in which ssp. latifolia is found[1] summers may be dry and include a period in which soil moisture becomes deficient. Coastal areas have a very narrow seasonal temperature range, while inland it is generally quite wide. At high elevations frost may occur at any time (Tackle, 1959).

It is generally agreed that in the Rocky Mountains fire has played a large role in the development of ecosystems. The serotinous cone of lodgepole pine, which remains closed at maturity and is opened by temperatures of 40° C. or greater (Clements, 1910) represents an adaptation to fire and promotes the recolonization of burns by this species. Once established, the high degree of shade intolerance in lodgepole seedlings very often prevents the stand from perpetuating itself and, in the absence of fire, other species, usually Douglas fir at low elevations and subalpine fir and Englemann spruce at high elevations take over the site as the original lodgepole stand ages and dies.

Although the principal niche of lodgepole pine in the Rocky Mountains is as a major component of the fire sere, in some areas it may form stands which persist in the absence of fire. In Colorado Moir (1969) found that deep soils between 2500 and 2850 meters

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[1]The area in which the Rocky Mountain form of lodgepole pine is found includes not only the Rocky Mountains but the intermountain region, the Washington Cascades, and the Blue Mountains of Oregon (Critchfield, 1957).

elevation might have 60 to 100-year old lodgepole stands with no advanced reproduction of other conifers. He related this to high summer soil surface temperatures and summer drought. In Yellowstone Park, on sites with combination of low rainfall and nutrient-poor soils, lodgepole pine forms pure stands which appear to persist over long periods. Despain (1973) related this to the inability of spruce and fir to become established on these sites. Similarly, in the northwest Oregon Cascades lodgepole pine forms pure, relatively stable stands on very droughty and nutrient-poor soils (Stephens, 1966).

There are few physiological limitations to lodgepole pine's ability to occupy various habitat types. In colonizing burns it encounters a wide variety of edaphic, topographic, elevational, and moisture conditions (Tackle, 1959). Its role seems to be that of a pioneer tree taxon on sites where other species, either temporarily or permanently, seem unable to become initially established. If by its presence, conditions are ameliorated sufficiently for other trees to establish, lodgepole pine apparently cannot compete with them and is ultimately replaced. If conditions remain too stringent for others, it maintains occupancy of the site.

Although morphological variations in lodgepole pine have been well studied and such factors as rates of photosynthesis and growth have been compared between populations (Sweet and Wareing, 1963a; Buchert, 1971), little is known about the degree to which populations of lodge-

pole pine have adapted to specific factors of the environment. There are many conflicting reports of the conditions under which it grows, and Edwards (1954) states that "it is a most adaptable species, reacting in many different ways to the factors of the locality where it grows." Does the species have a high degree of phenotypic plasticity, or is it characterized by a great number of ecotypes? Edwards (1954) reviews provenance studies that have been conducted in Europe.[2] These experiments demonstrated growth differences among provenances, as well as a tendency for individuals to perform better in climates similar to the place of their origin than they do in other climates. He concludes that lodgepole pine is differentiated into ecotypes which form an ecocline "ranging from the coastal shore pine to the most continental form of lodgepole growing east of the Rocky Mountains, and distributed between 64° and 36° N. latitudes." Edwards cites other researchers, however (Whitford and Craig, 1918; Davidson and Abercrombie, 1927), who maintain that the varieties within the species are "environmental forms," presumably implying that differences are due to phenotypic plasticity rather than genetic differentiation.

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[2]Provenance is defined by Hanson (1962) as "the place of origin of seeds or other propagules." The term provenance study is used by foresters to describe studies which compare the performance of trees of the same species but different geographic origin, when tested under common conditions.

This paper compares growth and phenology among lodgepole pine seedlings from five provenances, when subjected to conditions of varying daylength, temperature, and moisture stress. The objectives of the research are to determine (a) if there are significant differences in seedling response among samples of the various provenances and (b) whether such differences, if they exist, are dependent on the environmental factors tested.

THE CONCEPT OF THE ECOTYPE

Although this paper is solely an analysis of phenotypical differences among various populations of Pinus contorta, "lodgepole pine," and does not purport to determine genotypical variation, the role which the genotype undoubtedly plays in ecotypic variation warrants a brief examination of the genetic factors which contribute to the nature of variation in a species.

Early studies of infraspecific variation relating to habitat variation were of European forest trees. Langlet's (1971) historical review mentions work by Duhamel du Monceau (circa 1745), de Vilmorin (circa 1820), Kienitz (1879), Cieslar (1887-1907), and Engler (1905-1913). These investigations were in the nature of what foresters know today as provenance studies. Seed was collected from trees of contrasting locales and planted in one or several common gardens (See Heslop-Harrison, 1964, for a discussion of the limitations of the common-garden

method.) The observation that differences in plant growth and other characteristics often were related to habitat variation were and maintained in a common environment led to the concept that different habitats are occupied by different genotypes of a species, each genotype tending to "fit best" the set of environmental factors characteristic of its particular habitat.

Although this idea existed as early as the mid-eighteenth century, it was not effectively articulated until Turreson published "The genotypical response of the plant species to the habitat" in 1922. Turreson transplanted individuals of several European herbaceous species from varied habitats to a common garden. As a result of his observations he proposed a terminology to deal with various levels of genotype-environment interaction. In fact this was more than a terminology; it was a defining of new modes of thought concerning the genotypical organization of living systems. Among the terms proposed was ecotype, which Turreson defined as the genotypical response to a particular habitat.[3] In 1923 Turreson introduced the term "genecology" for the study of ecotypic

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[3]Other terms proposed by Turreson were:

Coenospecies: the total set of genetic combinations possible to the gene pool of the Mendelian species.

Ecospecies: the set of genotypes within the coenospecies which have been elicited by environmental requirements, i.e., those found in nature (roughly equivalent to the Mendelian species).

Ecophene: the set of non-genetic modifications of a particular ecotype.

variation in plants. Heslop-Harrison (1964) summarizes the basic propositions of genecology as follows:

> (1) wide ranging plant species show spatial variation in morphological and physiological characteristics; (2) much of this infraspecific variation can be correlated with habitat differences; (3) to the extent that ecologically-correlated variation is not simply due to plastic response to the environment, it is attributable to the action of natural selection in moulding locally adapted populations from the pool of genetical variation available to the species as a whole.

A controversy soon developed, and continues today (Spurr and Barnes, 1973) over the validity of the ecotype concept. The school which developed in opposition maintained that, since most environmental factors very in a continuous fashion, genotypes would also tend to vary continuously. This 'clinal' viewpoint was stressed in the studies of Gregor (1936, 1938, 1939, 1950, 1961), Langlet (1959); and Callaham (1962), among others. Expressing the opposing viewpoint, Clausen et al. (1940, 1945, 1948, 1948a) reported that population changes were rather abrupt in the species studied by them

The idea of continuity is a difficult one to deal with. Modern physics has demonstrated to the satisfaction of most people that, with the possible exception of time, there is no such thing as a continuous phenomenon in nature. Our perception of continuity is a function of the level at which we choose to look and the sensitivity of our measuring devices. The closeness with which some trait ("T") is able to vary with some environmental factor ("F") is dependent on the relative sizes of minimum ΔT and minimum ΔF. Although it is theoretically possible for a

nucleic acid molecule to respond to energy changes at the quantum level, the instabilities that this would introduce into the genome would probably prohobit maintenance of an organized system. Thus, it seems reasonable that a single gene is active over a range of environmental values, and that genomes do not vary continuously in their response to the environment. Mather (1943) indirectly made this point when he observed that the finest detectable level of variation would occur in those traits controlled by several genes, and hypothesized that, since much genetic variation appears to be continuous, traits which show ecotypic variation are polygenically controlled.[4]

It seems likely that, because of the limitation on the number of genetic combinations available, discontinuous variation in environmental response does exist. Whether this variation appears as ecotypical or ecoclinal depends perhaps on many factors, chief among them the size of

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[4] Clausen and Heisey (1958a) estimated that a minimum of 100 loci controlled 19 characters in Potentilla glandulosa. In contrast to Mather, they hypothesized that a high number of loci involved in a trait would increase the chance of linkage between genes involved in several traits, thus creating trait "complexes" and increasing the chance of discontinuous variation.

Langridge (1963) states that adaptations of the physiological trigger type are probably based on simple genetic systems. He cites research which has shown photoperiodism to be under the control of one gene in tobacco (Allard, 1914), maize (Singleton, 1950), and rice (Chandraratna, 1955); and cold requirement for flowering under single gene control in sugar beet (Abegg, 1936) and Hyoscyamus (Lang, 1948). Langridge goes on, however, to express mild despair about the ability to analyze the genetic basis of climatic adaptation because "a major part of the genome is concerned in any adaptive process that is a reasonably general feature of the organism."

the discontinuity compared to the degree of homeostasis of individuals (Levins, 1963), the heterogeneousness of the habitat (Levins, 1963), and the degree of gene flow within the population (Heslop-Harrison, 1964). Where a given trait is distributed in space normally around its adaptive norm, as would be expected if gene exchange is random and selective forces nondisruptive, mean response to a given environmental factor may well appear to be continuous. If gene exchange is restricted to selection disruptive, homogeneous ecotypic subsets may develop within a population.[5]

Table 1 (Heslop-Harrison, 1964) shows the relationship between the nature of gene recombination in a species and various other features. Forest trees, it would seem, fit in the category of free gene recombination and clinal variation. However, the evidence for this is contradictory and inconclusive.

Pollen distribution by pine is probably not extensive, although reports in the literature vary widely. Colwell (1951) found that Pinus coulteri pollen is generally transported only 10 to 30 feet downwind, and very little goes over 150 feet. At the normal density of forest

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[5]Thoday and Gibson (1962), in a set of classic experiments with Drosophila melanogester, demonstrated that disruptive selection would produce racial divergence despite a high level of intercrossing. They cited this experiment as evidence that distinct populations could be formed by an intermingling of habitat types, despite a high degree of intimacy between the populations.

Table 1 (from Heslop-Harrison, 1964)

Relationship between Some Components of the Genetic System and Longevity, Community Type, Physiological Features and Variation Pattern

Free gene recombination resulting from a high recombination index and outbreeding.	Restricted gene recombination resulting from a low recombination index or inbreeding.
Associated with:	Associated with:
(a) Protracted lifespan of individuals reaching maturity	(a) Short life span of individuals
(b) High and selective seedling mortality; dispersal capacity moderate to poor	(b) Low seedling mortality during colonization of suitable habitats; efficient seed dispersal
(c) Membership of closed climax communities in stable or but slowly changing habitats	(c) Membership of impermanent communities in ephemeral, fluctuating or shifting habitats
(d) High range of physiological tolerance in the adult, frequently dependent upon precisely adjusted developmental rhythms but not necessarily associated with phenotypic plasticity.	(d) Avoidance of adverse conditions in the seed state, with or without an associated capacity for adaptive plastic response to environmental stress.
(e) Continuous, clinal variation	(e) Discontinuous variation

stands an effective breeding radius of 30 to 50 feet would result in considerable genetic drift (Wright, 1943).[6] Rehfeldt and Lester (1969) felt that forest tree populations may subdivide themselves into distinct breeding units as one general method of obtaining a fitness-flexibility compromise, and cited research by Squillace and Bingham (1958), Habeck (1958), Muller (1952), and Benson et al. (1967) as evidence. Heslop-Harrison (1964) concluded that ". . . in a continuously dispersed, wind-pollinated species the average area within which there is an appreciable chance of two individuals mating will normally be quite small in relation to the total range." Koski (1967), on the other hand, in a study conducted in the pine stands of northern Finland, found significant pollen exchange over relatively long distances. He concluded that gene exchange between stands located tens of kilometers apart was efficient, and that breeding within stands approached panmixis. Although this resulted, he said, in a great deal of genetic variation between individuals, the formation of local races was seriously hampered by the gene flow.

The effectiveness of pollen distributed long distances from its

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[6] In lodgepole pine stands, where the majority of seed following fire will come from those trees which are serotinous, drift in individuals of the parent stand might conceivably result in a patchwork of progenies from single trees, each patch being fairly homogeneous but varying from other patches in a random fashion. This would be most evident for stands in which the preceding generation had a low proportion of serotinous trees.

parent tree will eventually be negated by differences in phenology.[7] However, pathways for gene migration do exist throughout any area over which the species is relatively continuous, i.e., no discontinuities larger than can be bridged by pollen (Heslop-Harrison, 1964). A particularly appropriate example of gene migration is the probable introgression of jack pine (Pinus banksiana lamb.) genes into lodgepole pine populations. Although closely related and freely interbreeding, the terpene composition of the resin in these two pines is very different (Mirov, 1961). Evidence of terpenes commonly found in jack pine in lodgepole pine turpentine has been found in Montana (Lotan and Joye, 1970), British Columbia (Zavarin et al., 1969), and Colorado (Mirov, 1956). Sierra Nevada trees sampled by Zavarin et al. did not show notable shifts toward jack pine resin composition.[8]

Regardless of gene flow, extremes of selection will result in

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[7]Flowering times may overlap over fairly large areas, however. Koski (1970) reported overlap in the flowering of Scots pine in northern and southern Finland four out of ten years.

[8]Turpentine composition of lodgepole pine at various points gives a measure of how far away from the point of contact of the two species (central Alberta) jack pine genes have moved and therefore, if the period in which they have been in contact is known, an estimate of the range of effective pollen transfer. If one accepts the estimates of Yeatman (1967) and Schoenike (1962) that the two species have been in contact only since the late post glacial, gene spread to Colorado during this period would require an effective rate of pollen spread of roughly 1000 feet per year. However, Argus (1966) and Zavarin et al. (1969) feel that the two pines have been in contact for a much longer period.

divergent populations (Levins, 1963; Heslop-Harrison, 1964). An unanswered question is the degree of environmental difference required to negate the effects of gene flow. Local ecotypic variation in forest trees has been reported for northern white cedar between well-drained and swampy areas (Habeck, 1958), western white pine between dry and moist sites (Squillace and Bingham, 1958), and Douglas fir between north and south slopes (Hermann and Lavender, 1968). The question is confounded considerably by the high degree of random variation which is apparently found in most forest stands. Rather than being merely adaptive "noise," however, the degree and nature of random variation may present a question equal to or surpassing in interest that concerning environmentally correlated local variation, since it is probably the source of much ecotypic differentiation (Stebbins, 1950), and represents a buffering capacity within the population against temporal environmental changes (Rehfeldt and Lester, 1969).

CHAPTER 2

HYPOTHESES

Hypothesis I

There is significant variation among stands in the response of lodgepole pine seedlings to different (a) temperatures, (b) daylengths, and (c) moisture stress regimes.

Hypotheses II

There is no significant variation within stands in the response of lodgepole pine seedlings to different (a) temperatures, (b) daylengths, and (c) moisture stress regimes.

CHAPTER 3

PROCEDURE

Seed Collection

Seed was collected from five open-cone and five closed-cone trees in each of four stands located in the Uinta range of Utah and Wyoming; the Gallatin range of southwestern Montana; the Nez Perce National Forest of central Idaho; and the Colville National Forest of northeastern Washington. Seed from ten closed-cone trees located in central British Columbia was provided by the British Columbia Forest Service. A small amount of seed was collected from four trees in an exceptionally low-elevation stand on the Colville National Forest. Location, elevation, and habitat type of each stand are listed in Table 2, along with site index, which is the average height in feet of dominant trees at 100 years of age, and is considered to be one measure of site quality (Davis, 1954). Parent tree data are given in Appendix I.

Stands were selected so as to represent as far as possible uniform habitat factors. This was difficult to do on a factor-by-factor basis because of the myriad possibilities for factor interaction and the many ways in which they could vary over the range of seed collection. In order to approximate as closely as possible the desired uniformity, stands were chosen from the Abies lasiocarpa/Pachistima myrsinites habitat type, or its ecological equivalent where that habitat type was not represented (Daubenmire and Daubenmire, 1968).

Table 2

Locations, Elevations, Habitat Types, and Site Indexes of Stands Sampled

Stand	Location	Elevation (Meters)	Habitat Type	Site Index (Alexander, 1966)
Washington #1	Sherman Pass, Colville N.F., Lat. 48° 36' N.	1,600	*Abies lasiocarpa/ Pachistima myrsinites*	90
Washington #2	Colville N.F., Lat. 48° 36' N.	750	*Abies lasiocarpa/ Pachistima myrsinites*	100
Montana	Butte Meadows, Gallatin N.F., Lat. 45° 26' N.	2,200	*Abies lasiocarpa/ Pachistima myrsinites*[a]	60
Utah	Gilbert Creek, Wasatch N.F., Lat. 40° 54' N.	2,500-3,500	*Abies lasiocarpa/ Pachistima myrsinites*[a]	45
Idaho	Little Slate Creek, Nez Perce N.F., Lat. 45°40'N.	1,550	*Abies grandis/ Xerophyllum tenax*	90
British Columbia	Cariboo Land District Lat. 53° 25' N.	700	Unknown, but probably *Abies lasiocarpa/ Clintonia uniflora*	100

[a]These habitat types did not fit well into any of those proposed by Daubenmire. There was no *Pachistima myrsinites* present. However, *Galium triflorum* was present, indicating that they would fit better into the *Abies lasiocarpa/Pachistima myrsinites* than in the *Abies lasiocarpa/Vaccinium scoparium* habitat type.

Seed was collected from dominant or codominant trees located a minimum of 60 m. apart. In most cases all parent trees were taken from an area no greater than five to ten ha. in extent, with no appreciable change in elevation or severe aspect differences. In the Uintas stand, however, low frequency of serotinous trees required seed collection over a considerable altitudinal range.

Seed was collected from both current-year cones and cones up to four years old where both were available, however all tests were done with one- to four-year-old seed from closed-cone trees and current-year seed from open-cone trees. The exception was the British Columbia seed, the age of which was not known.

Serotinous cones were opened by immersion in a water bath at 60° C. (Lotan, 1972). Extracted seed was dewinged and stored at 1° C.

The term "family" is used through this paper to designate the progeny from one wind-pollinated parent tree.

Temperature and Photoperiod Tests

Seedlings were grown in a greenhouse under four daylengths in each of two temperature regimes.

In all tests seedlings were exposed to the same period of natural daylength, generally eight hours per day. During the balance of the 24-hour period each treatment was covered by a black plastic hood and its photoperiod extended to the desired length by two gro-lux fluorescent

bulbs. Each hood was fitted over the top of the fluorescent light fixture and draped down over its treatment bench in the manner of a tent. It was loose fitting enough around the base of the treatment bench to ensure adequate ventilation, and yet effectively excluded all external light. Temperatures under the hood varied little from those outside the hood, but humidity was maintained at a higher level.

Daylengths used were (World Almanac, 1969);

14 hours - the mid-June photoperiod at 30° N latitude, the southern limit of the species.

15-1/2 hours - the mid-June photoperiod at 45° N latitude.

16-1/2 hours - the mid-June photoperiod at 50° N latitude.

22 hours - the mid-June photoperiod at 65° N latitude, the northern limit of the species.

Daylengths were chosen to include a range of photoperiods common to the seed collection zone as well as a range similar to that experienced by the species as a whole. The mid-June figure was picked as a convenient one within the period of maximum growth activity.

Each set of daylength treatments was grown under one of two temperature regimes. Generally these temperature regimes have been classified as warm and cool. Precise temperature control in the greenhouse, however, was not always possible. Cooling in the greenhouse wing selected for the cool temperature treatment turned out to be less efficient than in the warm temperature wing, with the result that day-

time temperatures in June, July, and August often peaked higher on the cool side than on the warm side.

The duration of high temperatures during the day was always considerably less on the cool than on the warm side, however, and nighttime temperatures were consistently 5° to 10° lower. The pattern of temperature variation for the two treatments is briefly summarized in Tables 3 and 4.

Temperatures in the greenhouse, especially during the cooler months, tended to vary with changes in the outside temperatures, and thus changes from day to night were usually smooth and somewhat gradual rather than abrupt.

Seed was stratified by soaking in cold water for 24 hours, then storing moist in plastic bags at 1° C. for two weeks (Lotan, 1972). In each treatment, seed from each parent tree was planted in rows, each row containing approximately 15 seeds spaced 1.5 to 2 cm. apart. Each parent tree was replicated three times per treatment, making a total of 150 rows per treatment. These 150 rows were in turn arranged into four rows, so one entire treatment was contained in a space 1.2 x 1.5 meters. Assignment of replications to planting spaces was done by random selection of replication numbers from a hat.

Seedlings were grown in a mixture of 20% sand, 40% peat, and 40% vermiculite. In the first few weeks nutrients were applied by watering once a day with full strength Shive's solution (Shive and Robbins, 1938)

Table 3

Approximate Temperature Range per Treatment (°C)

Treatment	Dec. through May	June through August	August through Nov.
Warm	30° day - 20° night	30° day - 20° night	30° day - 20° night
Cool	20° day - 5° night	30° day - 12° night	20° day - 5° night

Table 4

Average Hours per Week in Which the Temperature Exceeded 27°C and 32°C and in Which the Temperature was Lower Than 15°C and 10°C

	Dec.-April		May-Aug.		Sept.-Nov.		Dec.-May		June-Aug.		Sept.-Nov.	
	Hours Above		Hours Above		Hours Above		Hours Below		Hours Below		Hours Below	
Treatment	27°	32°	27°	32°	27°	32°	15°	10°	15°	10°	15°	10°
Warm	44	16	41	11	12	0	1	0	10	0	19	1
Cool	1	0	27	11	4	1	46	18	49	5	99	47

diluted 4:1. This regime resulted in a salt buildup and increased pH and so was changed to an application of two quarts Shive's solution once per week to each treatment. Seedlings were watered with tap water whenever the soil began to dry, generally twice a day in the summer and once a day in winter, spring, and fall.

Seedlings in both the warm and cool treatment were planted in mid-January. In February cool-side seedlings began to show symptoms of what was thought to be a damping-off fungus, and within two weeks their condition was such that it was decided to dig them up and replant in fumigated soil. Thus cool-side and warm-side seedlings were seven weeks out of sequence with each other, and a soil difference between treatments was introduced. In order to evaluate the effect of fumigation on seedling performance, a small test was set up in which approximately 50 seedlings from the Washington, Montana, and Utah stands were grown in soil from the cool treatment, and the same number of seedlings from the same parent trees were grown in soil from the warm treatment. Temperature and daylength were the same for both sets of seedlings. Each soil type was replicated three times.

Before describing the phenological measurements which were made, it would perhaps be useful to describe the development of pine seedlings. Following germination, the first foliage to appear consists of a whorl of cotyledons. Development of the stem soon results in the appearance of juvenile leaves, which are spirally arranged, linear, and single

(i.e., not in groups defined by a single fascicle) (Harlow and Harrar, 1958). Juvenile leaves are followed by acicular, fascicled adult leaves which develop in the axils of the juvenile leaves (Harlow and Harrar, 1958). The timing of the appearance of adult leaves is not clear. Harlow and Harrar (1958) state that, depending on the species, it may be one to several seasons. Mirov (1967), on the other hand, says that adult needles may appear during the first season. Under certain conditions many pines undergo a period of dormancy in midsummer which is broken in late summer or early fall (Mirov, 1967), and observations of lodgepole pine (Morsby, 1972) indicate that this secondary flush of growth may result in the production of adult needles. In the present study appearance of adult needles in relation to terminal bud activity varied with temperature. In the warm treatment adult needles were never produced before a terminal bud was set, and their appearance in the axils of juvenile leaves invariably signaled resumption of terminal growth. In contrast, cool treatment seedlings produced adult needles well before appearance of a terminal bud.

Cessation of subapical meristem activity, and consequently shoot elongation, is usually marked in pines by the appearance of a terminal bud, which is an unextended portion of stem containing the apical meristem and primordial leaves and their internodes, and which is covered by primordial leaves (Romberger, 1963). Because it is an obvious and easily recognized feature the terminal bud is often taken as a sign of

dormancy in the plant, but this is not necessarily an accurate interpretation. Activity of the various plant meristems--apical, subapical, cambial and root--is very seldom simultaneous, and other regions of the plant may be actively growing, or at least producing primordia, at the same time that the terminal bud has signaled cessation of subapical meristematic activity (Romberger, 1963; Mirov, 1967). Nevertheless, the terminal bud does have value as an indicator of dormancy in at least one part of the plant. It is quickly and easily seen and provides a reliable common basis for comparing developmental activity between seedlings. For these reasons it has been used as a measure of comparative phenology in this study.

With these comments as background, it is now appropriate to describe the phenological measurements made in this study. At two-week intervals for a period of 18 weeks the number of seedlings with terminal buds and the number with adult needles were recorded. In both temperature regimes the appearance of a terminal bud was taken to indicate the beginning of one phase of dormancy, and in this paper the length of time from planting to appearance of the terminal bud is defined as the growing period. The growing period of a given family has been taken as the number of weeks from planting till 50% of its seedlings have terminal buds.

In the warm temperature treatment appearance of adult needles, either from the apical meristem or axillary buds, was taken to indicate

cessation of subapical meristem dormancy. The use of axillary bud break to indicate subapical meristem activity was considered valid because the author's observations consistently revealed that, in these seedlings, appearance of new needles from axillary buds very closely preceded terminal bud burst (they did not of necessity precede it, however). The number of weeks from budset to appearance of adult needles is defined here as the dormant period, and the dormant period of a family is taken as the number of weeks from 50% of seedlings with terminal buds to 50% of seedlings with adult needles. In some daylength treatments, especially 22 hours, trees tended to set and break buds in very rapid sequence, one tree producing as many as three to four terminal buds in the course of the experiment. Data given here, however, is concerned only with appearance of the initial terminal bud and its subsequent burst.

In the cool temperature treatment adult needles appeared before budset and therefore were not appropriate as a measure of cessation of dormancy. In fact, once buds were set in these temperatures, they showed no signs of bursting during the duration of the experiment, approximately three months after the time of bud set.

It should be stressed that the terms, "growing period" and "dormant period," as used here refer only to subapical meristem activity. The total physiological state of the plant cannot be safely extrapolated from just this information.

Seedlings were lifted from the beds by hand. Essentially the method was one of running the hands down underneath each row and, with gentle movements of the fingers, loosening the soil medium from around the roots until the seedlings could be freed without forcing. Roots were considerably intertwined and, despite all precautions, some of the fine roots were torn and lost. It is difficult to estimate the amount of root lost in this manner but, in terms of mass, it was probably quite small.

Before lifting, the height of each seedling from ground level to terminal bud tip or growing tip was recorded to the nearest millimeter. After lifting, roots were washed and seedlings dried for 24 hours at 100° C. to 105° C. Total and top mass for each row (one replication of the seedlings from one parent tree) were measured to the nearest .01 grams.

Moisture Stress Tests

Seed from four parent trees in each of the stands used in the daylength-temperature tests, as well as four parent trees from the low-elevation Washington stand (herein called Washington #2), were used in the moisture stress tests. Polyethylene glycol 6000 was mixed with distilled water and nutrients to give solutions with osmotic pressures of 5.2, 3.2, and .2 bars. Amounts of polyethylene glycol 6000 necessary to give 5 and 3 bars pressure were 215 grams per liter and 160 grams

per liter respectively (Cox and Boessma, 1967). One-quarter strength Shive's nutrient solution was estimated (Mills, 1974) to have the same osmotic pressure as one-quarter strength Hoaglands Solution, which is approximately .2 bars (Cox and Boessma, 1967). Thus the control solution had an osmotic pressure of .2 bars.

Each moisture stress level was replicated twice. One replication of one level consisted of an aluminum baking pan (U.S. Army issue) with dimensions 54 cm. x 40 cm. x 4 cm., into which 4 liters of the proper solution was placed. Seeds were planted in plastic-coated paper cups 12 cm. in height, 8 cm. in diameter at the top, and 6 cm. in diameter at the base. Planting medium was vermiculite. Four triangular openings were punched in the bottom of each cup to allow moisture to enter.

Approximately 10 seeds of one parent tree were planted per cup. After germination these were reduced to three seedlings per cup. Each cup was initially placed in distilled water and nutrient solution until it contained 85% by volume moisture. Thereafter, once each week, cups were placed in the proper stress solution and allowed to imbibe solution for approximately 30 minutes. They were then removed from solution until the time of the next dunking, one week later. Weighing of selected cups showed that in the 10-minute immersion period cups were able to return to approximately 85% by volume moisture.

Evaporation at the time of year of the test (January-March) was

low, and during the seven days that cups were out of solution their moisture content per cup declined to about 30% by volume. However, moisture content in the lower portion of the cup--the root zone--stayed consistently high, and after a week it was little if any lower than the original moisture percentage. Assuming that vermiculite behaves like sand in its water retention properties (Ferguson, 1973), 30% water content by volume would result in a soil suction due to drying of approximately .1 bars, and at 40% water content soil suction would be zero (Gardner, 1960). For these reasons it is assumed that little or no extra moisture stress was introduced by allowing the vermiculite to dry for a week.

PH of the stress solution was adjusted to 4.0 in order to reduce microbiological activity. After one dunking of seedlings it increased to approximately 7.5, so the solution was changed after each placement of seedling cups in it, i.e., once a week. This procedure not only kept pH constant, but eliminated the problem of increasing polyethylene glycol concentration in the stress solution due to evaporation.

During the first two weeks of the test procedures were slightly different than described above. In order to avoid physiological shock in the seedlings by sudden exposure to high stress conditions small amounts (40 grams per liter) of polyethylene glycol were added at three-day intervals and the cups immersed with each addition, until the proper osmotic pressure levels were attained.

Tests were conducted in a greenhouse. Illumination was by two gro-lux fluorescent bulbs. Daylength was 18 hours, and temperature a fairly constant 15° to 20° C.

Seed was planted January 5 and seedlings were taken up April 1. As in the daylength-temperature tests the height of each seedling was measured to the nearest mm., and the top and total mass of groups of three seedlings (one replication of one family) was taken to the nearest .01 g.

Analysis

Analyses were done on an analysis-of-variance program provided by the Montana State University Statistical Laboratory. In the case of height and mass, variation in the natural logarithm of the dependent variable was tested. Although the value of the dependent variable is given in tables within the test, all significances reported are based on tests of logarithms. The variance of growth and dormancy period data was not distributed in a way that lent itself to transformation (there was no dependence of variance on mean in the dormant period data, and growth period variance plotted against mean looked like the top half of a sine curve) so analyses were done on the untransformed variables.

In all cases significant variation has been considered as 5% or less probability that means are drawn from the same population. Where not mentioned explicitly in the text, the term significance implies this criterion.

Two criteria of variation within populations have been used--the number of factors for which a given dependent variable has a significantly high F-value, and the error mean square of a given variable--both derived from the analysis of variance within stands. The F-value indicates the significance of variation among families and in the way in which they perform under different daylength and temperature regimes, while the error mean square is an indication of the degree of variation within each family. The usefulness of the error mean square is limited, but when coupled with the degree of significant variation among families, it may give useful insight into the pattern of variation within a population. For example, a low error mean square coupled with a high degree of significant variation among families suggests that within family variation may be small compared to that among families, while a large error mean square coupled with low significant variation among families may indicate just the opposite. These may thus suggest the most productive avenues upon which to plan management procedures.

CHAPTER 4

RESULTS

Temperature and Daylength Treatments

Mass[9]

Table 5 summarizes the significance of variations in mass for the factors of stand, temperature, daylength, and their interactions. Figures 1-4 show graphically variation between treatments for each stand separately.

Variation among temperature and daylength treatments. Table 6 gives the relative magnitude and significance of the various measures of mass for each temperature-daylength treatment. For all stands taken together variations in total, top, root mass, and top mass/root mass among temperature and daylength treatments were significant.[10] Daylength response varied with temperature treatment and this also was significant. In both warm and cool temperatures highest total mass was achieved under the 22-hour photoperiod and lowest under the 15-1/2 hour photoperiod. However, in the warm treatment 14 hours gave the second highest total mass, while in the cool treatment the second

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[9]Appendix II gives mass height, and phenological data for individual stands in each test.

[10]Unless otherwise stated, through the paper probability of 5% or less that means are drawn from the same population will be considered significant variation.

Table 5

Significance of Variations in Log_e Mass, Log_e Height, Growing Period and Dormant Period Among Stands, Temperature, and Daylength Treatments

	Provenance Stands	Temperatures	Daylengths	Stand X Temp.	Stand X Daylength	Temp. X Daylength	Stand X Temp. X Daylength
Total Mass	*	*	*	-	-	*	-
Top Mass	*	*	*	-	-	*	-
Root Mass	-	-	*	*	-	*	-
Top Mass/ Root Mass	*	*	*	*	-	*	-
Height	*	*	*	*	*	*	*
Growing Period	*	*	*	-	*	*	*
Dormant Period	*	No MSR	*	No MSR	-	No MSR	No MSR

* indicates significance at the 5% level of probability.

- indicates not significant at the 5% level of probability.

No MSR means No Measure

FIGURE I. AVERAGE TOTAL MASS OF SEEDLINGS, BY STANDS, AS A FUNCTION OF TEMPERATURE AND DAYLENGTH.

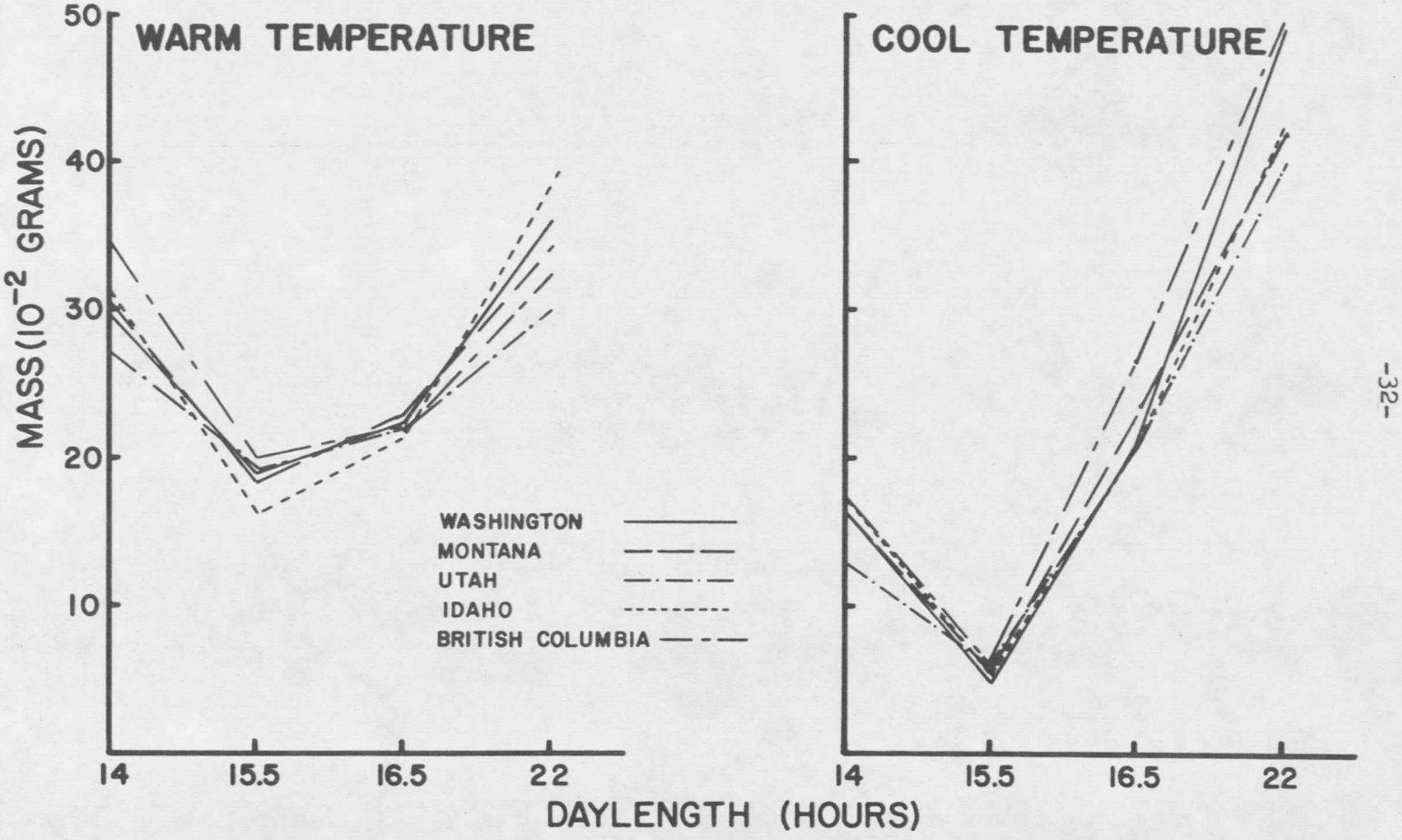

FIGURE 2. AVERAGE TOP MASS OF SEEDLINGS, BY STANDS, AS A FUNCTION OF TEMPERATURE AND DAYLENGTH.

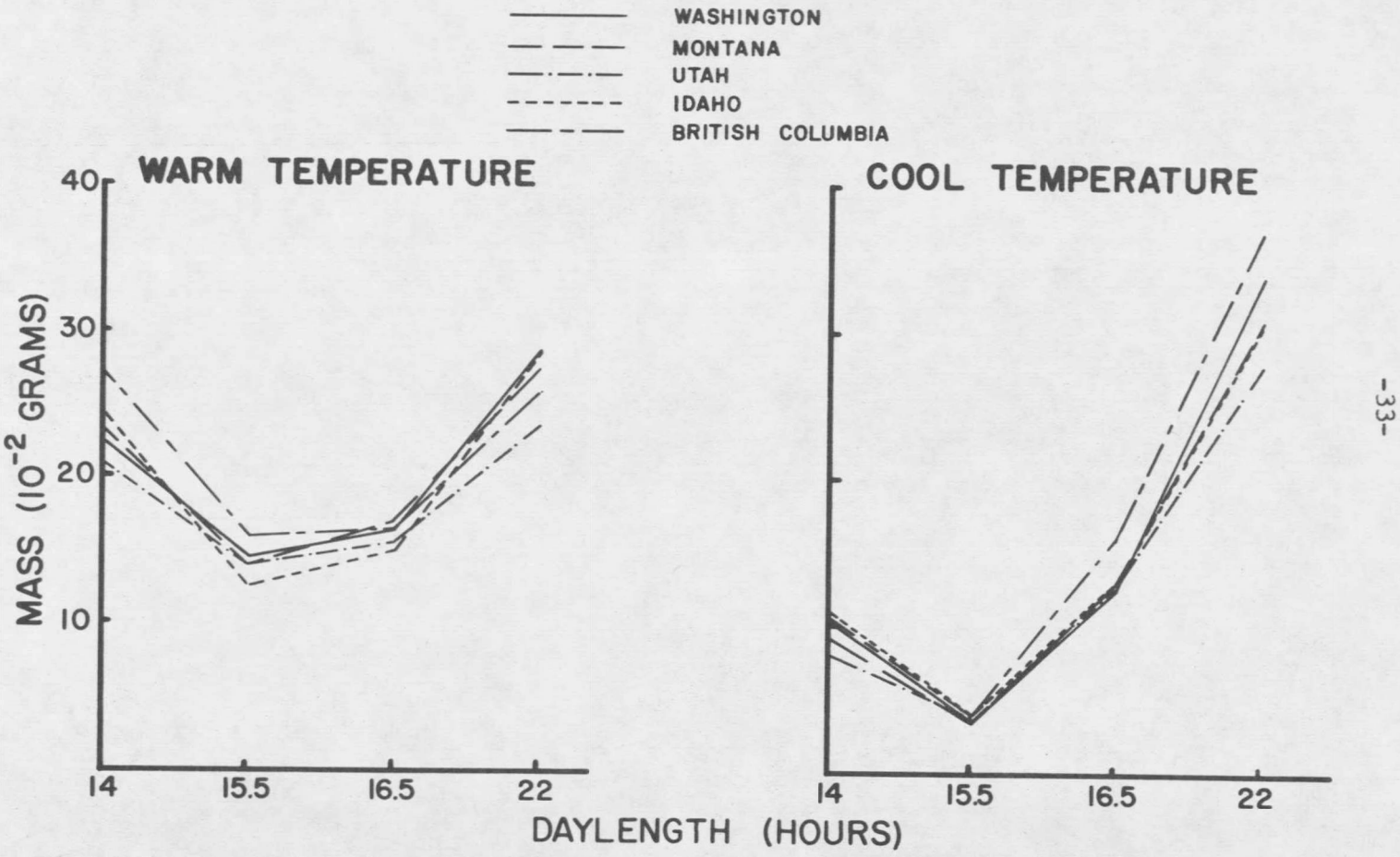

FIGURE 3. AVERAGE ROOT MASS OF SEEDLINGS, BY STANDS, AS A FUNCTION OF TEMPERATURE AND DAYLENGTH.

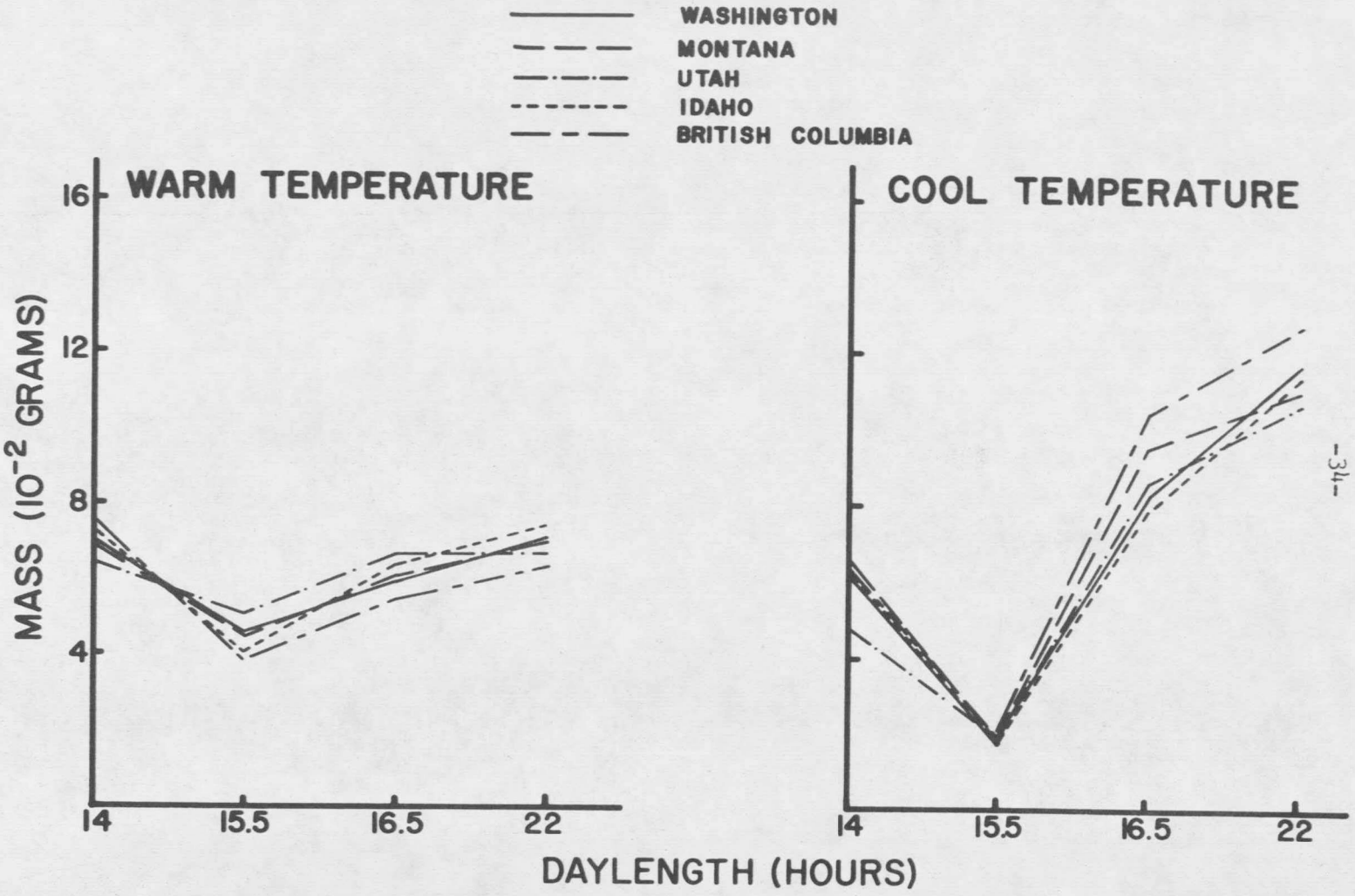

FIGURE 4. AVERAGE TOP MASS/ROOT MASS, BY STAND, AS A FUNCTION OF TEMPERATURE AND DAYLENGTH.

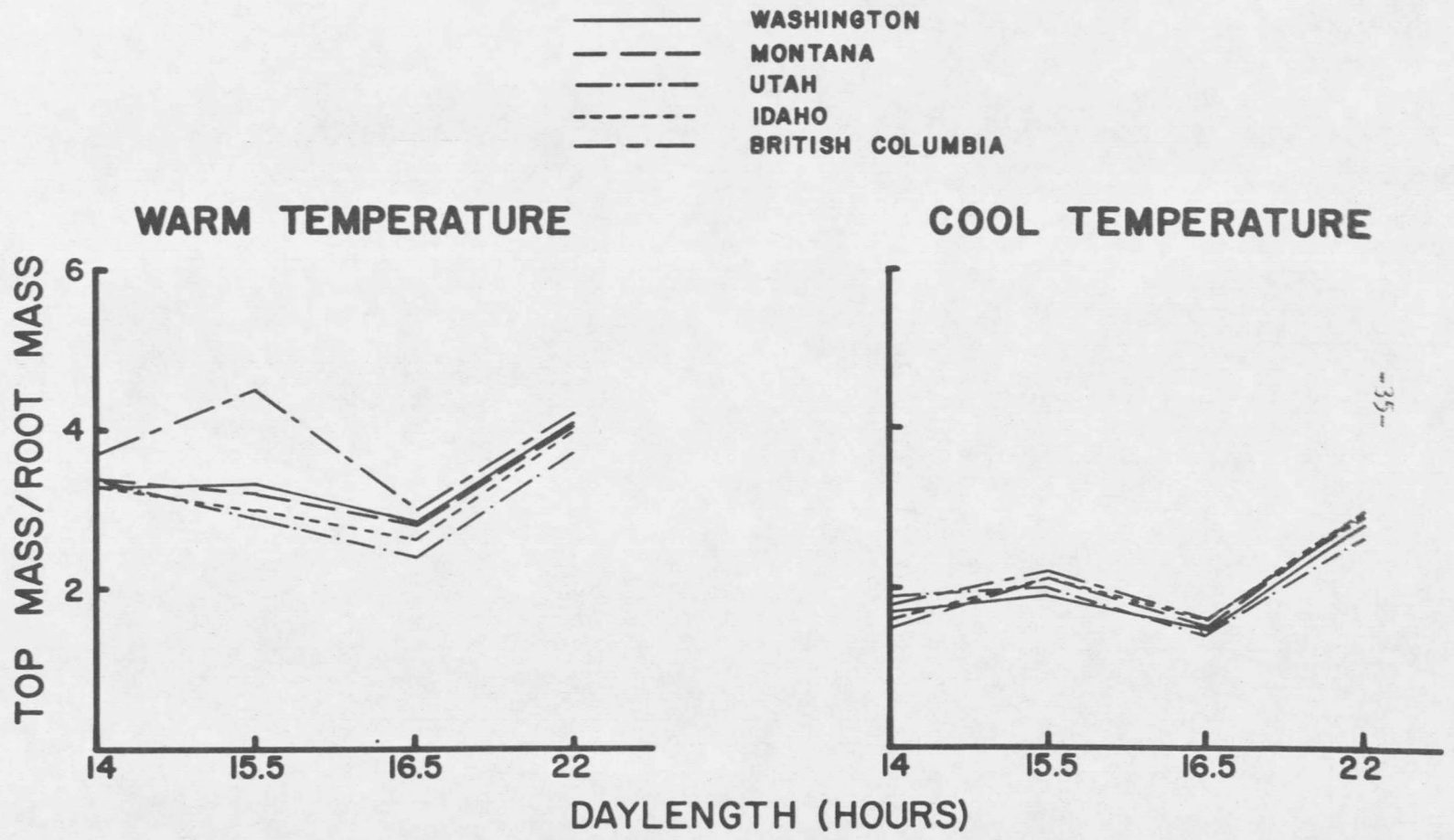

Table 6

Relative Magnitude and Significance of the Various Measurements of Mass, Height, Growing Period, and Dormant Period for Each Temperature-Daylength Treatment[a]

Total Mass	Top Mass	Root Mass	Top Mass/ Root Mass	Height	Growing Period	Dormant Period
24[b]	24	24	14	14	22	13
14	14	23	11	11	21	11
11	11	11	12	24	23	12
23	13	14	24	12	24	14
13	23	21	13	13	14	
12	12	13	22	23	13	
21	21	12	21	21	12	
22	22	22	23	22	11	

[a]Treatments are listed in order of decreasing magnitude of the dependent variable. (Treatments included in the same bracket are not significantly different at the 5% level of probability.)

[b] First digit identifies the temperature treatment:

1 = Warm
2 = Cool

Second digit identifies the photoperiod:

1 = 14 hours
2 = 15-1/2 hours
3 = 16-1/2 hours
4 = 22 hours

highest was in the 16-1/2 hour photoperiod. Top and root mass followed by the same pattern of variation with respect to photoperiod as total mass, with the exception of root mass in the warm treatment which was higher in the 14-hour photoperiod than in the 22-hour.

Except for the 22-hour photoperiod, total mass was less in the cool treatment than in the warm. This was true also for top mass, but not for the root, which was not significantly affected by cooler temperatures. Consequently the distribution of mass between top and root was quite different among temperature treatments. Among all treatments top mass/root mass was lowest for the 14, 15-1/2, and 16-1/2 hour photoperiods in the cool treatment, and only the 15-1/2 hour warm was lower than 22-hour cool treatment.

In summary, for both temperature treatments, greatest total mass was attained under the longest photoperiod--22 hours--and smallest total mass was in an intermediate daylength--15-1/2 hours. The relative magnitude of total mass between the 14 and 16-1/2 hour photoperiods was dependent on temperature. Total growth increased with cool temperatures at the longest photoperiod, but decreased in the three shorter daylengths. Root mass wasn't affected by temperature, and top mass/root mass was considerably lower in the cool than in the warm treatment.

Variation Among Stands. There is significant variation among stands in all variables except root mass. Analysis without the British Columbia seedlings included, however, gives no significant differences

between populations.[11] Table 7 gives mass values and their significance for each stand. The pattern of variation among stands is the same for total and top mass and for top mass/root mass. Because of the uniformity in root mass, total mass differences are largely explainable by top mass variation. Despite differences in top mass among stands, top mass/root mass remains surprisingly uniform, only the British Columbia source being significantly different.

There were no significant differences among the various stands in the manner in which their mass values varied with daylength. Similarly, stands behaved the same with respect to their total and top mass between temperature treatments, with values for the warm treatment significantly larger for each stand. British Columbia seedlings were the only ones for which there were significant differences in root mass between the two temperature treatments, their roots being considerably smaller in the warm treatment than in the cool. This effect was of such magnitude that British Columbia seedlings went from first in magnitude of root mass under the cool treatment to fifth in the warm treatment.

There are high correlations among total, top, and root masses for all stands combined. The correlation between top mass/root mass

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[11] The term population is used interchangeably with the term stand throughout the paper.

Table 7

Average Mass Values Per Seedling by Stands[a]

	MASS (10^{-2} g)			
	Total	Top	Root	Top Mass/ Root Mass
British Columbia	26.20	19.31	6.89	3.02
Washington	24.54	17.89	6.64	2.70
Montana	24.15	17.39	6.75	2.67
Idaho	24.03	17.31	6.67	2.65
Utah	22.20	15.78	6.41	2.54

[a]Mass values included in the same bracket are not significantly different at the 5% level of probability.

and other mass variables was relatively low, however (Table 8).

In summary, there were significant differences among stands in all variables except root mass. Stands reacted in the same way to different daylengths, and top mass varied in the same way among stands with respect to temperature treatments, being uniformly greater under warm temperatures. Root mass did not change significantly between temperature treatments except in the British Columbia stand. All significant variation in mass variables, in fact, was due to the British Columbia source.

Variation Within Stands. Table 9 gives the significance of variations in mass with respect to treatment factors for each stand. All sources except British Columbia had significant variation between families in total, top, and root mass. Among British Columbia families only root mass and top mass/root mass varied significantly. In the Washington and Utah stands, also, families varied significantly in top mass/root mass.

Within stand variation in family interaction with temperature and daylength varied among stands. Montana seedlings had no significant variations with respect to these factors, and British Columbia seedlings only in top mass/root mass. Total and top mass varied significantly within the Idaho stand for the family-temperature, family-daylength, and family-temperature-daylength interactions. Top mass/root mass was not affected. In the Washington stand variation of top mass was significant

Table 8

Correlation Among Mass Variables
for All Stands Combined

	Total Mass	Top Mass	Root Mass	Top Mass/Root Mass
Total Mass	1.000[a]			
Top Mass	.983	1.000		
Root Mass	.850	.741	1.000	
Top Mass/Root Mass	.153	.274	-.229	1.000

[a]Correlation coefficient (r^2).

Table 9

Significance of Variation in Log_e Mass with Respect to Treatment Factors for Each Stand

	Log_e Total Mass				Log_e Top Mass				Log_e Root Mass				Log_e Top Mass/Root Mass			
	F	FxT	FxD	FxTxD	F	FxT	FxD	FxTxD	F	FxT	FxD	FxTxD	F	FxT	FxD	FxTxD
Washington	*	-	*	-	*	*	*	-	*	-	-	-	*	*	*	-
Montana	*	-	-	-	*	-	-	-	*	-	-	-	-	-	-	-
Utah	*	*	*	*	*	*	*	*	*	*	*	-	*	-	-	-
Idaho	*	*	*	*	*	*	*	*	*	*	-	-	-	-	-	-
British Columbia	-	-	-	-	-	-	-	-	*	-	-	-	*	-	*	*

* indicates significance at the 5% level of probability.

- indicates not significant at the 5% level of probability.

F = family; T = temperature; D = daylength.

for the family-daylength and family-temperature interactions, while root mass reacted the same way among families to temperature and daylength variations. The top mass/root mass ratio also varied significantly for both family-temperature and family-daylength interactions.

Mean square error values (Table 10) show a somewhat different pattern of within-family variation for the various stands than between-family variation. The Washington and Idaho stands, with a relatively large amount of inter-family variation, also had a great deal of within-family variation. The Utah stand, however, with the largest amount of variation between families, had the lowest amount within families, and the British Columbia source, reacting in just the opposite way, had a comparatively high degree of variation within families, but very little between. The Montana stand seemed to be overall the most uniform.

In summary, compared to the other stands, British Columbia was remarkably uniform with respect to inter-family variation, having significant variation only in root mass, but within-family variation was comparatively high. The Montana stand was also quite uniform. There was significant variation between families in nearly every category, but all families reacted to temperature and daylength in the same way. Within-family variation was low. The Utah, Washington, and Idaho stands had a great deal of variation, not only between families, but in the way families reacted to daylength and temperature differences. In the Washington and Idaho stands, this was coupled with a high degree of

Table 10

Error Mean Squares for Dependent Variables, by Stands
(From Analysis of Within-Stand Variance)

Stand	Error Mean Square Within Stand of						
	Log_e Total Mass	Log_e Top Mass	Log_e Root Mass	Log_e Top Mass/ Root Mass	Log_e Height	Growth Period	Dormant Period
Washington	.16	.18	.17	.09	.094	4.9	8.2
Montana	.10	.12	.14	.06	.078	4.1	6.4
Utah	.09	.10	.12	.08	.073	4.0	6.1
Idaho	.13	.14	.16	.07	.090	4.7	3.4
British Columbia	.14	.14	.14	.06	.087	3.5	7.6

variation within families, but intra-family variation in the Utah source was low.

Height

Variation among temperature and daylength treatments (Table 5). Heights in the warm treatment were generally greater than in the cool, although under the 22-hour photoperiod and cool temperatures seedlings were taller than those in either the 15-1/2 or 16-1/2 hour photoperiod in the warm treatment. The pattern of height variation with respect to photoperiod in the cool treatment was the same as that of mass, with 22 hours greatest, followed by 16-1/2, 14, and 15-1/2 hours. In the warm treatment 22 hours had the greatest heights and 14 hours the second greatest, as was true in mass, but the heights of trees in the 15-1/2 hour photoperiod were greater than in the 16-1/2 hour, although their mass was less.

Variation among stands (Tables 5 and 11; Figure 5). In all photoperiod-daylength combinations except two, British Columbia seedlings were significantly taller than those from all other stands. Washington seedlings were slightly but not significantly taller in the 22-hour warm temperature treatment, and in the 15-1/2 hour cool treatment British Columbia and Utah seedlings were not significantly different.

In all warm temperature treatments and in the 22-hour cool treatment stands behaved much the same way with respect to height, with

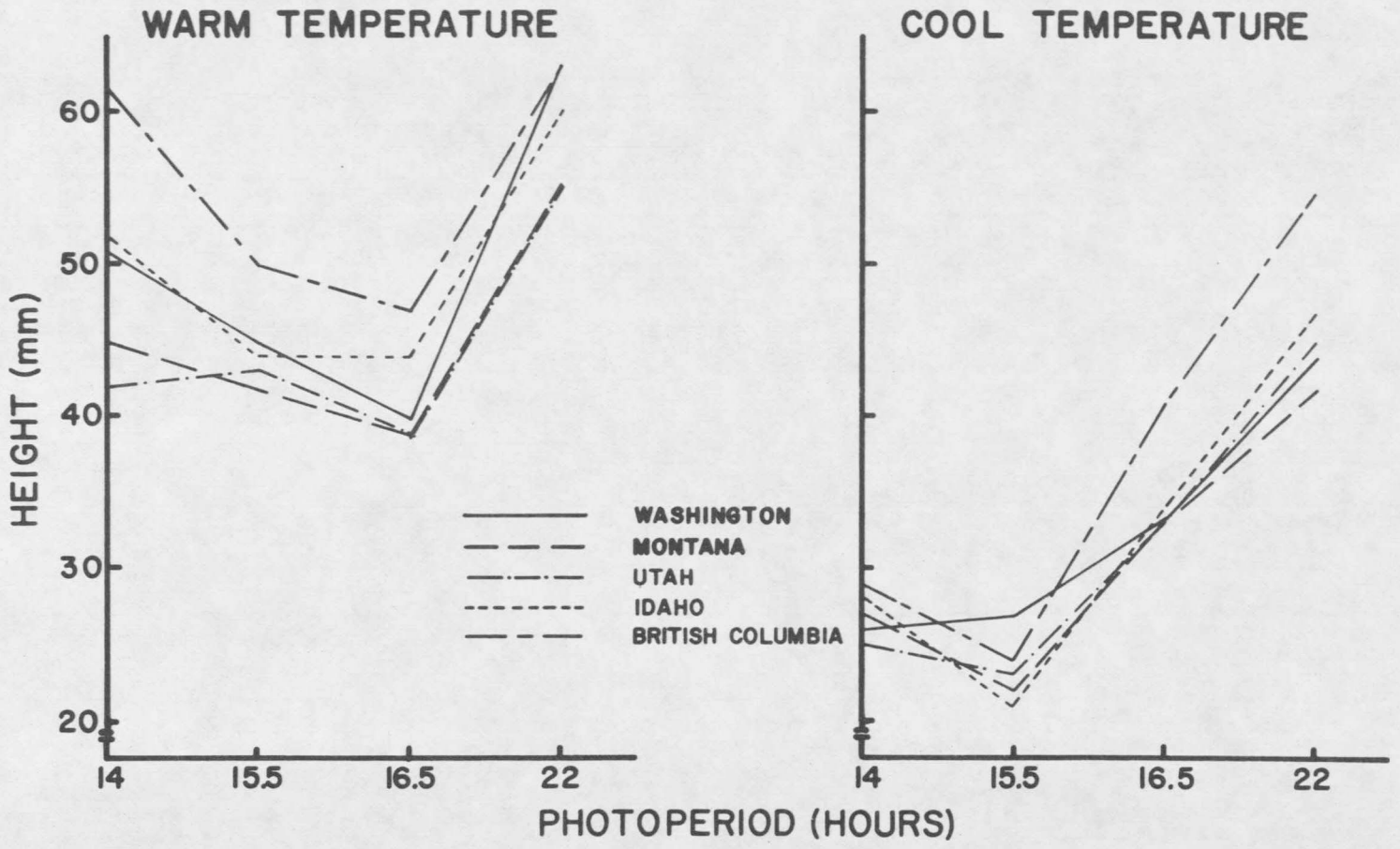
Table 11

Average Heights in mm. of Seedlings by Stands, Photoperiod, and Temperature*

	WARM TREATMENT				COOL TREATMENT			
	Photoperiod (hours)				Photoperiod (hours)			
	22	16-1/2	15-1/2	14	22	16-1/2	15-1/2	14
British Columbia	63[a]	47	50	62	55	41	24[a]	29
Washington	63[a]	40[a]	45[a]	51[a]	44[a,b]	33[a]	22[c]	26[a]
Idaho	60	44[a,b]	44[a,b]	52[a]	47[a]	34[a]	21[c]	26[a]
Utah	55[b]	39[b]	43[a,b]	47[b]	45[b]	33[a]	23[a,b]	25
Montana	55[b]	39[b]	42[b]	45[b]	42[b]	33[a]	22[b,c]	27[a]

*Heights within a column with the same superscript are not significantly different (5% level of probability).

FIGURE 5. AVERAGE HEIGHT GROWTH OF SEEDLINGS, BY STANDS, WITH RESPECT TO DAYLENGTH AND TEMPERATURE.



British Columbia seedlings the tallest (with the exception pointed out in the previous paragraph), Utah and Montana the shortest and very similar to each other, and Washington and Idaho forming an intermediate group not significantly different from each.

In the three shorter daylengths of the cool treatment, Montana and Utah seedlings were relatively much taller, and this effect had an interesting dependence on daylength. In the 16-1/2 hour photoperiod, Utah seedlings were second tallest and Montana seedlings shortest, with the difference between them significant. In the 14-hour photoperiod, this effect was reversed, with Montana seedlings second greatest in height and significantly taller than Utah seedlings, which were shortest. In the 15-1/2 hour photoperiod, Utah and Montana seedlings were second and third, respectively, in height and were not significantly different from each other. In each of these three treatments, there were no significant differences between Washington and Idaho seedling heights.

Unlike mass, analysis of variance with the British Columbia data removed did not affect the significance of height differences among stands.

Variation Within Stands (Table 12). Height was extremely variable among seedlings from the different parent trees within each stand. Families were not only different with respect to their heights, they reacted differently to daylength and temperature. This was true regardless of whether heights or $\log_e$ heights were analyzed. None of this

Table 12

Significance of Within-Stand Variation in Log_e Height with Respect to Families and Their Interactions with Temperature and Daylength Treatments

Stand	Family	Family x Temperature	Family x Daylength	Family x Temperature x Daylength
Washington	*	*	*	*
Montana	*	*	*	*
Utah	*	*	*	*
Idaho	*	*	*	*
British Columbia	*	*	*	*

* indicates significant variation at the 5% level of probability.

variation was explained by differences in closed-cone and open-cone trees.

Phenological Development

Variation Among Temperature and Daylength Treatment (Tables 5 and 13). There were significant differences in the growing period of seedlings among temperature and daylength treatments, and in the pattern of daylength response at the two temperatures. Budset was considerably slower at cool temperatures, ranging from three weeks behind the warm treatment in the 22-hour photoperiod to eight weeks behind in the 15-1/2 hour photoperiod.

Growing period with respect to daylength was almost exactly the opposite in the two temperature greatments. In the warm temperatures, growth was longest at 22- and 16-1/2 hour daylengths, and shortest at 15-1/2 and 14 hours. In the cool treatment, growing periods were again not significantly different between the 22- and 16-1/2 hour photoperiods, but in this case the former two photoperiods had growth periods significantly shorter than the 15-1/2 hour and 14-hour photoperiods. For reasons that will be discussed in the Discussion section, differences in growing period between temperature treatments should be interpreted very cautiously.

The length of the dormant period, taken here as the number of weeks from 50% budset to 50% of seedlings with adult needles (See the

Table 13

Temperature and Daylength Dependence of Growing and Dormant Periods*

Daylength (Hours)	Growing Period (Weeks)		Dormant Period (Weeks)
	Warm Treatment	Cool Treatment	Warm Treatment
14	18.6	25.2	10.6[a]
15-1/2	19.4	27.5	7.7
16-1/2	19.9[a]	23.2[a]	11.0[a]
22	19.9[a]	22.9[a]	5.3

*Weeks with the same superscript are not significantly different at the 5% level of probability.

Methods section), varied significantly between daylengths in the warm treatment. No measure was made in the cool treatment. The pattern of variation in the dormant period between daylengths was somewhat unusual, with the 22- and 15-1/2 hour photoperiod seedlings having significantly shorter periods of dormancy than those in the 14- and 16-1/2 hour daylengths. Dormant periods between the former two daylengths were also significantly different than each other, with 22 hours giving the shortest, while in the latter two, differences were not significant.

Variation among stands (Table 5: Figure 6). Stands varied significantly among themselves in both growth and dormancy period. There were significant differences in the way stands reacted to the various daylengths, but not in their responses to temperature.

In the Montana, Idaho, and Utah stands, there were no significant differences between growth periods at 22, 16-1/2, and 15-1/2 hour photoperiods, while growing time was significantly shorter in the 14-hour daylength. The Washington stand was somewhat similar except that the growing period in the 15-1/2 hour daylength was significantly shorter than in the 22 and 16-1/2 hour photoperiods. The British Columbia stand was quite different in its reaction to photoperiod, with the period of growth not significantly different at 16-1/2, 15-1/2, and 14-hour photoperiods, but significantly shorter at the 22-hour daylength.

In the 14- and 16-1/2 hour daylengths the pattern of variation in growing time between stands was quite similar, with British Columbia,

FIGURE 6. AVERAGE GROWING PERIOD OF SEEDLINGS, BY STANDS, WITH RESPECT TO DAYLENGTH AND TEMPERATURE.

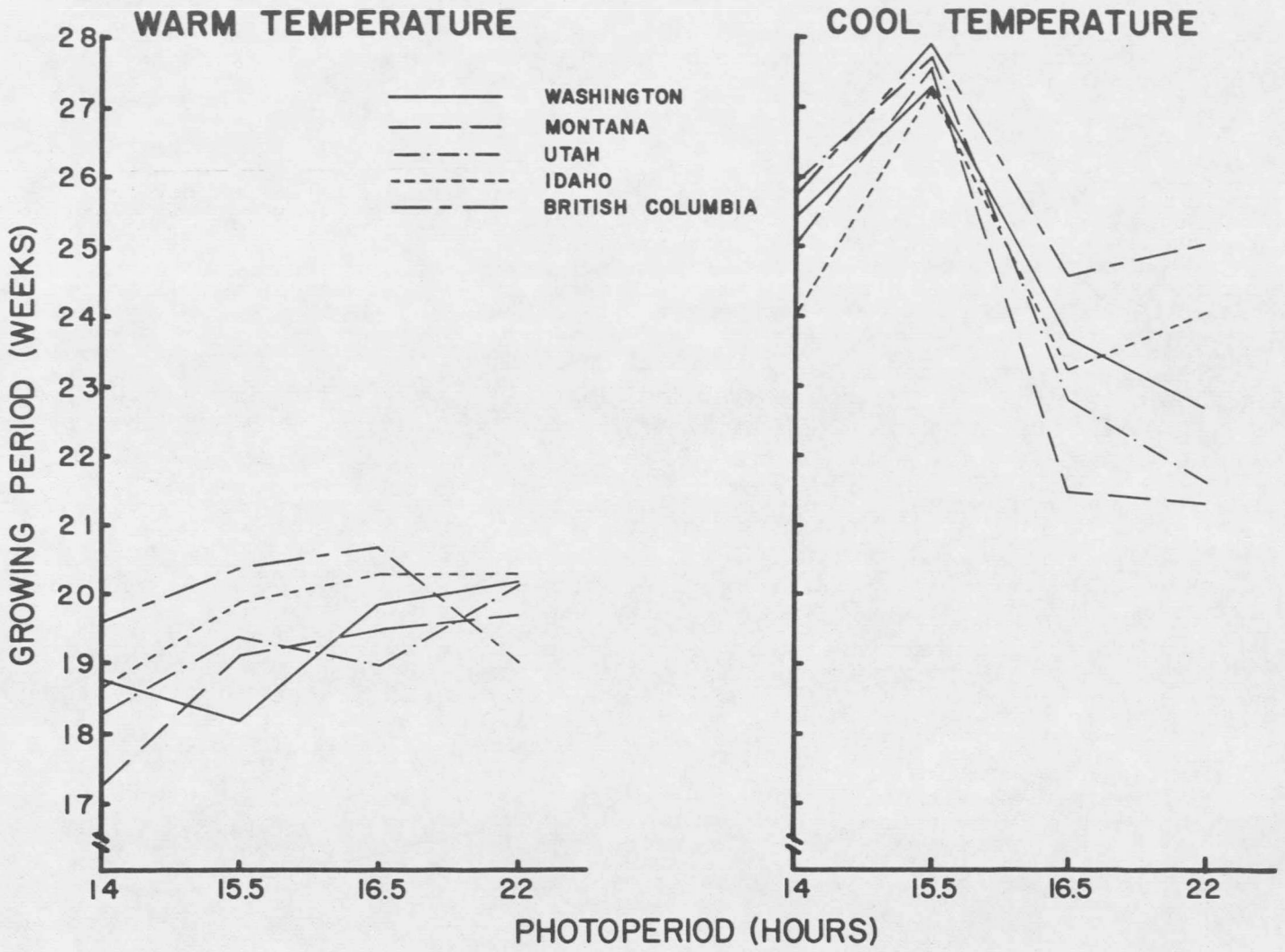
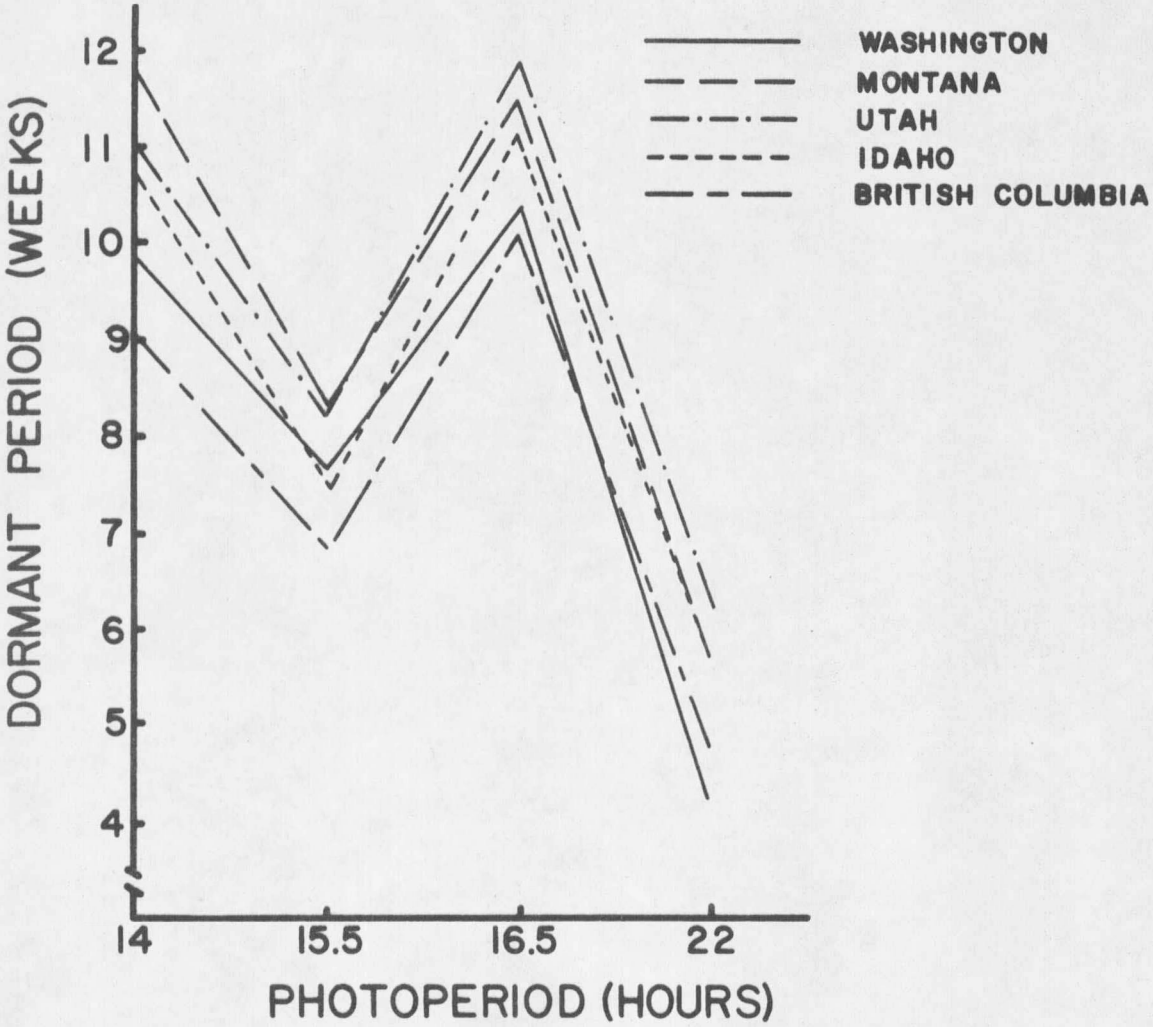


FIGURE 7. AVERAGE DORMANT PERIOD OF SEEDLINGS, BY STAND, WITH RESPECT TO DAYLENGTH (WARM TEMPERATURE).



Washington, and Idaho forming a group with a relatively long growing period, and Montana and Utah with shorter growth periods. At 15-1/2 hours the pattern was somewhat the same, however, here the growth period of the Washington stand was shortened considerably. It had, in fact, the shortest growing period of the group at the 15-1/2 hour daylength. In the 22-hour photoperiod the British Columbia source was affected in the same way that trees from Washington had been at 15-1/2 hours, the growing period being shortened drastically. This behavior on the part of British Columbia seedlings was very different from that of the other stands, which tended to increase their growth period at 22 hours compared to the other daylengths.

Stands varied significantly among themselves in the length of their dormant periods, but there was no variation in the way they reacted to daylength. British Columbia and Washington sources had the shortest dormancy periods, Montana and Utah the longest, and the Idaho stand was intermediate.

Variation within stands (Table 14). Variation in growth period among seedlings from different parent trees was significant in all stands except Washington. Conversely, no stand except Washington had significant differences in the way seedlings from different parent trees reacted in their growth period to daylength or temperature.

Dormant period was considerably more uniform within stands than growth period. Only two stands, Montana and Utah, had significant dif-

Table 14

Significance of Within-Stand Variation in Periods of Growth and Dormancy

Stand	Growing Period				Dormant Period	
	F	F x D	F x T	F x T x D	F	F x D
Washington	-	*	*	*	-	-
Montana	*	-	-	-	*	*
Utah	*	-	-	-	*	-
Idaho	*	-	-	-	-	-
British Columbia	*	-	-	-	-	-

* implies significance at the 5% level of probability.

F = Family; D = Daylength; F = Temperature.

- indicates not significant at the 5% level of probability.

differences among families, and families reacted differently to day-length only in the Montana source.

Variation in Growth of Seedlings in Fumigated and Non-Fumigated Soil (Table 15). Seedlings grown in fumigated soil (cool treatment) had significantly greater top and total mass than those grown in non-fumigated soil (warm treatment). Root mass, top mass/root mass, and height were not different between the two soil types.

Moisture Stress Tests

There were significant differences between moisture stress levels in all mass variables, but not in height. There were also significant differences in the manner in which the various stands reacted to moisture stress, but these differences were restricted to root mass, top mass/root mass, and height. Stands varied in the same way in top and total mass (Table 16).

For all stands except Utah and British Columbia, the decrease in top mass of seedlings with water stress was very close to linear. Among Utah and British Columbia seedlings the decrease in top mass was appreciably more between the 0.2 bar and 3.2 bar treatments than between the 3.2 bar and 5.2 bar treatments (Figure 9).

With the exception of the low elevation Washington stand, root mass was sharply lower in the 3.2 bar as compared to the 0.2 bar treatment, while in the 5.2 bar treatment, it was only slightly lower or, in

Table 15

Mass in 10^{-2} grams and Height in mm. per Seedling by Fumigated and Non-Fumigated Soil, Along with Probabilities for the Significance of F-values from Analysis of Variance Between Soil Types

	Total Mass	Top Mass	Root Mass	Top Mass/ Root Mass	Height
Non-fumigated soil	.053	.036	.018	2.50	33
Fumigated soil	.095	.078	.021	3.74	37
P value for the significance of F between soil types	.039	.026	.650	.227	.637

Table 16

Significance of Variation in Log_e Mass and Log_e Height Among Stands and Moisture Stress Treatments

	S	R	M	S x R	S x M	M x R	S x R x M
Total Mass	*	-	*	-	-	-	-
Top Mass	*	-	*	-	-	-	-
Root Mass	*	-	*	-	*	-	-
Top Mass/Root Mass	-	-	*	-	*	-	*
Height	*	-	-	-	*	*	-

* indicates significance variation at the 5% level.

- indicates not significant at the 5% level.

S = stands; R = replication; M = moisture stress.

FIGURE 8. AVERAGE TOTAL MASS, BY STANDS, AS A FUNCTION OF MOISTURE STRESS LEVEL.

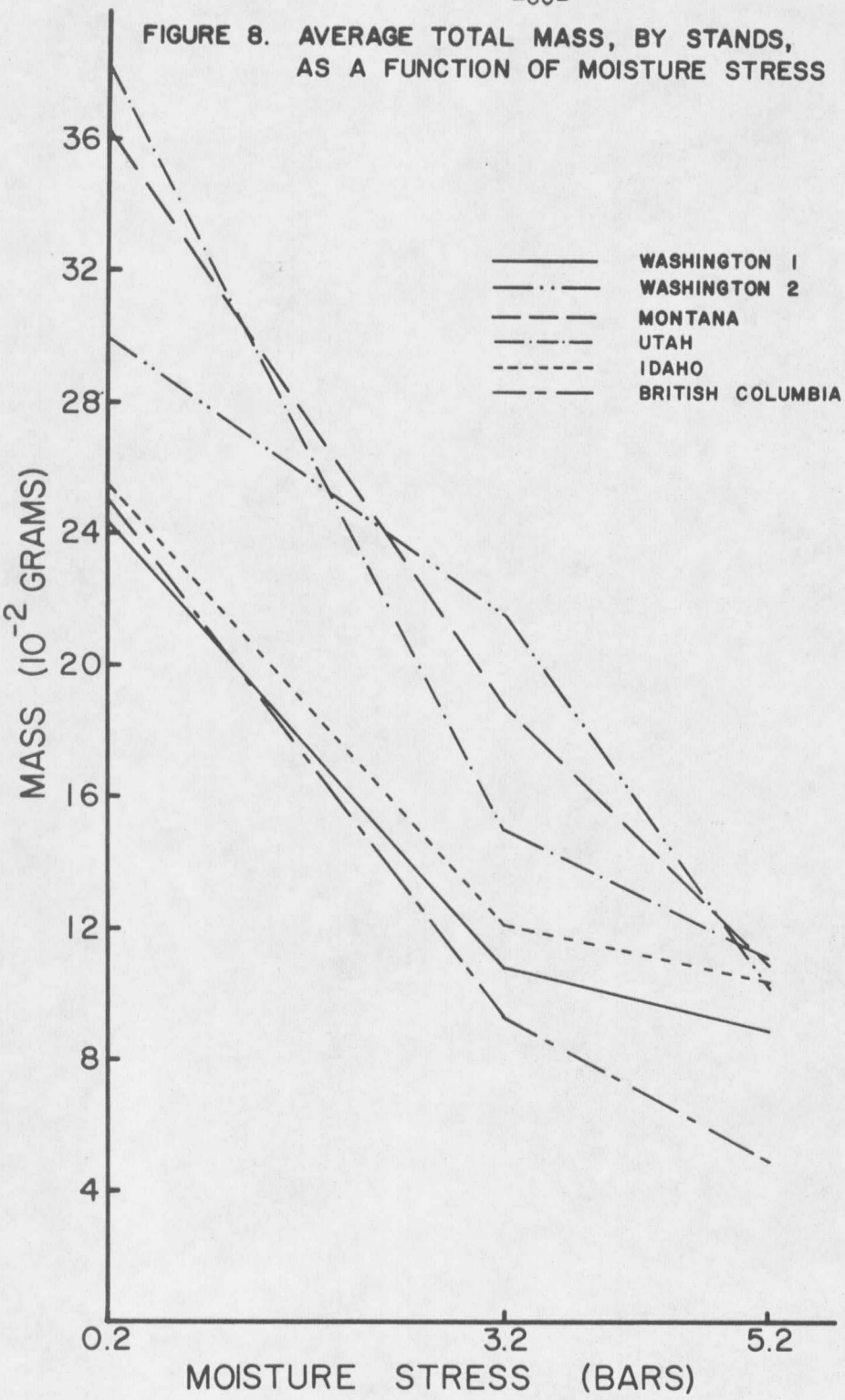
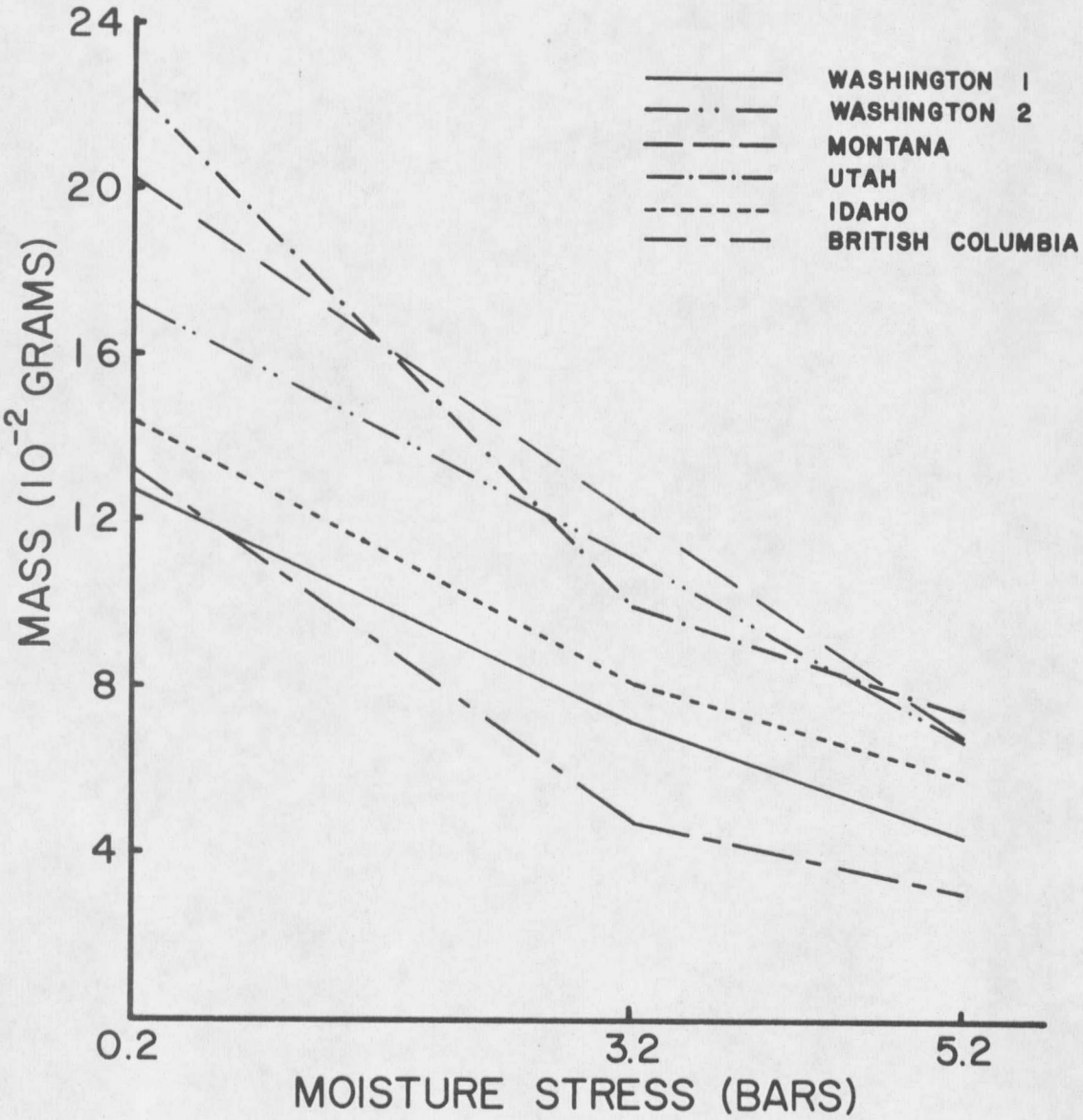


FIGURE 9. AVERAGE TOP MASS, BY STANDS, AS A FUNCTION OF MOISTURE STRESS LEVEL.



the case of the high elevation Washington and Idaho seedlings, higher in the 3.2 bar treatment. The behavior of the low elevation Washington seedlings was the opposite of the others, with the greatest reduction in root mass between the 3.2 bar and 5.2 bar treatments (Figure 10).

This different behavior of top and root masses in response to moisture stress resulted in considerable differences in the top mass/root mass among treatments. Again with the exception of the low elevation Washington seedlings, top mass/root mass was sharply higher in the 3.2 bar treatment as compared to the 0.2 bar, and then lower again in the 5.2 bar treatment. Top mass/root mass at 5.2 bars compared to 0.2 bars varied among stands. In the high elevation Washington and Idaho seedlings the ratio was very close to the same at the two levels, while among Montana, Utah, and British Columbia seedlings top mass/root mass at 5.2 bars remained appreciably higher than at 0.2 bars. In the Utah seedlings, the ratio at 5.2 bars was little changed from that at 3.2 bars. In the low elevation Washington stand top mass/root mass was the same at 0.2 and 3.2 bars, and sharply higher at 5.2 bars (Figure 11).

Heights were not significantly affected by moisture stress except among British Columbia seedlings. In seedlings of that stand, heights at 3.2 and 5.2 bars were significantly lower than at 0.2 bars.

FIGURE 10. AVERAGE ROOT MASS, BY STAND, AS A FUNCTION OF MOISTURE STRESS LEVEL

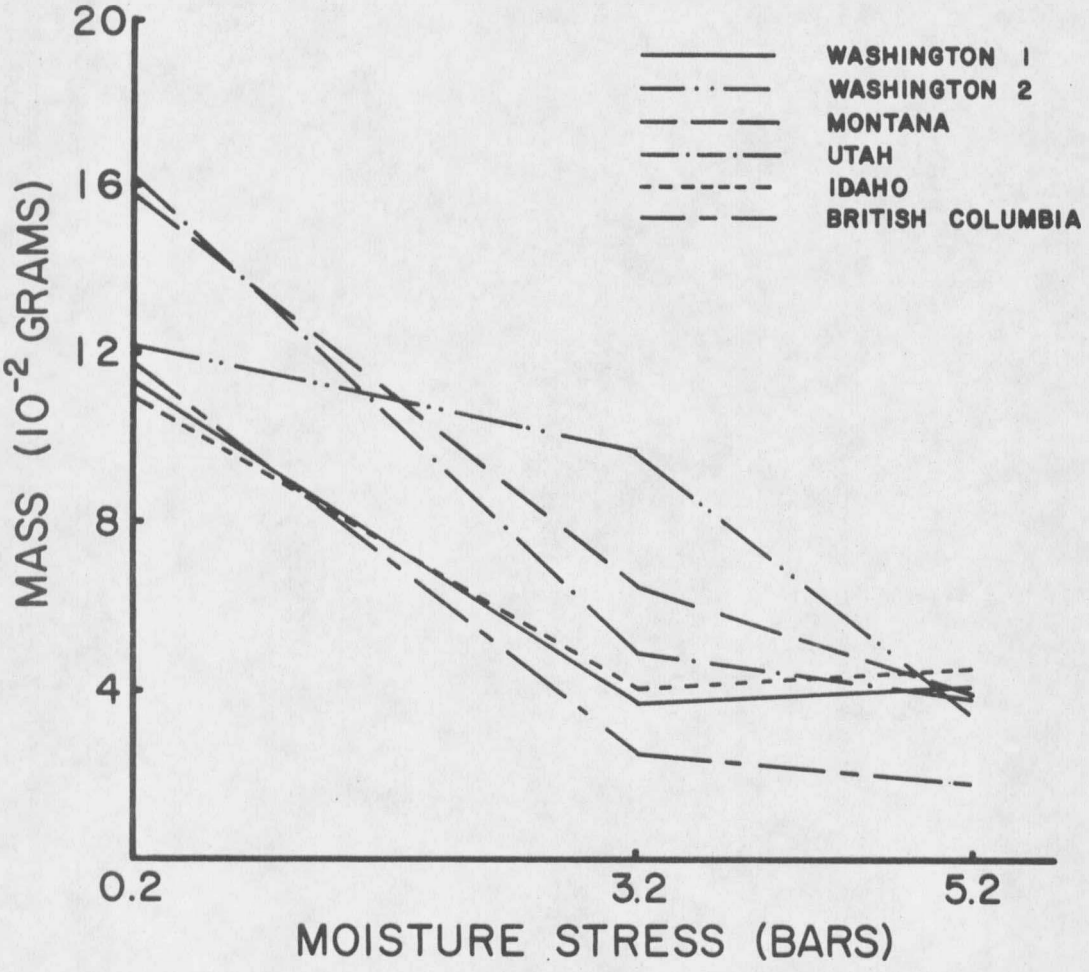
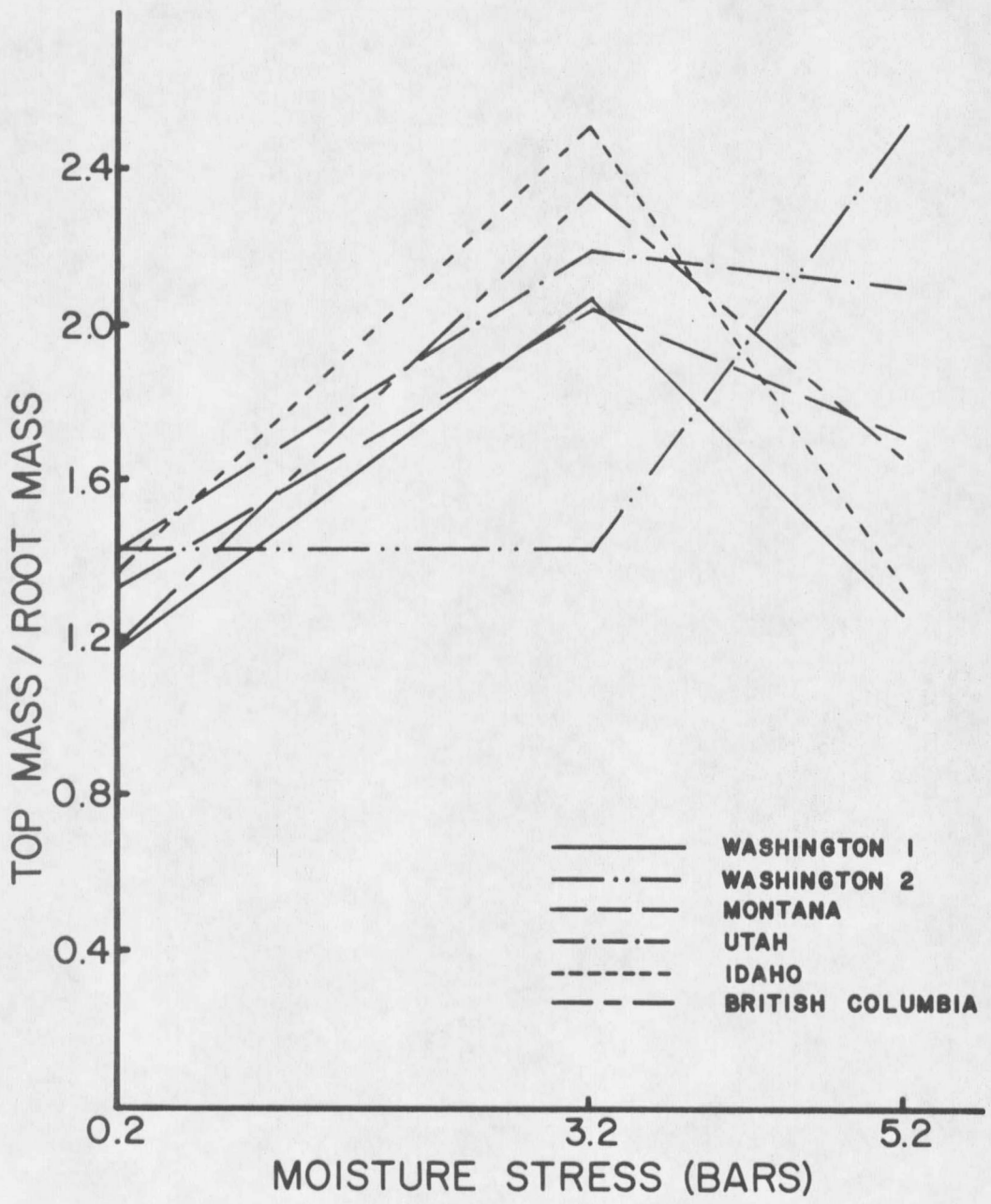


FIGURE 11. AVERAGE TOP MASS/ROOT MASS, BY STANDS, AS A FUNCTION OF MOISTURE STRESS LEVEL



Seedling mortality[12] averaged 27% at 3.2 bars and 43% at 5.2 bars (Table 17). At 3.2 bars mortality rate varied little among stands, ranging from 20% in the low elevation Washington and Montana stands to 35% in the high elevation Washington stand. At 5.2 bars mortality in the Montana, Idaho, and British Columbia stands was less than 10% greater than in the 3.2 bar treatment, while in the two Washington stands mortality was considerably higher at 5.2 bars than at 3.2 bars. The Utah stand behaved in a manner intermediate to these two groups.

With the exception of the low elevation Washington stand, each population had families which suffered less than 20% mortality at 5.2 bars, and at 3.2 bars every stand had families that suffered less than 20% mortality (Table 4). This relative resistance was most evident in the British Columbia, Montana, and Idaho stands. However, in the analysis of variance of mass and height changes within stands with respect to moisture stress only the Utah stand showed significant differences in the behavior of families with respect to moisture treatment, and this was only in height (Table 18).

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[12]Mortality figures include seedlings dead as well as those living but in such poor condition that their survival was not judged probable.

Table 17

Seedling Mortality by Stand and Moisture Stress Level

Stand	0.2 Bars	3.2 Bars		5.2 Bars	
	% Mortality	% Mortality	% of Families With Greater Than 20% Mortality	% Mortality	% of Families With Greater Than 20% Mortality
1	0	35	50	63	67
2	0	20	0	64	100
3	0	20	50	20	50
4	0	26	25	42	75
5	0	28	75	35	50
6	0	25	67	33	50
Average all Stands		27		43	

Table 18

Significance of Within-Stand Variation in Log_e Mass and Log_e Height With Respect to Moisture Stress

Stand	Total Mass			Top Mass			Root Mass			Top Mass/ Root Mass			Height		
	F	M	FxM	F	M	FxM	F	M	FxM	F	M	FxM	F	M	FxM
Washington #1	-	*	-	-	*	-	-	*	-	-	-	-	*	-	-
Washington #2	No MSR	*	No MSR	No MSR	*	No MSR	No MSR	*	No MSR	No MSR	-	No MSR	No MSR	-	No MSR
Montana	-	*	-	-	*	-	-	*	-	*	*	-	-	-	-
Utah	-	*	-	-	*	-	-	*	-	-	*	-	-	-	*
Idaho	*	*	-	*	*	-	*	*	-	-	*	-	*	-	-
British Columbia	No MSR	*	No MSR	No MSR	*	No MSR	No MSR	-	No MSR	No MSR	-	No MSR	No MSR	-	No MSR

* indicates significant variation at the 5% level. - indicates not significant at the 5% level.

F = family; M = moisture stress.

No MSR means no measure. In the Washington #2 and British Columbia stands progeny from only two parent trees survived at all moisture stress levels. It was felt that this number was inadequate to compare within stand variation

Summary of Results

Variation Between Treatments

At a given daylength seedlings were consistently taller under warm temperatures than in cool. The variation in mass with temperature was photoperiod dependent, with long photoperiods tending to give larger masses in cool temperatures than in warm, and short photoperiods the opposite. Top mass/root mass was always greater in the warm treatment than in the cool.

Within each temperature treatment greatest growth was always at 22-hour daylengths and least at 15-1/2 hour daylengths. In warm temperatures, growth at 14 hours was better than at 16-1/2 hours. In cool temperatures this was reversed.

There was little obvious correlation between either growing period or dormant period and size. In the cool treatment, growing period in the various daylengths was inversely related to size of seedlings. In the warm treatment, length of growing period was directly related to daylength, while the second greatest seedling size was in the shortest photoperiod.

Variation Among Stands

Mass values tended to be uniform among stands. The British Columbia stand was significantly higher than the others in top mass and Utah significantly lower, but there were no differences in root

mass. Height was more variable. British Columbia seedlings were consistently taller, with Washington and Idaho forming a middle and Utah and Montana a lower group, except at the two shorter photoperiods under cool temperatures, where 15-1/2 hours favored the Utah stand and 14 hours the Montana.

There were no differences in the way the masses of the various stands reacted to daylength, and in the stand-temperature interaction, only root mass and top mass/root mass gave significant differences, primarily due to the effect of warm temperatures on root mass of British Columbia seedlings. Stands behaved somewhat differently in their heights with respect to daylength and temperature, with 16-1/2 hour daylengths and cool temperatures favoring Utah seedlings and 14-hour daylengths with cool temperatures favoring Montana seedlings relative to those from other stands.

With respect to growing period, there were significant differences in the manner in which stands reacted to daylength, but none in their reaction to temperature. Differences in daylength-stand interaction were primarily due to British Columbia seedlings which, in contrast to the other stands, had their shortest growing period in the 22-hour photoperiod. At all other daylengths, British Columbia seedlings had the longest growth period, Montana and Utah seedlings the shortest, with Idaho and Washington seedlings intermediate in their growth period.

Mass was affected by moisture stress but not height. Stands reacted the same in their top mass to moisture stress treatments, but not in their root mass or height. Root mass was consistently lower in stress treatments than in the control, however two stands--Idaho and Washington #1--had higher root masses at 5.2 bars water stress than at 3.2 bars, while for the other stands it was lower. Mortality differences among stands were small at 3.2 bars, but at 5.2 bars the two Washington stands suffered considerably higher seedling loss than the others.

Variation Within Stands

British Columbia seedlings had greater variation within families than between, while in Utah seedlings the opposite was true. Washington and Idaho seedlings seemed to vary considerably both within and between families, while those from Montana were relatively uniform both within and between.

CHAPTER 5

DISCUSSION AND CONCLUSIONS

Climatic Differences Between Parent Stand Locales

As Wright (1973) has pointed out, in testing various populations of tree species one finds many differences which are difficult to explain "in terms of adaptation to modern climatic and site conditions." "Purely statistical data on noninterpretable interactions," Wright concludes, "are of little practical value." Certainly on a macroscale, i.e., interpopulation differences, the inclusion of observations into a useful model requires that we deal only with those effects to which some cause may be reasonably (although perhaps not conclusively) assigned. As pointed out in the introduction to this paper, however, within-population variation, even though it has a large random component, is of interest because it is the stuff of evolutionary change.

Thus, I take two approaches in discussing the data of this study. First, and primarily, I will be concerned with the reactions of seedlings to the various experimental conditions, and the similarities and differences of these reactions among the different seed sources. Where differences between sources occur, I will discuss these in relation to factors of the native habitat, such as photoperiod, temperature regime, and moisture conditions. Secondly, I will look at variation between seedlings in a stand and compare this intrapopulation variation among stands.

Table 19 gives climatic data for the various stand locations. Because of the interaction of elevation, latitude, and macroclimatic factors, the most northerly provenances are not the coolest. The Montana and Utah stands occupy the most severe sites in terms of temperature, with extremely short frost-free periods and temperatures that commonly dip close to freezing in the warmest part of the summer. The Washington, Idaho, and British Columbia stands are very similar in climate, the more northerly location of the Canadian source being counteracted by its lower elevation (the low elevation Washington stand--Washington #2--was not included in the daylength-temperature tests, and therefore will not be included in the discussion of these effects).

Daylength is a function only of latitude, and photoperiod during the height of the growing season increases with latitude. It does not follow from this, however, that phenological effects such as budset should be keyed to longer daylengths in the more northerly provenances, if indeed they are keyed at all to photoperiod. The more severe climatic conditions of the southern sources suggest that they may cease growth earlier in the fall than seedlings from the north, and thus the relative photoperiod dependence one would expect among stands is confounded.

Precipitation during the growing period is relatively high in the British Columbia, Montana, and Utah stands; low in Idaho and the low-elevation Washington stand; and intermediate in the high-elevation Wash-

Table 19

Weather Data for Stand Locations (United States data from Baker, 1944; British Columbia data from Canada Department of Mines and Technical Surveys, 1957)

	Growing Scale (Average Consecutive Days With T° Above 5.5° C)	Average Consecutive Days With T° Above 0° C.	Mean July Daily Low Temp. (°C.)	Mean July Daily High Temp. (°C.)	Average Yearly Precip. (Inches)	Inches Precip. in June	July	Aug.
Washington #1	150	60	5	22	45	2.8	1.7	1.5
Washington #2	210	135	10	28	25	1.6	1.0	0.8
Montana	130	15	4	22	22	3.5	2.0	1.4
Utah*	138	35	2	21	29	2.1	2.5	2.4
Idaho**	165	77	6	27	37	2.2	1.1	1.1
British Columbia	160	60	(Mean July Temp.--13)		20	(Mean Precip. June-July--.8)		

*Baker could find no weather data for the Uinta Mountains. He speculated that climate there was very similar to that in his Western Colorado and Western Wyoming zones. The data given here is an average of those two.

**The Idaho stand sampled in this study is located on the border of Baker's Northern and Central Idaho regions. The author felt that the area was not typical of either region, and yet somewhat like both. Consequently, data given here is an average of the two.

ington stand. Variability of precipitation is approximately equal in all United States stands, with about one year out of five having less than one-half the average rainfall (Baker, 1944). No similar estimate is available for the locale of the Canadian source.

Variation Among Treatments

Photoperiodism, thermoperiodism, and their interaction in pines is a complex phenomenon. For excellent reviews of the subject see Mirov (1967), Downs (1962), and Hellmers (1962). In seven species of pines tested by Downs (1962), both height and mass increased monotonically with increasing photoperiod, up to 16 hours of light. Downs and Piringer (1958) found that the height growth of ponderosa pine and both height and weight of loblolly pine were decreased by continuous light. Vaartaja (1959), testing seed from British Columbia, found a ratio of height at 18 hours photoperiod to height at 12 hours photoperiod of 2.1 in lodgepole pine. Giertych and Farrar (1962) found a ratio of dry weight at 17 hours photoperiod to dry weight at 10 hours photoperiod of approximately 1.4 in lodgepole seedlings from an Alberta source at 50°N. latitude. In this experiment the ratios of mass and height at two daylengths were dependent on temperature and the daylengths used. The lack of a significant difference between total mass at 14 and 22 hours daylength in the warm treatment indicates that extra light of itself was probably not the sole cause of size variation between treatments, and

therefore some photoperiodic dependence is indicated by treatment differences.

Greatest height and top mass growth in these tests were clearly at the longest photoperiod, but the effect of the three shorter daylengths shows no clear relation between growth and photoperiod. Results in the 16-1/2 hour warm temperature treatment were confounded by depressed growth of seedlings in the inner part of the planting bed. This effect has been noted by Voight (1962) as not uncommon in nursery beds and greenhouse cultures. Its cause is unknown, although it can usually be cured by aeration. The phenomenon was not seen in any other test bed, and the resulting depression of average growths in the 16-1/2 hour warm treatment relative to the 14-hour warm suggests that the cool treatment may give a more accurate measure of relative growth at the two photoperiods. Depression in growth at the 15-1/2 hour daylength was experienced at both temperatures, was not localized to any one area of the bed, and has no clear explanation. The effect seemed to be associated with a much more severe reaction to the conditions of high soil salts experienced early in the experiment (see the Methods section). Experimentation on the interaction between photoperiod and nutrient uptake is suggested.

Despite the fact that a soil difference was introduced between temperature treatments when the cool treatment soil was fumigated, valid conclusions can be drawn concerning temperature effects. The fact that

cool treatment soil produced seedlings with significantly larger top masses than that from the warm treatment when grown under the same temperatures serves to underscore the significance of smaller top masses produced under cool temperatures. Root masses, which were not significantly affected by soil differences, were not different in the two temperature treatments, indicating that tops and roots respond to different temperature stimuli in their growth patterns. Krugman and Stone (1966) found that root mass of ponderosa pine was not affected by cold night temperatures, while top mass and height were greater under cold nights (6°C.) and warm days. A daylength component of the differential root-top reaction seen in this experiment is also indicated, with root growth greater at the shortest daylength than at the longest in the warm temperature treatment.

The suggestion that lodgepole pine root growth is favored over top growth at cool temperatures or, in warm temperatures, at short daylengths, is supported by observations in the literature. These have been many reports of root growth in the spring, fall, and winter, when aerial portions of the tree are apparently dormant (see Romberger, 1963, for a review). Kaufmann (1945) reported that Jack pine in Minnesota began root growth in the spring when the temperature in the upper six inches of soil reached 5° C. Preston (1942) found that lodgepole pine roots grew continuously "from the time the frost leaves the ground in the spring until it freezes again in the fall." He excavated lodgepole

roots that were actively growing on November 2, with a foot of snow on the ground. These facts indicate that the smaller top mass/root mass ratios in the short daylength warm temperatures and in the cool treatments were in part a result of the relatively shorter total growing times of aerial portions in these treatments, while root growth was continuous. (Recall that while growth period as defined for purposes of this paper--weeks to first budset--was shorter in the warm treatment than in the cool, buds were broken and growth resumed in the warm treatment, while in the cool treatment, once set, buds were not again broken). Sweet and Wareing (1968a) found a close association between top mass/root mass and length of time required to set a terminal bud in lodgepole pine.

It might be logically inferred from the above discussion that differences in top mass between treatments were primarily due to differences in growth period of the seedlings. The effect of growth period on differences in height and mass among populations will be discussed later in the paper, however, subjective evaluation of seedling size at various stages of development gave the very clear impression that cool temperature seedlings were generally smaller and less vigorous than warm temperature seedlings of the same age. Undoubtedly growth period plays a role in temperature-dependent size differences, but rate of growth is slowed at low temperatures and elongation may cease altogether below 5.5° C. (Kienholz, 1934). This undoubtedly contributed to

to differences in top mass and height between temperature treatments. Apparently the enzymatic machinery responsible for root growth is less susceptible to low temperatures than that of tops.

The effect of temperature on phenological sequence in lodgepole pine is striking. The tendency to set buds in mid-summer and then resume growth in the fall is not uncommon in tree species (Romberger, 1963). In lodgepole pine, it occurs in at least some nurseries, although among trees in the wild it is apparently not normal (Dahlgren, 1973). A possible implication of the delay in first budset under cool temperatures is that trees did not undergo this period of mid-summer dormancy. Bonner and Hellmers (cited in Hellmers, 1962) found that high night temperatures caused both an increased tendency to form terminal buds and an increased tendency to break them. Vegis (1956) suggested that high temperatures promoted bud formation in trees, and that this was caused by oxygen deficiency in buds. Pollack (1953) also felt that oxygen became limiting in buds during high temperatures, resulting in the accumulation of a growth inhibitor. Another interpretation is possible, however. The production of adult needles by cool temperature seedlings well in advance of budset suggests that they experienced a physiological change which, in the warm treatment, was associated with termination of the first dormant period. This, coupled with the somewhat anomalous (Vaartaja, 1959) fact that buds were set first in the longest daylengths of the cool treatment, suggest that cool treatment

seedlings may have undergone a period of dormancy without setting a terminal bud. Such a case has not been reported before to the author's knowledge, but it remains a possibility.

Temperature seems to also alter the relation between growing period and daylength. As a rule, growing period increases with increasing daylength (Downs and Borthwick, 1956; Nitsch, 1957; Vaartaja, 1957; Wareing, 1950), as it generally did in the warm temperature treatments of this test. Cool temperatures, however, seem to negate the effects of long days on growth period of lodgepole pine. This effect has been noted in other species (Downs, 1962). Among individual stands the relationship of growth period at 22 hours photoperiod to that at 16-1/2 hours in the cool treatment is the mirror image of the same relation in the warm treatment, with those stands which had longer growth periods in the 22-hour treatment at warm temperatures having shorter growth periods under 22 hours in the cool treatment, and vice versa. There seems to be no ready explanation for this, but it serves to illustrate the extent of daylength-temperature interaction in the phenology of lodgepole pine.

Variation Among Stands

Critchfield (1957) observed that time of year seemed to have no effect on the growth period of greenhouse-grown lodgepole pine seedlings. In his tests seed from locales with severe climates produced seedlings

which had a shorter growth period than those from milder climatic areas, but no daylength dependence was seen. Similarly, in this study seedlings whose parent stands had the mildest climates also had the longest growing periods but, in contrast to Critchfield's findings, there were small but significant differences in growth periods among the various daylengths.

The pattern of variation in growing period of individual stands with respect to photoperiod seems to bear no relation to the latitude of the parent stand. The two stands from the same latitude--Montana and Idaho--behaved the same way, with their shortest growth period at the shortest daylength. However, the behavior of seedlings from the other stands appears to have no orderly relation to latitude. It is concluded that no meaningful interaction exists between stand locations and daylength with respect to growth period. This is supported by observations at the U.S. Forest Service Lucky Peak Nursery in southern Idaho, where lodgepole pine from all sources start and stop growth at the same time of year (Morsby, 1972).

The uniformity of stands in their mass values and in the manner in which their masses reacted to daylength and temperature is remarkable. The significant differences that do exist among top masses of stands--British Columbia high and Utah low--may correlate positively with growing period at the stand site, as studies in other pines have shown (Squillace and Silen, 1960; Langlet, 1959; Giertych and Farrar, 1962).

However, the equality in mass between Montana seedlings (from the severest habitat) and those from Washington and Idaho cast doubt on this relation. Height growth under warm temperatures seemed to present a clearer correlation with climatic factors of the place of seed origin, the seed from low elevations producing taller seedlings. Barnes (1967) noted this same elevational effect on height growth in Western white pine, as did Callaham and Lidocoet (1961) in ponderosa and Jeffy pines. Wright et al. (1969), however, did not see any predictable differences between low and high elevation sources of ponderosa pine.

Sweet and Wareing (1968a), in a study of growth rates in four provenances of lodgepole pine, obtained results very similar to those of this work, with height differences among provenances related to the time period of height growth (time from germination to terminal budset), but no similar correlation existing with respect to differences in mass. They attributed this to the ability of lodgepole pine to continue dry matter accumulation long after height growth has ceased (Sweet and Wareing, 1968b).

Height in cool temperatures gave the clearest example seen in the experiment of ecotypic variation which could be related to climatic conditions at the place of origin, with height growth in seedlings from the more southerly, high-elevation stands favored in cool temperatures and short daylengths. Irgens-Moller (1957) noted a similar temperature-daylength interaction in Douglas fir, in which ecotypic photoperiodic

responses of high elevation trees were magnified by cool temperatures, and disappeared altogether with warm temperatures.

Stands reacted differently in their root mass with respect to temperature, but this was solely due to the British Columbia seedlings and their smaller root mass in warm temperatures. Apparently the distribution of photosynthate between root and top is affected by temperature in the British Columbia seedlings to a greater degree than is true in the other stands tested.

The above observations lead to the conclusion that small but significant geographic variation in growth and phenology of lodgepole pine exists, but only in height is there ecotypic variation with respect to temperature and daylength, and this is in response to elevational gradients rather than latitudinal. Perry and Lotan (1974) have described variation in the germination per cent of these same seed sources. Seed from Idaho, Montana, and Washington (high elevation) formed a high germinating group, while that from Utah, British Columbia, and Washington (low elevation) had poor germination per cents. Temperature did not appreciably affect these relation. Stratification requirements were greatly different among stands, with Utah seed requiring long periods of stratification and British Columbia seed affected adversely by even short periods (two weeks) of stratification. Rafn (1915), Haasis and Thrupp (1931), and Critchfield (1957) also demonstrated germination differences between various populations of lodgepole pine. Sweet and

Wareing (1968a) showed significant difference in duration of height growth, and consequently height, among four provenances of lodgepole pine, but found no significant differences in relative growth rate. It is impossible under the conditions of this experiment to determine whether mass differences were due to differences in rate of dry matter accumulation or period of dry matter accumulation.

The lack of latitudinally-correlated photoperiodic ecotypes in lodgepole pine seems to be unique among pines (and perhaps among all tree species that have been studied). Ecotypic variation in photoperiodic response has been shown to exist in at least six other species of pines (Vaartaja, 1959; Downs and Piringer, 1958; Giertych and Farrar, 1962; Wassink and Wiersma, 1955; Wells, 1964a, 1946b; Wright, 1973) based on latitudinal correlations. Karschon (1949) suggested that photoperiodic ecotypes of Scots pine existed along elevational gradients. Support for the observations of this study comes from Critchfield (1959) however, who found variation in morphological characters of lodgepole pine well correlated with elevation, but poorly correlated with latitude. This latitudinal uniformity lends credence to the argument of Bates (1917) that lodgepole pine spread throughout its present range in fairly recent times and quite rapidly. Rickleffs (1973) has pointed out that, if a population is relatively flexible genetically, its uniformity could be due to the rapid spread of a small, uniform population.

The variable response of root mass in response to moisture stress

seems to have some relation to habitat of the parent stand, with seedlings from the area of summer drought (Washington and Idaho) maintaining their root mass at the high moisture stress levels better than those seedlings from other areas (with the exception of the low-elevation Washington seedlings whose parent trees were growing adjacent to a stream). Although the analysis of variance shows no significant variation in the root mass of British Columbia seedlings with moisture stress, Figure 10 seems to argue differently. It is felt that a low sample size in the British Columbia seedlings, due to poor germination, gave undependable results in the analysis of variance.

Variation Within Stands

Two factors which would seem to bear on the nature of diversity within a given population are the stability of the local environment and the length of time which a population has had to adapt to this local environment. Pianka (1966) says that stable local climates allow the evolution of more specialized adaptedness. Carson (1959) has suggested that chromosome polymorphism, and thus adaptive flexibility, is greater in the center of a species range, while peripheral populations are a "more prolific field of genetic experimentation" (Dobzhansky, 1970). Thus, at the limits of a species range one would expect to see a great deal of diversity among families in a given population, as is seen in the seedlings of the Utah stand while, near the

center of the range, the increased heterozygosity which Carson postulates should produce increased variation within families, but if the climate is stable, different families may vary little among themselves. This latter situation is what is seen in the British Columbia seedlings. If one draws a gradient of increasing inter-familial variation and decreasing intra-familial variation from north to south, the Washington and Idaho stands fit quite well, a further indication that the spread of lodgepole pine has been from north to south. The high degree of variation among families in response to daylength and temperature in the Washington, Idaho, and Utah stands raises the intriguing possibility that these stands are in an active and, because of small differences between them, early stage of adaptation to the local conditions. The Montana stand doesn't fit into this scheme, having the least total variation in all (in perhaps the least stable habitat). However, by changing elevation with latitudinal progression, populations could migrate down the backbone of the Rocky Mountains with very little change in environmental factors other than daylength, and thus might retain a relatively high degree of uniformity among families. Why, if this is true, the amount of intra-familial variation (and thus heterozygosity) should be less in the Montana stand than in the British Columbia stand is not clear. Perhaps, for some reason, a high degree of heterozygosity is of negative adaptive value in severe habitats.

Summary of Conclusions

1. Except for the 22-hour photoperiod, top mass and height growth of lodgepole pine are reduced significantly in cool temperatures, while root growth is not affected.

2. Phenological sequence of lodgepole pine is temperature-dependent, with cool temperatures delaying budset.

3. Photoperiodic dependence in the growth of lodgepole pine is temperature-dependent, growth increasing with increasing daylengths in cool temperatures, but the same relation not necessarily holding in warm temperatures.

4. There are significant differences among stands in height growth and these differences seem to correlate with length of growing season at the place of origin. Although there are some differences in mass and phenology, stands tend to be more uniform in these factors than in height, and the differences that exist are not correlated with growing season at the place of origin.

5. British Columbia seedlings are generally superior to those from the United States in height and mass growth.

6. There are no photoperiodic ecotypes with respect to mass or phenology. There are elevational ecotypes with respect to seedling height, however, there has been no significant differentiation in lodgepole pine along a latitudinal gradient. Hypothesis I(a), that there

is significant difference among stands in the response of lodgepole pine seedlings to different temperatures, is accepted and I(b), that there is significant variation among stands in the response of lodgepole pine seedlings to different daylengths, is rejected.

7. Stands react differently in their height and root mass to moisture stress, but not in their top mass. Seedlings from areas of summer drought withstand stress better than those from areas of high summer moisture. Hypothesis I(c), that there is significant variation among stands in the response of lodgepole pine seedlings to different moisture stress regimes, is accepted.

8. A north-south cline exists in the degree and nature of variation within stands (excepting the Montana stand). Lodgepole pine probably originated in Canada and has spread rapidly south. Some stands in the United States are in a state of active adaptation to local conditions. Hypothesis II(a) and II(b), that there is no significant variation within stands in the response of lodgepole pine seedlings to different temperatures and daylengths, are accepted for the British Columbia and Montana stands, and rejected for all others. Hypothesis II(c), that there is no significant variation within stands in the response of lodgepole pine seedlings to different moisture stress regimes, is accepted for all stands.

APPENDICES

APPENDIX I

Table 20

Parent Tree Data

Stand	Tree No.	Age (yrs.)	Height (meters)	Diameter (Breast Hgt.) (cm.)	Length of Live Crown (meters)	Elevation (Meters)	Aspect
Washington (High elev.)	101	64	21.0	22.4	6.3	1590	N
	102	64	22.8	23.1	7.8	1590	NW
	103	67	21.9	22.9	9.0	1590	NW
	104	67	20.4	23.1	6.6	1590	NE
	105	66	20.7	19.8	9.0	1590	N
	106	67	21.9	24.1	9.9	1590	N
	107	68	23.7	22.9	12.0	1590	N
	108	65	22.8	26.4	12.9	1590	N
	109	68	17.4	20.1	11.7	1590	N
	110	67	23.7	27.7	10.4	1590	N
Washington (Low elev.)	201	35	20.4	20.6	7.2	735	Flat
	204	36	16.5	14.7	6.9	735	Flat
	206	36	15.6	19.6	9.0	735	Flat
	207	38	15.9	18.3	8.7	735	Flat
Montana	301	138	22.5	37.6	15.0	2160	Flat
	302	176	23.7	26.7	8.1	2190	N
	303	198	22.5	27.7	9.3	2160	Flat
	304	77	17.7	21.6	8.7	2160	Flat
	305	159	21.3	29.0	11.7	2160	Flat
	306	111	20.4	28.4	17.3	2160	Flat
	307	85	22.2	27.2	12.3	2160	Flat

(Continued)

Table 20 (Cont.)

Stand	Tree No.	Age (yrs.)	Height (meters)	Diameter (Breast Hgt.) (cm.)	Length of Live Crown (meters)	Elevation (Meters)	Aspect
Montana (Cont.)	308	96	17.1	20.3	8.1	2160	Flat
	309	122	19.8	22.1	13.1	2160	Flat
	310	97	14.7	18.3	9.6	2160	Flat
Utah	401	178	13.5	23.6	7.2	2500	NW
	402	103	15.9	25.4	8.1	2560	Flat
	403	103	15.3	16.5	7.2	2560	W
	404	88	11.1	21.8	6.9	2790	Flat
	405	88	12.9	19.8	7.8	2790	E
	406	116	14.6	19.0	6.3	2500	NW
	407	107	15.9	18.5	6.9	2580	Flat
	408	87	11.7	18.8	6.6	2790	Flat
	409	165	18.0	23.6	8.4	2745	NW
	410	86	14.4	19.0	6.9	2700	NW
Idaho	501	96	29.7	36.3	13.8	1530	E
	502	104	20.1	21.1	10.8	1530	E
	503	104	29.4	36.1	16.8	1530	E
	504	60	19.8	20.8	11.7	1530	SE
	505	111	24.3	21.1	8.4	1530	Flat
	506	93	25.2	29.5	9.0	1530	W
	507	117	28.2	31.2	14.1	1530	W
	508	74	24.0	29.2	14.1	1530	E
	509	120	28.2	25.1	9.9	1530	E
	510	74	25.2	28.4	33.6	1530	E

(Continued)

Table 20 (Cont.)

Stand	Tree No.	Age (yrs.)	Height (meters)	Diameter (Breast Hgt.) (cm.)	Length of Live Crown (meters)	Elevation (Meters)	Aspect
British Columbia	601	106	23.7	30.5	--	690	Flat
	602	72	24.6	32.5	--	690	Flat
	603	70	22.2	30.0	--	690	Flat
	604	69	23.1	36.3	--	690	Flat
	605	79	26.4	36.8	--	690	Flat
	606	56	24.6	36.8	--	690	Flat
	607	86	27.3	34.0	--	690	Flat
	608	50	21.6	22.9	--	690	Flat
	609	86	25.5	42.9	--	690	Flat
	610	64	21.0	22.1	--	690	Flat

APPENDIX II

Table 21

Mass, Height, and Phenological Measurements by Stands and Treatments*

Washington (High Elevation)

Temp.	Day-Length (hours)	# OBS for Mass and Phenology	Total Mass		Top Mass		Root Mass		Top Mass/ Root Mass		Growing Period		Dormant Period		# OBS for Height	Height	
			Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.		Mean	S.D.
Warm	14	28	29.8	10.6	22.7	8.3	7.1	2.7	3.3	0.9	18.8	2.6	9.9	3.3	202	51	16
	15½	28	19.3	10.2	14.7	7.9	4.6	2.6	3.4	1.0	18.1	1.1	7.7	1.9	223	45	14
	16½	28	22.6	8.4	16.6	6.5	6.0	2.3	2.8	0.7	19.9	2.1	10.4	3.4	206	40	15
	22	26	36.0	15.0	28.8	12.8	7.2	2.8	4.1	1.1	20.2	3.9	4.2	1.9	188	63	18
Cool	14	27	16.5	5.3	10.3	3.5	6.3	2.1	1.7	0.6	25.4	2.8	--	--	143	26	6
	15½	26	5.2	1.4	3.4	1.1	1.8	0.5	1.9	0.6	27.3	1.2	--	--	110	27	66
	16½	25	21.1	6.6	12.7	4.2	8.4	2.6	1.5	0.2	23.7	3.2	--	--	146	33	9
	22	25	45.8	29.3	34.0	24.5	11.8	5.4	2.8	1.0	22.7	2.9	--	--	94	44	15

*All mass values given in 10^{-2} grams. Height in mm.; growing and dormant periods in weeks.

APPENDIX II (Cont.)

Table 22

Mass, Height, and Phenological Measurements by Stands and Treatments*

Montana

Temp.	Day-Length (hours)	# OBS for Mass and Phenology	Total Mass		Top Mass		Root Mass		Top Mass/ Root Mass		Growing Period		Dormant Period		# OBS for Height	Height	
			Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.		Mean	S.D.
Warm	14	30	30.3	9.4	23.3	7.6	7.0	2.3	3.4	0.8	17.3	2.0	11.9	3.7	243	45	13
	15½	30	18.7	9.9	14.2	7.8	4.5	2.3	3.2	0.7	19.1	1.6	8.3	1.7	275	42	11
	16½	30	22.9	9.1	16.8	6.7	6.1	2.6	2.8	0.5	19.5	1.9	11.5	2.9	248	39	14
	22	30	34.7	12.2	27.6	9.7	7.1	2.9	4.1	1.0	19.7	2.4	5.7	3.1	250	55	16
Cool	14	30	16.3	5.9	9.6	3.3	6.7	2.7	1.5	0.2	25.0	2.8	--	--	234	27	7
	15½	29	5.3	1.6	3.5	1.1	1.8	0.6	2.0	0.7	27.5	1.7	--	--	135	22	6
	16½	29	22.8	7.7	13.1	4.3	9.6	4.3	1.5	0.5	21.5	2.8	--	--	204	33	42
	22	30	42.2	12.3	31.1	9.3	11.1	3.9	2.9	0.8	21.3	2.7	--	--	163	42	13

*All mass values given in 10^{-2} grams. Height in mm.; growing and dormant periods in weeks.

APPENDIX II (Cont.)

Table 23

Mass, Height, and Phenological Measurements by Stands and Treatments*

Utah

Temp.	Day-Length (Hours)	#OBS for Mass and Phenology	Total Mass		Top Mass		Root Mass		Top Mass/ Root Mass		Growing Period		Dormant Period		# OBS for Height	Height	
			Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.		Mean	S.D.
Warm	14	30	27.5	8.7	21.0	6.9	6.5	2.3	3.4	1.0	18.3	1.7	11.1	2.5	277	47	13
	15½	30	19.3	12.9	14.2	9.5	5.1	3.6	2.9	0.8	19.4	1.6	8.2	2.9	334	43	11
	16½	29	22.0	8.4	15.3	6.3	6.7	2.8	2.4	0.7	19.0	1.9	11.9	2.9	286	39	13
	22	30	30.0	12.0	23.3	10.0	6.7	2.9	3.7	1.2	20.1	2.4	6.3	2.8	260	55	16
Cool	14	29	13.0	4.2	8.1	2.8	4.9	1.7	1.9	1.1	25.9	2.4	--	--	205	25	7
	15½	28	5.8	1.5	3.8	1.0	2.0	0.8	2.0	0.6	27.7	1.0	--	--	157	23	6
	16½	28	21.0	7.1	12.3	4.5	8.6	3.0	1.4	0.3	22.8	3.2	--	--	220	33	8
	22	28	38.9	17.9	28.1	13.8	10.8	4.6	2.6	0.5	21.6	2.8	--	--	156	45	56

*All mass values given in 10^{-2} grams. Height in mm.; growing and dormant periods in weeks.

APPENDIX II (Cont.)

Table 24

Mass, Height, and Phenological Measurements by Stands and Treatments*

Idaho

Temp.	Day-Length (hours)	# OBS for Mass and Phenology	Total Mass		Top Mass		Root Mass		Top Mass/ Root Mass		Growing Period		Dormant Period		# OBS for Height	Height	
			Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.		Mean	S.D.
Warm	14	30	31.8	17.2	24.4	13.6	7.3	3.8	3.3	0.6	18.7	1.1	10.8	1.5	249	52	16
	15½	29	16.4	7.3	12.3	5.8	4.1	1.7	3.0	0.7	19.9	1.2	7.4	1.5	299	44	13
	16½	30	21.4	8.9	15.0	5.8	6.4	4.0	2.6	0.7	20.3	1.9	11.3	2.4	256	44	19
	22	30	35.8	17.0	28.3	13.7	7.5	3.8	4.0	1.2	20.3	2.4	5.7	2.0	218	60	19
Cool	14	30	17.6	6.1	10.9	4.1	6.7	2.2	1.6	0.3	24.0	2.9	--	--	221	26	7
	15½	29	5.7	2.2	3.8	1.7	1.9	0.7	2.1	0.7	27.1	1.8	--	--	140	21	6
	16½	30	20.8	6.0	12.8	4.5	8.0	1.8	1.6	0.4	23.2	2.2	--	--	216	34	10
	22	27	42.7	20.2	31.3	14.3	11.5	6.8	2.9	0.8	24.0	3.2	--	--	140	47	15

*All mass values given in 10^{-2} grams. Height in mm.; growing and dormant periods in weeks.

APPENDIX II (Cont.)

Table 25

Mass, Height, and Phenological Measurements by Stands and Treatments*

British Columbia

Temp.	Day-Length (hours)	# OBS for Mass and Phenology	Total Mass		Top Mass		Root Mass		Top Mass/ Root Mass		Growing Period		Dormant Period		# OBS for Height	Height	
			Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.		Mean	S.D.
Warm	14	30	30.5	14.7	27.5	12.4	7.6	2.9	3.7	1.0	19.6	1.3	9.1	2.8	226	62	20
	15½	29	20.1	11.7	16.1	10.4	3.9	2.0	4.5	4.0	20.4	1.8	6.9	2.7	266	50	15
	16½	30	22.1	9.2	16.5	7.3	5.5	2.1	3.0	0.7	20.7	1.2	10.1	2.1	246	47	18
	22	29	32.4	10.5	26.1	8.9	6.4	2.4	4.3	1.3	19.0	2.8	4.8	3.1	238	63	18
Cool	14	29	17.6	5.8	11.2	3.5	6.5	2.6	1.8	0.4	25.7	2.5	--	--	224	29	8
	15½	30	6.0	1.8	4.1	1.2	2.0	0.8	2.2	0.7	27.9	0.5	--	--	162	24	6
	16½	29	26.7	6.8	16.2	4.7	10.5	3.0	1.6	0.4	24.6	2.2	--	--	199	41	12
	22	27	49.7	14.5	36.9	11.3	12.8	3.8	2.9	0.6	25.0	2.2	--	--	112	55	17

*All mass values given in 10^{-2} grams. Height in mm.; growing and dormant periods in weeks.

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