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GENETIC AND ENVIRONMENTAL VARIATION IN SHOOT
GROWTH AND OTHER TRAITS OF BLUE SPRUCE (*PICEA*
PUNGENS). *

MICHIGAN STATE UNIVERSITY, PH.D., 1978

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GENETIC AND ENVIRONMENTAL VARIATION IN SHOOT
GROWTH AND OTHER TRAITS OF BLUE SPRUCE
(*PICEA PUNGENS*)

By

Bruce C. Bongarten

A DISSERTATION

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1978

ABSTRACT

GENETIC AND ENVIRONMENTAL VARIATION IN SHOOT GROWTH AND OTHER TRAITS OF BLUE SPRUCE (*PICEA PUNGENS*)

By

Bruce C. Bongarten

A rangewide seed collection of 260 half-sib families from 61 native stands of blue spruce (*Picea pungens*, Engl.) was made in 1969. Seeds were grown outdoors in a nursery and also in a greenhouse with continuous light. Trees in the latter group, referred to as "accelerated," were field planted in southern Michigan after 6 months of continuous growth. Trees grown in the outdoor nursery were field planted at the same height after 3 years, adjacent to the "accelerated" trees, and also at eight other locations from Montana to Maine. After 7 years from seed, the trees were compared for genetic variation. This work describes the genetic variation of blue spruce and focuses particularly on factors of shoot growth that have lead to different patterns of height growth in the accelerated and nursery-grown trees. Three other western conifers are compared to blue spruce in their reaction to accelerating conditions and Douglas-fir is compared to blue spruce for several components of shoot growth variation.

For the nursery-grown blue spruce, results were similar at all nine plantation locations. Trees from southern Arizona and New Mexico

were the fastest growing, but had mostly green foliage. Trees from northern Arizona and New Mexico and southern Colorado were also above average in height and were the bluest. Trees from Utah, Wyoming, and northwest Arizona were least susceptible to spring frost damage although even the most susceptible were damaged infrequently. Trees of all origins suffered heavy terminal bud mortality each winter. This was a cause of forking and diminished height growth. Significant variation in height, color, and date of leafing out was found for region, stand and family of origin, although blue spruce showed less total genetic variation than other Rocky Mountain conifers for all traits but color.

At the same age, accelerated trees were taller, had bluer foliage color, later date of leafing out, less frost damage, less winter needle browning, less terminal bud mortality and higher survival than the nursery-started trees. Except for height, differences were small. For height, accelerated trees were 70% taller at age 7. However, if growth was measured from time of field planting, heights were equal at 4 years from planting.

Genotype x plantation interaction for the accelerated and nursery-grown trees in Michigan was pronounced only for height. Much of the interaction was evident in the regional patterns of height. In the first year, accelerated seedlings from northern regions were taller than southern trees, while the reverse was true in the nursery seedlings. After 7 years, southern trees were taller in both tests, although the differences were smaller in the accelerated test.

First year differences resulted directly from the different photoperiods. Blue spruce under natural photoperiods, whether outdoors

or in the greenhouse, set buds when the night period reached a critical length. Trees from southern origins required longer nights before being induced to dormancy, and were taller by virtue of their longer period of growth. Under continuous light, all blue spruce were able to grow continuously during the 6-month growing period. In these northern trees had a tendency for faster rate of growth.

Genotype x seedling treatment interaction was also found in testing Engelmann spruce and Douglas-fir under 24-hour and natural photoperiods. Southern trees, having late bud set, were relatively taller, and northern trees, having early bud set, were relatively shorter in the natural photoperiod regime than under continuous light.

After field planting, the accelerated trees began a slow reversion to the geographic pattern of the trees grown outdoors. Southern trees were faster growing at 8-years-of-age because they had larger preformed buds.

Taken as a group, they had more needle primordia in the buds because their period of initiation was almost a month longer than the northern ones. Rate of needle initiation was not important in regional differences in needle number; however, differences within regions were large and resulted from differences in rate of needle initiation.

In Douglas-fir, like blue spruce, northern trees beginning fast and finishing early compared to the southern trees. However, regional differences in Douglas-fir also depended to some degree on rates of needle initiation. Furthermore, southern trees seemed to have longer distances between needles.

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My thanks also go to the many graduate students and technicians who went out of their way to assist me in collecting data for this study.

I am especially indebted to my close friend and colleague, Don DeHayes, whose friendship, assistance and discussions were invaluable to me.

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INTRODUCTION

In its native range, blue spruce rises as a tall spire from the deep ravines of the central and southern Rocky Mountains. There its aesthetic and watershed values far outweigh its importance for commercial timber.

Despite its Rocky Mountain grandeur, blue spruce has become most commonly known as an endemic of suburbia where it is, perhaps, the most commonly planted ornamental conifer. Its symmetric, full crown, wide adaptability and striking blue color are responsible for its widespread popularity which has spread from ornamental to shelterbelt use, and from Dayton, Ohio, to Moscow, Russia.

In spite of its commercial importance for ornamental, shelterbelt and Christmas tree purposes, there has been little work done on the genetics of blue spruce. Such basic questions as "What are the degree and geographic distribution of variation in blue spruce?" have not yet been answered.

There is good reason to suspect that blue spruce is genetically variable. First, climatic conditions within the range of blue spruce, from southern Arizona and New Mexico, to northern Wyoming, are quite variable. Adaptation to these conditions would lead to genetic differentiation. These adaptive differences would be further encouraged by the discontinuous range of blue spruce which prevents gene flow from other areas.

Adaptations arising in the native range would undoubtedly differentially affect performance when planted outside that range. Identification of the best adapted races of blue spruce would therefore be the starting point for any genetic improvement of this species.

For that reason, a rangewide half-sib progeny test of blue spruce was organized in 1969 at Michigan State University. The trees were grown in a nursery in East Lansing, Michigan, and after 2 years, sent to cooperators throughout the United States and Canada.

Because of the slow juvenile growth of blue spruce under natural conditions, attempts to hasten the growth and testing were also made. Trees were grown in a greenhouse with continuous light to promote continuous growth and were regularly watered and fertilized. This procedure has become known as the "accelerating" treatment. Under this regime, trees could be field planted after 6 months, 2 years before nursery-grown trees.

However, it soon became apparent that the height variation patterns were different between the nursery and accelerated treatments. While the variation pattern has been relatively stable through 7 years of growth in the nursery test, it has changed in the accelerated test, becoming similar to that of the nursery-grown trees.

The objectives of this work were to: 1) describe the natural variation in blue spruce for the purposes of defining superior seed collection areas and determining what steps might next be taken for the genetic improvement of blue spruce, 2) describe and determine the cause of differences between the "accelerated" and nursery grown

trees, 3) determine if other species react to accelerating conditions in the same manner as blue spruce, and 4) to determine how differences in meristematic activity are responsible for geographic variation in the amount of shoot growth.

CHAPTER I

GENETIC VARIATION IN BLUE SPRUCE

Blue spruce (Picea pungens, Engelm.) inhabits the deep canyons and grassy meadows of the central and southern Rocky Mountains. There, it occurs in isolated, pure groves, surrounded by ponderosa pine (Pinus ponderosa), Douglas-fir (Pseudotsuga menziesii), white fir (Abies concolor) and Engelmann spruce (Picea engelmannii). Because of its inaccessibility and watershed and aesthetic values it is rarely cut for timber in its native range. But, its stately form, blue color and wide adaptability have made it among the most commonly planted ornamentals in the northern United States. These attributes have also made blue spruce a valued shelterbelt species and an increasingly popular Christmas tree.

Variation in foliage color of blue spruce has long been recognized. Since the 1880s trees of exceptionally blue color have been clonally propagated as horticultural cultivars (DenOuden and Brown, 1965). Such propagules are usually grafts of lateral branches and may never establish apical dominance, remaining shrubby throughout their life. As a result, most nurserymen obtain blue trees, referred to as "shiners," from selection within nursery beds of trees grown from seed.

In spite of the commercial importance and known variation in foliage color of blue spruce, there have been almost no genetic studies of this species. The work of Cram (1961-68), Dawson and Rudolph (1966) and Hanover (1975) comprises the total knowledge of

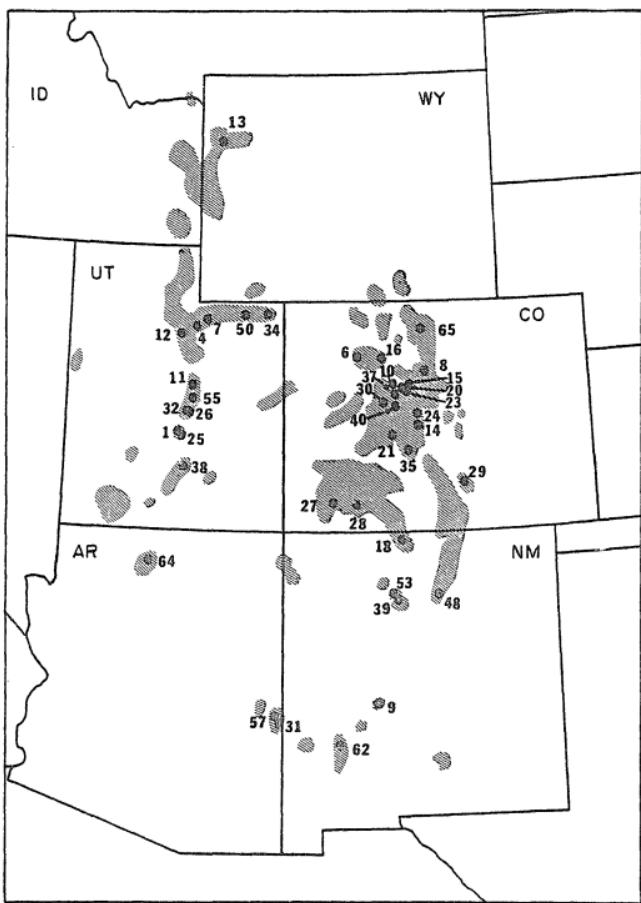
blue spruce genetics. Cram, working with locally grown trees in Saskatchewan, found that certain parents could transmit blue color to their progeny. Dawson and Rudolph reported significant differences in growth rate and survival among trees from six locations in Colorado, Utah and Wyoming when grown in North Dakota. Hanover also found differences in seedling growth rate, foliage color and monoterpenes composition among blue spruce from 61 native stands grown in Michigan.

The present study was undertaken primarily to determine the degree and pattern of genetic variation in blue spruce for the purposes of defining superior seed collection areas and providing information and material for future breeding. A second objective was to compare blue spruce with its less commonly planted cousin, and high altitude Rocky Mountain companion, Engelmann spruce.

MATERIALS AND METHODS

Through the courtesy of the United States Forest Service and other agencies, seeds were obtained from natural stands of blue and Engelmann spruces from throughout the central and southern Rocky Mountains (Figure 1). On the average, seven randomly chosen trees per stand were sampled. Seeds were kept separate by individual parent tree. They were sown in spring of 1970 at East Lansing, Michigan using a randomized complete block design of four replicates with row plots 1.17 m long and 10 cm apart, containing 20 trees per row. Excess seed was mass sown in rectangular plots in a fifth replicate having a density of about 5000 trees per square meter.

FIGURE 1. Natural range of blue spruce and
location of stands used in this
study.



In 1973 3+0 stock was used to establish permanent half-sib family test plantations in southern and northern Michigan. Cooperators in the United States and Canada received 2+0 seedlings bulked by stand. These were lined out in transplant beds (except in Nebraska and Montana where they were potted) until large enough for field planting. Permanent plantations were established in 1973-1975 at 13 places. Data from nine plantations are included in the present paper. Their locations are shown in Figure 2.

Each plantation followed a randomized complete block design of three to 10 replicates with four tree plots and a spacing of 1.8 x 2.4 m or 2.4 x 2.4 m. Herbicides and mowing were used as needed to control weeds and grass at all but the northern Michigan, Montana, and Quebec plantations. In these no weed control was provided, although chemical elimination of red maple sprouts was begun in Quebec in 1977.

The plantation sites differ markedly in their climatic conditions (Table 1). They also represent a wide range of edaphic conditions. For example, the Nebraska plantation is on a heavy textured prairie soil, the southern Michigan plantation on a sandy-loam soil, and the northern Michigan plantation on a sterile sandy soil where bracken fern is the major competition.

In each plantation mortality and height were measured several times, the last time in 1977. Color and frost damage were also rated in each plantation in 1977. At the southern Michigan plantation winter needle browning and death of terminal buds were

FIGURE 2. Locations of the Montana (MT), Nebraska (NE), northern (Chippawa County) Michigan (NMI), southern (Kalamazoo County) Michigan (SMI), Delaware County, Ohio (DOH), Coshocton County Ohio (COH), Pennsylvania (PA), Maine (ME), and Quebec, Canada (QUE) plantation sites at which blue spruce was grown.

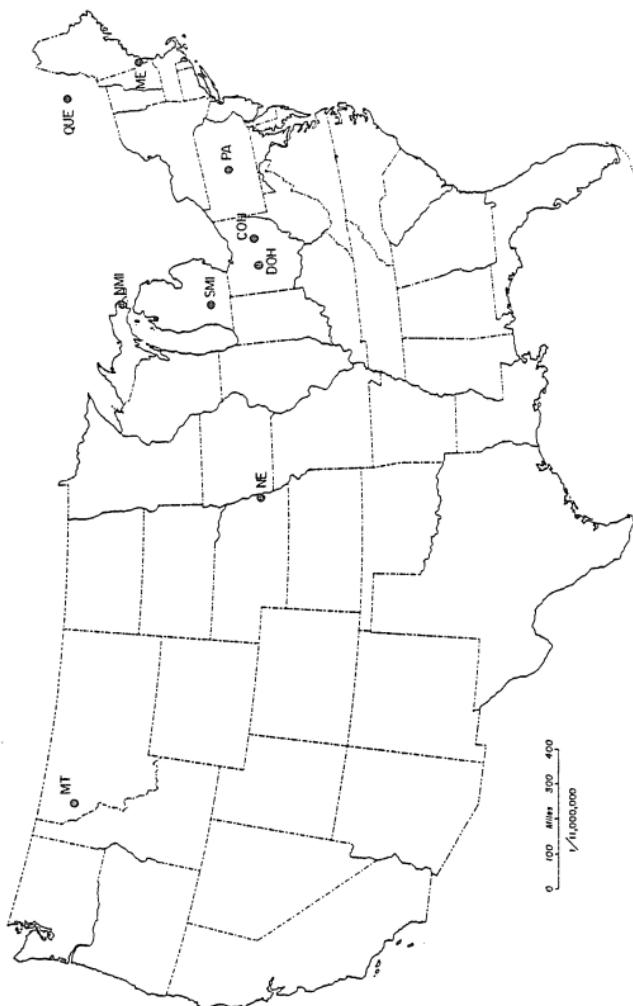


Table 1. Climatic data for stations close to test plantations (after USDA, 1941).

Plantation location County, state or province	Avg. temp., C° Jan.	Avg. temp., C° July	Length of growing season (days)	Precipitation (mm)
Lincoln, Montana	- 7	17	100	350
Cass, Nebraska	- 4	26	164	710
Delaware, Ohio	- 2	23	157	940
Coshocton, Ohio	- 2	24	162	1030
Kalamazoo, Mich	- 4	23	153	860
Chippewa, Mich	-10	18	142	740
Centre, Penn	- 3	22	156	990
York, Maine	- 6	21	134	1070
Quebec	-12	19		1070

additionally measured. Data from each plantation and from the combined data were subjected to an analysis of variance.

RESULTS AND DISCUSSION

Mortality. Mortality ranged from 10-50% among the measured plantations. Nearly all of the mortality occurred in the first year after field planting and was unrelated to seed source. There was no relationship either between mortality and subsequent plantation growth. For example, the two Michigan plantations had the least mortality, but represented the fastest and slowest growing plantations. The degree of mortality at any plantation was apparently dependent on the specific conditions of the stock and site at the time of planting. Once established, blue spruce could survive ensuing periods of extended drought and cold well.

Genotype-environment interaction. Genotype-environment interaction occurs when the relative performance of provenances is unlike at different plantation sites. Data from the nine blue spruce plantations were analyzed together to detect the occurrence of provenance-plantation interaction. Degrees of freedom for plantations, provenances, block, provenance-plantation interaction and error were 8, 39, 48, 312, and 1715, respectively, when analyzed on a plot basis. No statistically significant provenance-plantation interaction was found for height or color. That is, the relative performance of the provenances was unaffected by the handling and environmental conditions at the different locations.

For growth rate genotype-environment interaction often implies differential adaptability. For several coniferous species, trees of southern origin are cold damaged in the northern Lake States and grow poorly compared to their performance in the southern Lake States (Wright, 1973). This is an obvious case of interaction caused by differential adaptability. Another is the poor performance of Inland Empire Douglas-fir in Nebraska, but not Michigan for drought related reasons (Read, 1977). The absence of major interaction in blue spruce suggests that its physiological tolerances are not substantially different throughout its range.

Because provenance-plantation interaction was lacking, all plantations will be considered together in the remainder of this paper.

Geographic variation patterns. The geographic variation pattern was different for each trait. For height, southern trees were faster growing than northern trees. For budburst, eastern trees leafed-out before western trees. For foliage color, the highest frequency of blue trees was found in northern Arizona-New Mexico and southern Colorado; trees from north or south of this area had greener foliage. For winter needle browning, only trees from the southern most stands were affected.

Stands were grouped into five regions for descriptive purposes (Table 2). The division was based on geographic proximity and similarity in the above mentioned traits. In some cases natural boundaries mark the division between regions. The Southern Arizona-New Mexico region is separated from the others by an extensive desert-

Table 2. Data on location of origin and growth for the 39 blue spruce stands represented in the provenance test.

Region, stand no., and state	North latitude	West longitude	Elevation	Trees per stand ^{1/}	Relative height	Foliage color	Date of leafing out		% of leaves
							% of mean	0=green 12=blue	
Intermountain									
13	WY	43.3	110.8	1860	1000+	97	4.5	30	1
50	UT	40.9	109.8	2410	1000+	93	5.6	28	0
7	UT	40.6	109.4	2590	25	94	4.6	27	0
4	UT	40.5	110.3	2130	200	110	4.6	-	-
12	UT	40.5	110.3	2290	25	95	4.5	29	2
11	UT	39.7	111.7	2360	-	91	5.3	30	0
55	UT	39.4	111.2	2230	50	115	4.8	-	-
32	UT	39.3	111.5	2560	-	97	4.5	31	2
26	UT	39.3	111.5	2500	1000+	98	5.0	30	2
1	UT	38.8	111.7	2360	25	100	6.8	29	0
25	UT	38.8	111.3	1980	300	92	6.2	30	2
38	UT	38.1	111.4	2560	400	83	5.8	31	0
Average							94	5.2	30
Kaibab									
64	AR	36.8	112.2	2360	-	109	8.7	30	0
N.W. Colorado									
65	CO	40.6	105.5	2440	1000+	93	5.5	30	0
16	CO	40.1	107.1	2590	40	84	4.9	38	2
6	CO	40.0	107.5	2220	-	109	4.6	25	1
8	CO	39.8	105.5	2510	-	104	5.4	28	0
15	CO	39.6	106.4	2390	1000+	92	5.1	28	0
20	CO	39.6	106.6	2490	-	92	6.0	25	1
23	CO	39.5	106.5	2590	30	99	4.9	25	0
10	CO	-	-	2900	20	88	7.1	28	1
37	CO	39.4	107.0	2470	30	94	5.9	27	0
30	CO	39.7	107.2	2510	100	95	6.2	27	0
40	CO	39.2	106.8	2510	1000+	111	5.3	26	1
24	CO	39.0	106.0	2900	20	88	7.1	28	0
14	CO	38.9	107.0	2870	1000+	95	5.4	26	0
21	CO	38.8	107.2	2710	10	90	4.7	26	0
35	CO	38.2	106.8	2800	500	88	6.2	28	0
29	CO	38.1	106.0	2390	-	87	8.0	28	0
Average							97	5.6	27
No. New Mexico									
S. Colorado									
27	CO	37.8	108.2	2440	1000+	116	8.5	24	2
28	CO	37.5	106.9	2440	1000+	112	7.8	26	1
18	NM	36.9	106.1	2740	-	83	6.0	29	1
53	NM	36.5	106.5	2620	1000+	111	8.1	25	1
39	NM	36.0	106.2	2590	35	102	6.4	27	1
48	NM	35.8	105.8	2340	1000+	122	7.5	27	2
Average							108	7.4	26
S. Arizona									
New Mexico									
9	NM	33.9	107.5	2600	35	112	8.5	24	6
57	AR	33.8	109.3	2800	5	125	4.8	27	3
31	AR	33.5	109.3	2590	50	121	5.3	26	8
62	NH	33.3	107.9	2590	5	124	4.3	26	3
Average							121	5.7	26
Approximate									
LSD (%)							5.2	0.5	2
Region							7.0	0.7	-

^{1/}This column represents the number of trees in a contiguous stand as estimated by the seed collector.

grassland range gap. The western regions are likewise isolated from the eastern ones. Boundaries between the Southern Colorado-Northern New Mexico and the Northern Colorado regions and the Kaibab and Intermountain regions are, however, ill defined. This is due in part to inadequate sampling in southern Utah and Colorado, and in part to the artificial nature of the regional groupings.

Stand variation within each region was considerable for each trait, but was not related to latitude or longitude. One should, therefore, not expect to find trees from the southern part of a region faster growing than trees from the northern part or trees from the eastern part earlier to leaf out than trees from the western part. Identification of superior stands within a region cannot be accomplished on the basis of geographic location.

Data from the two Michigan plantations also revealed large differences among families within a stand. The relative importance of regional, stand within region and family within stand variation for height, color and time of leafing out are presented in terms of variance components in Table 3. For each trait, differences at each level of variation were highly significant. Furthermore, regional, stand and family variance components were approximately equal in each trait. This implies that selection at each level of population structure should be effective in providing genetic gain.

Of particular interest is the smallness of regional variation. The 8 year height superiority of blue spruce from Arizona and New Mexico over trees from northern Colorado and Utah is much less than

Table 3. Proportion of total genetic variation due to region, stand and family.

Source of variation	Height	Foliage color	Date of leafing out
% of total variance			
Between regions	36	38	41
Stands within regions	35	37	32
Families within stands	29	25	26

in other species occupying the same range (Table 4). Differences in Douglas-fir, white fir, and limber-southwestern white pine were 4 to 8 times as great (Kung and Wright, 1972). In ponderosa pine repeated winter injury has reduced the initially large growth differences, but unlike blue spruce, the region of origin can easily be identified by numerous twig and needle characteristics.

Differences in blue spruces from different elevations. Elevation is one of the most often mentioned sources of local population variation. Such variation is considered as an adaptational response to large climatic differences which may occur over short distances as one increases in altitude. To test the possible influence of elevation of origin on growth rate, neighboring stands were compared on a paired basis. Differences in elevation were plotted against differences in growth rate (Figure 3). In 11 of the 13 comparisons trees from lower elevations outgrew those from higher elevation. This was significant at the 5% level. However, the correlation of difference in growth rate with difference in elevation was low ($r = .05$) and nonsignificant. In other words, decreasing elevation did not result in consistently increasing growth rates. While a comprehensive rule cannot be drawn from this data, seed collectors would probably do best to collect from low elevation stands of blue spruce, which are also likely to be the most accessible.

No elevational trends were detected for color or date of budburst.

Effect of small stands on growth rate. Population differentiation is also promoted by isolation and small population size. Both

Table 4. Relative height superiority of Rocky Mountain conifers from Arizona and New Mexico over those from No. Colorado and Utah.

Species	Percent height advantage of Arizona-New Mexico trees over No. Colorado-Utah trees	
	age 2	age 8-10
Blue spruce	26	25
Douglas-fir ^{1/}	109	103
White fir ^{2/}	30	38
Ponderosa pine ^{3/}	83	20
Lumber and southwestern ^{4/} white pines	250	419

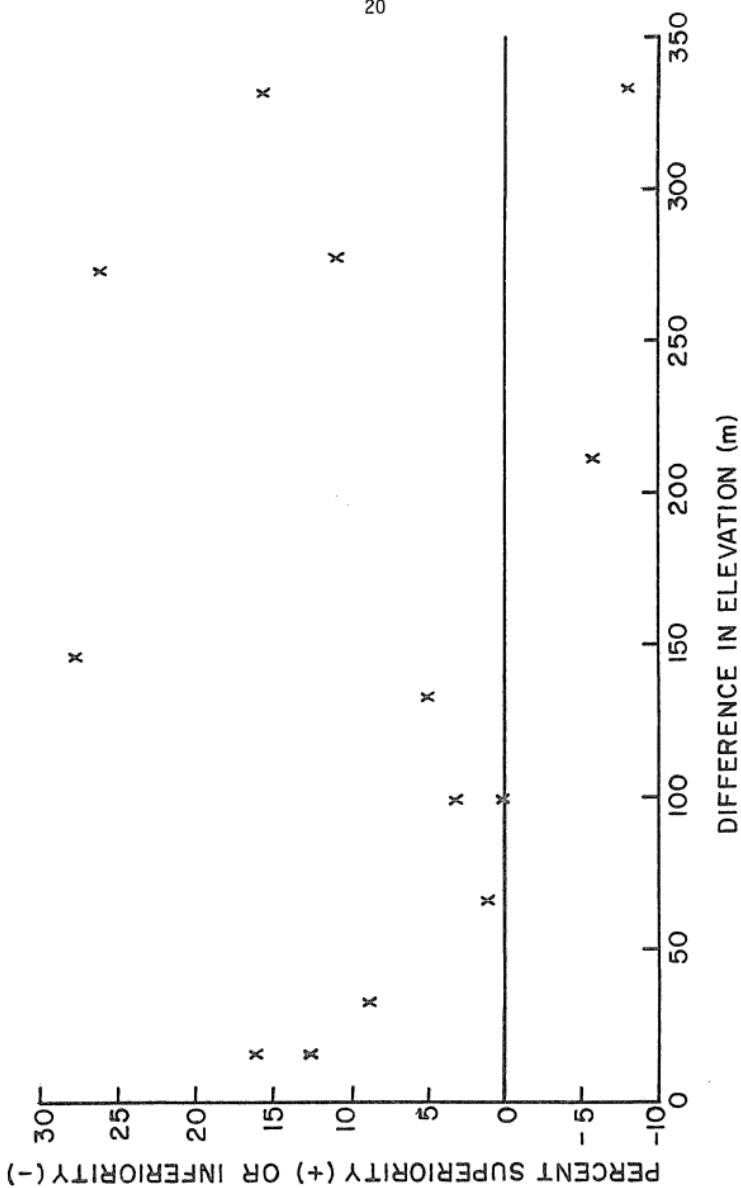
^{1/} Wright, Kung, Read, Lemmien and Bright, 1971.

^{2/} Wright, Lemmien, and Bright, 1971.

^{3/} Wright et al, 1969

^{4/} Wright, Kung, Read, Steinhoff and Andresen, 1971.

FIGURE 3. Relative height superiority (+) or inferiority (-) of low to high elevation stands as related to elevation differences between them. Each point represents a comparison between two nearby stands.



of these conditions commonly occur in blue spruce. Small, isolated stands are also prone to inbreeding and therefore depression of growth rate. In this study progeny from stands containing as few as 6-10 individuals showed no depression of growth rate (Table 2). However, progeny of one isolated tree from Utah (population 34) showed marked inbreeding depression. After 8 years of growth in southern Michigan it averaged only 29 cm compared to 47 cm for trees from neighboring stands.

Growth rate. Blue spruce is a slow growing species, at least in its youth. After 8 years from seed the overall mean height was 48 cm. The southern Michigan plantation was the tallest. Its average height was 73 cm. Plantations in Nebraska, Pennsylvania, Maine and Wooster, Ohio had mean heights between 54 and 60 cm. The Montana, Quebec and northern Michigan plantations had mean heights of 39, 37, 35 cm, respectively, reflecting the lack of maintenance and the droughty conditions of the northern Michigan site.

Differences in height among plantations were larger than differences among seedlots. Two-to-one differences in height were present between the tallest and shortest plantations while the difference between seedlot extremes was only 50%. Growers should pay as much, or more, attention to plantation establishment and maintenance as to seed source.

Trees from southern Arizona-New Mexico were the fastest growing. They averaged 62 cm over all plantations. Trees from the Kaibab Plateau in northern Arizona as well as trees from northern New Mexico and southern Colorado grew more slowly, but most trees were

also well above average. Trees from further north in Colorado, Utah, and Wyoming were generally below average in height, although trees from a few provenances were as tall as those from further south (Table 2).

The correlation between nursery height at age 2 and 8 year field height was $r = .73$. In practical terms the nursery measurements were predictive of the regional trends in growth rate, but were not useful for early selection of fast growing stands within a region.

Foliage color. The blue foliage of blue spruce and other conifers is due to wax deposited onto the surface of the needles by the epidermal cells. It can be rubbed off by hand revealing the green chlorophyllous color beneath. The greater the wax deposition, the more intense is the blue color (Hanover and Reicosky, 1971; Reicosky and Hanover, 1976).

Although some wax was apparent on year-old seedlings, the distinctive blue color for which blue spruce is noted, was not evident for several years. By age 8, however, several individuals were as blue as the commercial cultivars. Like these cultivars, blue trees varied from steel blue to almost white.

Many individuals remain green throughout their lifetime because they produce little surface wax. Most tested seedlots, though, yielded at least some trees of blue color, but the frequency and intensity were greatly dependent on geographic origin. Blue color was most frequent on trees from Kaibab, northern New Mexico and southern Colorado seedlots. In the best provenances one of three

trees were "shiners". One stand in southern New Mexico (population 9) also produced a high frequency of blue trees, but other trees from this region had a uniquely yellow-green cast.

Within a half-sib family color segregation was striking, but separation of genetic and environmental components of variation among these trees requires clonal testing. The inheritance of color in blue spruce does not appear to be simple (Cram, 1968).

Leafing out and spring frost damage. Blue spruce leafs out later than other spruces grown in the north central States and it is therefore less often damaged by late spring frosts ($r = .77$). Even so, frost damage was reported in all but the Quebec and Montana plantations in 1977. Frost damage also occurred in 1974 and 1976 in Michigan and Ohio.

Trees from the western regions leafed out later than eastern trees and were less prone to spring frost damage. However, even in the most susceptible seedlots, trees generally had less than one-third of their buds killed and recovery was good. Damage was heaviest in terrain depressions which trapped cold air. Such depressions were not necessarily deep. For instance, at the northern Michigan plantation trees just 1 meter below the level surface were badly damaged regardless of origin.

Winter injury. Winter damage has not been a serious problem on blue spruce and is limited to trees from southern Arizona and New Mexico. It was first manifested in the nursery as browning of the needle tips. In the harsh winter of 1976-77, whole needle browning was observed in southern Michigan, but was restricted to

the bottom of the trees. Damage to white fir and ponderosa pine grown at the same location was far more severe.

In the southern Michigan plantation two-thirds of the terminal buds died during the winter of 1975-76. Bud death was unrelated to region of origin. The same phenomenon was repeated during the winter of 1976-77 at both Michigan plantations and in Ohio. The degree of terminal bud death in the other plantations was not measured.

Linquist et al. (1963) described terminal bud death as one of the primary effects of winter desiccation in a controlled test with blue spruce. Winter desiccation was also the probable cause of terminal bud death in the exposed Michigan plantations.

In most cases a single lateral branch quickly assumed dominance and death of the terminal bud was apparent only upon careful examination. But, terminal bud death was also a common cause of forking which resulted when a single lateral failed to establish dominance.

Comparison of blue and Engelmann spruces. Wherever blue spruce is natively found, Engelmann spruce can generally be located by proceeding to higher elevation. The morphological similarity of these spruces often makes identification difficult although, side by side, the branches of blue spruce appear more planar and stiff and the foliage more prickly and less appressed to the twig than Engelmann. Ecologically and reproductively, however, they are quite distinct and rarely do they occur in the same stand or hybridize.

A comparison of blue and Englemann spruces grown in southern Michigan is given in Table 5. The Engelmann spruce results are drawn from four provenances in the present experiment and from 12

Table 5. Height growth, frost and winter damage, and foliage color of blue and Engelmann spruces at age 7 years in So. Michigan.

Character	Species	
	Blue	Engelmann
Height	73 cm	63 cm
Needles browned in winter, 1976-77	1 %	26 %
Buds damaged by spring frost, 1976	5 %	50 %
Foliage color (0 = green) (12 = blue)		
AR-NM	6.7	7.0
Others	5.4	4.0

others in an adjacent plantation supplied by the Institute of Forest Genetics at Rhinelander, Wisconsin. The trees represent most of the range of Engelmann spruce, but, because of high mortality, intra-specific variation could not be accurately evaluated for most traits.

Although morphologically alike, blue and Engelmann spruces are well differentiated physiologically. Engelmann spruce, adapted to the cool, moist conditions of the subalpine Rocky Mountains, is ill at home in the eastern United States and Canada. It was severely damaged by frost every spring because it leafed out a week to ten days before blue spruce. It was also regularly injured during winters by cold and desiccating winds in southern Michigan where protective snow, to which Engelmann spruce is accustomed, was often lacking. As a result, growth of Engelmann spruce was considerably depressed. Many Engelmann spruces, however, displayed the same striking blue color as blue spruce. In fact Engelmann spruce from southern Arizona and New Mexico are apt to be bluer than blue spruce from this region.

Cooperators received only two Engelmann spruce seedlots with the blue spruce. In their plantations, also, Engelmann spruce suffered heavy frost damage and were slower growing than most blue spruce.

Evolutionary considerations. Once established, blue spruce survived well in a wide range of environments. Although growth was much affected by cultural and site conditions, the reputation of blue spruce for adaptability is apparently deserved. The source of its adaptability may derive from circumstances in its canyon habitat.

There, daily temperature fluctuations are extreme as a result of radiational cooling through open timber and poor air drainage. Soil moisture also varies greatly with season. In spring, melting mountain snows send torrents of water through the valleys, but in summer months many streams are reduced to trickles and drought conditions prevail not far from their beds.

Although local topography modifies weather at any single point, there are broad climatic differences within the range of blue spruce. Arizona and New Mexico are characterized by mild winters and long growing seasons. In the blue spruce zone of Arizona and New Mexico the frost free period may be greater than 150 days compared to 90 days in Colorado and less than 60 days in Utah (Baker, 1944). In general, the longer growing seasons have favored more rapid growth.

On the whole, the Southwest is noted for its high level of solar radiation. Blue trees are probably an adaptation to this condition and most companion species exhibit this trait also. The exact cause-effect relationship between glaucousness and solar radiation has not been determined, however. Several attempts to relate blueness with decreased transpiration have failed, probably because the stomates of green foliage are also clogged with wax (Hanover and Reicosky, 1971). Glaucous foliage does reflect more light than nonglaucous foliage and this may help prevent solarization, the destruction of chlorophyll in plant tissue by high intensity light (Reicosky and Hanover, In press). While solarization is the probable cause of widespread mortality of unshaded Engelmann spruce in the Southwest (Ronco, 1970), it does not seem so serious a problem in blue spruce.

Although blue trees are the rule in the Southwest, green trees may dominate in some areas. For example, blue spruce from southern Arizona and New Mexico are quite green. Furthermore, green trees of other normally glaucous species also occur in some locations of the Southwest, but the geographic pattern is unique for each species. This randomness suggests that foliage color in these isolated stands was determined generations ago when populations were narrowed to small size. The persistence of green trees suggests that the conditions which favored glaucousness may no longer exist or that the selection pressure is low.

Date of leafing out is also an obvious adaptive trait. Trees that flush too early would suffer repeated frost damage and those leafing out unduly late would not utilize the whole growing season. Leafing out in blue spruce and other species is primarily dependent on heat accumulation. In an early spring blue spruce may flush in late April, but in a late spring not until late May. Trees from regions with short springs require less heat to flush than those from regions with long sporadic warming. In general this means that trees from colder climates leaf out before those from warmer climates when grown at the same location. Thus Engelmann spruce flushes before blue spruce and northern ponderosa pine before southern. In blue spruce the pattern is anomalous as eastern trees break bud before western trees. Although daytime spring temperatures do not greatly differ between these regions, the frost free period of the western region is considerably shorter (Baker, 1944) probably because of the frequent nighttime radiational frosts characteristic of the basin

and plateau provinces (J. Harmon, personal communication). To avoid frost damage a larger heat accumulation may be needed to initiate leafing out in western blue spruce. Confirmation of this hypothesis awaits further climatological study.

As mentioned previously, blue spruce displays a relatively small amount of genetic variation compared to other species occupying the same range. This also represents an interesting evolutionary problem. Three possible explanations are offered. 1. The habitat of blue spruce may be more or less uniform despite wide geographic distribution. Regional climatic differences are greater, except in summer, for Douglas-fir, white fir and limber-southwestern white pine because, unlike blue spruce, they grow at lower elevations in Arizona and New Mexico than in Colorado and Utah (Kung and Wright, 1972). Differences in length of growing season and winter temperature are thereby larger in these species than blue spruce.

2. The genus, Picea, may be evolutionarily more conservative, resisting change to a greater extent than other coniferous genera. As Wright (1955) first observed, variation among spruce species is small compared to species variation within other genera. Within species variation is also small for those Picea species tested. For example, genetic variation in Norway spruce, Picea abies, is much less than in Scotch pine, Pinus sylvestris, the only other intensively studied European species. In rangewide tests of the two species in New Hampshire and Czechoslovakia differences among seedlot extremes for height were two or three-to-one for Norway spruce and four or five-to-one for Scotch pine (Baldwin *et al.*, 1973; Wright and

Baldwin, 1957; Vincent and Polnar, 1953). In boreal North America, jack pine (Pinus banksiana) is more variable morphologically and adaptationally than white spruce (Picea glauca) although both have a wide range in growth rate.

3. Populations of blue spruce may only recently have become separated and have not had time to differentiate. This conforms with the hypothesis of Daubenmire (1972) and Taylor et al (1975) that blue spruce is a recent derivative of Engelmann spruce. Their proposal is based on the morphological similarity of the two species. But, cytologically blue and Engelmann spruces exhibit a complex incompatibility system, typical of more distant relatives (Kossuth and Fechner, 1973). Dobzhanski (1970) notes, however, that reproductive barriers can be established in relatively short periods.

Practical application. For ornamental purposes foliage color is probably the most important criteria in selecting seed source, especially because differences in growth rate and adaptability are not great. Of those tested, three stands stood out as producing the highest frequency of blue trees. These are stands 64, from the Kaibab Plateau in Arizona, 27 from the Dolores River in southwestern Colorado and 9, from Beartrap Canyon in southern New Mexico. All were also above average in height. The Kaibab trees have the advantage of being most frost resistant while the Dolores River and Beartrap Canyon trees are somewhat faster growing.

Seeds from the Kaibab Plateau have long been favored by nurserymen and are commercially available. Although seed from the Dolores River drainage and Beartrap Canyon may not always be obtainable,

seed from most other stands in southern Colorado and northern New Mexico will also produce a high frequency of blue trees with good growth rate.

Where blue color is not a selection criteria, as for shelterbelts, seed from Arizona's White Mountains (stands 31 and 57) will provide the fastest growing trees. At the present seed from this area are not commercially available.

Data from this experiment indicate that improvement in color and growth rate can be made by selecting at both the stand and individual tree levels. Progeny testing of additional trees from many stands in the best regions should provide better seed than available from any single stand when grown as a seed orchard and rogued to the best families. Progeny testing and seed orchard establishment of full-sib families derived from crosses among the best families in the present experiment should also be effective in achieving genetic progress. Because of the long generation time in blue spruce (20 years), however, investigation of the feasibility of developing grafted seed orchards should be considered as an alternative to seedling seed orchards.

SUMMARY

Blue spruce from 40 places in the central and southern Rocky Mountains were grown at nine locations in the northern United States and in Canada. Results, eight years from sowing, were similar in all plantations. Trees from southern Arizona and New Mexico were the

fastest growing, but had mostly green foliage. Trees from northern Arizona and New Mexico and southern Colorado were also above average in growth and were the bluest. Trees from Utah, Wyoming and northwest Arizona were least susceptible to spring frost damage although even the most susceptible were damaged just once every three years. Trees of all origins suffered heavy terminal bud mortality each winter which was a cause of forking and diminished height growth. Significant variation in height, color and date of leafing out was found for region, stand and family of origin although blue spruce showed less total genetic variation than other Rocky Mountain conifers in all traits but color.

Engelmann spruce from several southern sources were also grown. Compared to blue spruce, these suffered severe spring frost and winter cold damage resulting in poorer growth.

CHAPTER II

ACCELERATING SEEDLING GROWTH FOR GENETIC TESTING: I. RESULTS IN BLUE SPRUCE AFTER SEVEN YEARS

ABSTRACT

The juvenile growth of blue spruce (Picea pungens, Engl.) of 192 half-sib families from 48 native stands was "accelerated" through exposure to continuous light and regulated watering and fertilization in a greenhouse. Under these conditions, trees grew without setting bud for six months, at which time they were 22 cm in height and ready for field planting. The same material, grown in a nursery, was field planted at an equal size after three years. In the first 4 years, following plantation establishment, growth was equal in the accelerated and nursery tests, but when compared at equal age (7 years), accelerated trees were 70% taller than nursery-grown trees.

In the accelerated test, seedlings from northern origins were faster growing than southern trees, while the reverse was true in the nursery test. Seven years after field planting, southern trees were taller in both tests, although the differences were smaller in the accelerated test. Differences in night length causing growth cessation were responsible for the geographic pattern of

height growth in the nursery seedlings. Removal of this growth control in the accelerated test resulted in the different geographic growth pattern. Differences in seedlot rankings between the two tests at age seven were largely due to treatment in the first years. These differences suggest that trees should be tested under the same conditions in which they are to be commercially grown.

Differences in foliage color and date of bud burst could be measured at an earlier age in the accelerated trees, and there was no important genotype x test interaction for these traits or for frost damage, winter damage, or survival.

During the initial growth period, error variance was higher in the greenhouse than in the nursery.

INTRODUCTION

The juvenile growth rate of many important commercial tree species is slow. In genetic testing, this hampers accurate early evaluation because field tests are slow to be established and because the end product, the rotation size tree, is so far in the future. In some traits, such as wood fiber length, distinct juvenile and mature forms specifically hinder early selection. Methods for accelerating the early growth and maturation of trees have, therefore, drawn the attention of forest geneticists.

Among the techniques employed for accelerating juvenile growth are optimization of nutrient and water levels, atmospheric CO₂ enrichment, temperature regulation, and supplemental light. The most profound gains are made by lengthening the photoperiod with supplemental light. In some species longer photoperiods permit continuous growth without budset. In others, it encourages recurring flushes of growth without intervening periods of cold (Vince-Prue, 1975). These procedures may also hasten physiological maturation (Young and Hanover, 1976).

Reported here is a case study in acceleration of growth for genetic testing. A progeny test of 192 blue spruce $\frac{1}{2}$ -sib families is used. An "accelerated" treatment in which trees were grown in a greenhouse with continuous light, periodic fertilization, and frequent watering is compared to a "non-accelerated" treatment in which the trees were grown outdoors using conventional nursery practices.

This paper reports results for the first 7 years of growth.
Earlier papers report results at six months (Hanover and Reicosky,
1972) and two years (Hanover, 1974).

MATERIALS AND METHODS

Through the cooperation of the U.S. Forest Service, National Park Service and Colorado State University, seeds from 192 blue spruce from 48 native stands in the southern and central Rocky Mountains were collected in fall, 1969.

The seeds were divided into two groups. The first group was sown in January, 1970, in one gallon polyethylene rose pots placed in a greenhouse. The growing media was comprised of loam, peat moss, and sand (2:1:1), and the seeds were covered with quartz sand. Supplemental light was provided by VHO cool white fluorescent lamps which produced 450 ft-c at the soil surface at night. Temperature in the greenhouse was maintained at approximately 23 C day and night throughout the 6-month growing period. In July, 1970, the supplemental light was discontinued, allowing the trees to set bud. One month later the trees were placed outside for acclimation to natural conditions. In September the trees were removed from the pots, cleaned of soil and one-half were field planted in three replicates with four tree plots. The remaining trees were lined out in nursery beds and were used to establish two additional replications in spring, 1971. Trees treated in the above manner will be referred to as "accelerated."

The second group of seeds was sown in an outdoor nursery at East Lansing, Michigan, in May, 1970. Seedlots were sown in one meter row plots of 20 seeds with 30 cm between rows using a randomized complete block design of four replications. The nursery soil was sandy, and no irrigation or fertilizer was applied. In

May, 1973, the 3+0 seedlings were lifted and field planted in 3 replications adjacent to the accelerated plantation. Trees in this group will be referred to as "non-accelerated."

The plantations were established at the W.K. Kellogg Experimental Forest in Kalamazoo County in southern Michigan. The site was a level abandoned hayfield having a sandy-loam soil. Prior to establishment, simazine and Amitrol-T were applied in 60 cm strips at the recommended dosage to control grasses and weeds. Chemical weed control has been used in subsequent years and has been very effective. Spacing for both plantations was 2 x 2.6 m and crown closure had not yet occurred in either at the time of the last measurements.

Measurements were made several times through age seven. The data were reduced to plot means for tabulation and analysis.

RESULTS AND DISCUSSION

Acceleration of growth and maturity. Under the accelerating conditions, blue spruce averaged 22 cm in height after 6 months and were large enough for field planting. During the accelerating period, trees grew continuously without setting buds. Upon transfer to outdoor conditions, however, they quickly set buds and ceased height growth. Some trees were planted soon after budset in fall, while others were overwintered in the nursery and planted the following spring.

By contrast, blue spruce grown in the nursery were only 6 cm tall after 1 year and did not reach a height of 22 cm until age 3, at which time they were spring field planted.

Growth during the first 4 years after field planting was similar for all types of stock, resulting in average heights of 66, 60, and 64 cm, respectively, for accelerated fall planted, accelerated spring planted and nursery grown stock.

Accelerated trees were taller, however, when the comparison was made on the basis of equal age from seed. At the end of 1976, when all trees were 7 years old from seed, average heights were 115, 102, and 64 cm, respectively, for the three types of stock.

Foliage color, date of bud burst, frost and winter damage and mortality were also measured in the two tests. Plantation means differed for each trait at age 7 (Table 6). Differences were significant at the .01 level for all traits except frost damage and terminal bud death, which were significant at the .05 level.

TABLE 6. Comparison of blue spruce grown under accelerated and non-accelerated conditions after seven years from seed.

Treatment	Ht. cm	Foliage color 12=blue 0=green	Date of budburst April	Winter death foliage term. bud	Survival	Frost damage	
---% of trees---							
Accelerated	112	8.1	29	Only trees from S.Ar. & NM in the non-accel. test had measurable damage.	67	94	43
Non-Accelerated	64	7.1	28		75	85	50
<hr/>							
<u>Statistical significance</u> 1/							
Between treatments	**	**	**	**	*	**	*
Genotype x treatments	**	ns	ns	**	ns	ns	ns
<hr/>							

1/

ns = no statistical significance.

** = significant at $P = .01$

* = significant at $P = .05$.

On the average, trees in the accelerated test had bluer foliage color than those in the non-accelerated test. Furthermore, large color differences among seedlots became apparent before age 5 in the accelerated test, but not until later in the non-accelerated test. Evidently, accelerating seedling growth has also hastened the transformation from juvenile foliage color to mature, allowing earlier determination of genetic differences.

Trees in the accelerated test also burst buds 1 day later, on average, than trees in the adjacent non-accelerated test. Frost damage was therefore somewhat less on the accelerated trees as well. The later leafing out of accelerated trees may be further indication of advanced maturation as later bud burst has been associated with older trees in the Norway spruce, Picea abies (Langlet, 1960).

Accelerated trees were less prone to winter needle browning and terminal bud death, though the differences were small. Accelerated trees suffered no needle damage. Most non-accelerated trees also had no damage, but 6% needle browning on trees from southern Arizona and New Mexico was observed. The majority of trees in both tests, however, suffered death of their uppermost terminal buds. Two-thirds of the accelerated trees lost their terminal buds, while three-fourths of the non-accelerated trees had dead terminals. The reasons for the greater injury of the non-accelerated trees is not clear.

Mortality was also less in the accelerated test, but it is difficult to specify a reason since there were many differences in the two plantations due to year, site, and handling.

Seedlot x treatment interaction. For the purpose of genetic testing the effect of accelerating growth on relative seedlot performance is of primary interest. Differences in seedlot ranking between the accelerated and non-accelerated tests can be detected by testing for seedlot x treatment interaction.

As indicated in Table 6, only height and winter needle browning had statistically significant interaction at age 7 years. Relative seedlot rankings were similar in the two tests for foliage color, survival, terminal bud death, date of budburst and frost damage. For needle browning the interaction was a statistical artifact and unimportant. It was the result of slight damage occurring on trees of southernmost origin in the non-accelerated test, while accelerated trees were not affected.

Differences in ranking for height were large and of major importance as indicated by the low correlations between seedlot heights in the two tests (Table 7). Correlations were poor whether based on all seedlots or confined to stands within a region (as defined in Chapter 1) or trees from the same stands.

Seedlot rankings between the two tests became more consistent between the ages of 2 and 7, as indicated by the increased correlations, but even at age 7, only seven of 12 stands were among the top quarter in both tests. (Three would be in common if there were no correlation.) Almost half (5/12ths) of the best stands would be overlooked by selecting trees grown under one condition for growth in the other. Results at age 7 argue in favor of testing trees in the same environment in which they are to be grown.

TABLE 7. Correlations between the accelerated and non-accelerated tests at two ages.

Basis of Comparison	Age (Years)	
	2	7
All stands	.18 ^{NS(a)}	.61**
Stands within regions	.35*	.41**
Families within stands	.12 ^{NS}	.34**

(a)** = significant at $P = .01$; * = significant at $P = .05$;
 NS = not significant.

If trees are to be commercially started under accelerating conditions, then seedlot selection should be based on tests under accelerating conditions. Likewise, seedlot selection for trees grown outdoors are best made from trees grown under outdoor conditions.

Geographic component of the height interaction. The geographic pattern of height growth was very different in the two tests, especially in the first years. Much of the interaction can be explained by these geographic differences. After the second year of growth in the nursery, trees from southern regions were taller than trees from northern regions (Table 8). Differences between regional means were nearly 30%. At the same age there were no regional differences for height growth in the accelerated test. As a result, the correlation of seedlot heights between the two tests was close to zero at age 2.

The geographic pattern in the non-accelerated test changed very little between ages 2 and 7, but in the accelerated test there was a shift in the geographic pattern, southern trees emerging as taller than northern trees. Although southern trees were taller in both tests at age 7, the geographic differences were larger in the non-accelerated test. Regional differences were 30% of the plantation mean in the non-accelerated test and only 5% in the accelerated test. Although the tests were more similar at age 7 than age 2, seedlot x treatment interaction was still strongly present.

Photoperiod hypothesis for geographic interaction. In blue spruce seedlings, the duration of growth is determined photoperiodically in the absence of stress (Young and Hanover, 1977). When

TABLE 8. Relative heights of blue spruce from different geographic regions at ages 2 and 7.

Region of Origin	<u>Seedling growing regime</u>			
	<u>Accelerating</u>		<u>Nursery</u>	
	Age 2	Age 7	Age 2	Age 7
----- % of plantation mean -----				
S. AR-NM	99	104	126	124
S. CO - N. NM	99	107	116	112
N. CO	100	98	94	97
UT-WY	101	98	94	94

1/

S. AR-NM = southern Arizona and New Mexico

S. CO-N. NM = southern Colorado and northern New Mexico

N. CO - northern Colorado

UT-WY - Utah and Wyoming

a certain night length is reached bud set and growth cessation are triggered. Photoperiod similarly controls growth duration of a number of other species (Waring, 1956). For many of these, the critical night length for causing cessation of growth varies with the origin of the seed. In four Picea species and in many others in several genera, trees from southern regions commonly require longer nights for growth termination than northern trees (Pollard *et al.*, 1975; Pollard and Logan, 1976; Dormling, 1973; Vaartaga, 1959). Hence, southern trees grow longer into the season when grown at a common location.

In the non-accelerated test, growth was terminated when the critical night length was reached. The greater growth of southern trees was presumably a result of their longer duration of growth.

In the accelerated test, however, the photoperiodic control of growth was removed. Having no night period, the accelerated trees were able to grow continuously. Tree heights reflected growth rate differences in the absence of duration differences. There was a tendency for northern trees to grow faster in the accelerating regime, but this tendency was weak ($r=.22$).

Once removed from the greenhouse and subjected to natural photo-periods, the accelerated trees began a slow reversion to the geographic pattern of the non-accelerated trees. Southern trees began outgrowing northern trees immediately following outplanting, but by a lesser degree than in the non-accelerated test (Table 9). Apparently, in the seedling state, annual growth increment is influenced by the size of the plant so that early growth differences can persist for long periods. In the accelerated test, the advantage

TABLE 9. Percent growth increment advantage of southern blue spruce over northern for several periods of growth. Trees from Arizona, New Mexico and southern Colorado are considered southern. Trees from Utah, Wyoming and north and central Colorado are northern.

Growth Period	Accelerated	Non-accelerated
Years	-----% increment-----	
0-2	-2	25
3-5	8	32
6-7	14	19
Total Height	9	24

of southern trees has become increasingly pronounced, but at age 7 the greater growth increment of the southern trees in the accelerated test still was not as great as in the non-accelerated test. A number of years will yet be required before geographic differences in growth rate will be equalized in the two tests.

Early selection. In the non-accelerated test, early selection for regions having fast growing trees would have been effective as regional differences in heights were similar at ages 2 and 7. (Table 10). By contrast, identification of regions having fast growing trees would have been impossible at age 2 in the accelerated test since the expression of regional differences was not apparent until later. In testing trees having different photoperiodic requirements, accelerating growth through photoperiod extension should be avoided where selection for growth rate is important.

In choosing the best stands from within a region or the best families in a stand, at age 7, earlier selection would have been unsatisfactory in the present experiment, whether the trees were begun under nursery or accelerating conditions. The usefulness of early measurements for predictive purposes depends on the strength of the relationship between the early and final heights and on the time saved by selecting at an early age. Correlations of $r=.7$ or better are necessary to prevent the omission of half of the best seedlots under most circumstances. Correlations well above $r=.9$ are necessary for selection at ages close to the final age in order to justify the small savings in time achieved by selecting at these ages. In this study, correlations between heights

at ages 2 and 7 ranged between $r=.65-.31$ for stands within regions and families within stands for both testing regimes (Table 10). These were too low for accurate prediction of height at age 7. The correlations were stronger between heights at age 5 or 6 and height at age 7, but the year or two savings were insufficient to offset the loss in gain. In testing similar material in the future, measurements before age 7 should not be expected to be useful for selection purposes at a later age.

TABLE 10. Correlations between heights at age 7 and heights at earlier ages for the accelerated and non-accelerated tests. Correlations above .39 for stand and .21 for family are significant at the .01 level.

Age	Stand within region		Family within stand	
	Accelerated	Non-accelerated	Accelerated	Non-accelerated
<hr/>				
Years	-----	-----	r -----	-----
1	.50	--	.18	--
2	.65	.31	.53	.49
5	.80	.81	.77	.76
6	.91	.93	.89	.88

Increased error variance in the greenhouse. One of the reasons often given for greenhouse testing is that it reduces the environmental "noise" (error variance) which masks true genetic differences. One measure of such "noise" is the coefficient of variation.

In our test with blue spruce, the coefficient of variation, and therefore the error variance, was lower in the non-accelerated, outdoor treatment than in the greenhouse test (.14 vs. .20). The explanation for this involves distinguishing temporal from spatial variation effects. Temporal effects include day-to-day and day-night variations which are less generally in the greenhouse than in the outdoor nursery. These conditions have been shown to favor rapid plant growth and may therefore be commercially valuable. They do little, however, to reduce spatial variation which is the actual source of environmental "noise." Spatial variation occurs when each tree receives different treatment. It may be quite large in some greenhouses. For example, in a greenhouse, it is very difficult to obtain uniform watering, and if a water-carried fertilizer is used, differences in watering will also affect nutrient levels. Sizable temperature gradients and drafts are also common in greenhouses, and uniform radiation is rarely achieved when supplemental lighting is used. All of these effects contribute to spatial variation. Most are difficult to block out, and so they contribute to error variance because each tree is affected differently. Spacial variation is likely to be less in the outdoor nursery since temperature, wind and rain will be equivalent throughout the nursery. If the nursery bed is well prepared, and the test replicated, soil and nutrient effects may also be small so that error variance is minimized.

Applications of accelerating growth for genetic testing. For height, results through age 7 show that seedlot rankings were different for trees started under accelerating conditions compared with those begun in an outdoor nursery. On this short rotation basis, testing trees by accelerating growth is necessary if trees are to be grown commercially by the accelerating method. Similarly, if trees are to be nursery-grown commercially, testing should be done using nursery-grown stock.

For long rotations, however, some conditions may favor genetic testing with accelerated stock, while others may favor testing with non-accelerated stock, regardless of the commercial method of production. This is because early growth effects are likely to be overcome over long periods. The method which can be used for accurately predicting rotation first will be the preferred method of testing.

When differences in photoperiodic requirements are important in causing height growth differences, accelerating growth through photoperiod extension may delay accurate evaluation and be less preferred. Such is the case in blue spruce. In the non-accelerated test, the faster growth of southern trees was evident at age 2, while the same geographic differences were beginning to develop much later in the accelerated test.

When photoperiodic differences are minimized, though, accelerating growth may have applicability. An example of this is lodgepole pine, Pinus contorta, where photoperiodic differences are minor. Perry and Lotan (1978) found no evidence of daylength x height or dry weight interactions for populations from British

Columbia to Utah, and correlations 5 years after field planting were very strong. For these, supplemental light may hasten growth without inducing unnatural seedling differences. Another case is the testing of families or stands within a limited geographic range. For blue spruce accelerated and non-accelerated testing procedures were found to be about equally effective through age 7.

When strong genotype x field environment interaction exists, accelerated growth may be preferred since nursery effects would tend to be swamped by the field environment and early recognition of the interaction would be facilitated by the early field planting. This has not been the case with blue spruce, which showed remarkably little genotype x environment interaction when planted at nine sites from Montana to Maine (Chapter 1).

Accelerating growth may be most valuable, however, for early selection of non-growth traits. In the present study, rankings were similar in both tests at age 7, but most traits could be judged at an earlier age in the accelerated test. For example, foliage color differences could be judged at age 5 in the accelerated test, but not until age 7 in the non-accelerated test. This is especially valuable in blue spruce where color differences are as, or more, important than growth rate differences.

CHAPTER III

ACCELERATING SEEDLING GROWTH FOR GENETIC TESTING: II RESULTS WITH FOUR WESTERN CONIFERS AFTER SIX MONTHS

ABSTRACT

Blue and Engelmann spruce, Douglas-fir and white fir from several geographic locations were grown for six months outdoors, in a greenhouse with natural photoperiods, and in a greenhouse with 24-hour light. Trees grown outdoors formed winter buds in August and September 11 to 16 weeks after germination and averaged 48 to 130 cm tall depending on species. Trees grown indoors under natural daylength conditions set bud one week later and grew 20-65% taller. Trees grown under continuous light in the greenhouse did not set winter buds by age 6 months and grew tallest, averaging 45-140% taller than the outdoor-grown trees.

Genotype x regime interaction was absent before budset but was present at experiment's end for all species but white fir. Trees grown under continuous light had the same geographic pattern for height growth at 26 weeks as at 10 weeks. However, for trees grown under natural photoperiods, those from southern and coastal locations set bud later causing them to increase in relative height beyond 10 weeks. This difference was responsible

for the significant interaction. Since seedlot rankings were similar for trees grown under natural photoperiods, whether outdoors or in the greenhouse, extended photoperiod was shown to cause differences in seedlot rankings by eliminating differences in duration of growth among trees of wide geographic origin.

INTRODUCTION

The seedling growth of many tree species can be increased by postponing bud set through exposure to continuous light and by providing irrigation, fertilizer and temperature regulation in a greenhouse. The term "accelerated growth" has been coined to describe growth under such conditions (Hanover *et al.*, 1976).

The geographic pattern of growth rate for accelerated blue spruce (Picea pungens) was found to differ markedly from nursery grown blue spruce (Chapter 2). When grown under accelerating conditions, northern trees were slightly taller than southern trees after six months. Conversely, trees from southern locations were tallest when grown in an outdoor nursery. After several years in the field, the faster growth of southern trees was evident in both tests.

The different early growth patterns in the accelerated and nursery tests were proposed to result from photoperiodic differences in bud set in the nursery test and their absence in the accelerated test. Under natural daylengths, in the nursery, southern trees could continue growing longer into the season than northern trees because they could tolerate longer nights before being triggered to go dormant. By virtue of their longer duration of growth, southern trees were taller. Trees grown under continuous light did not set bud. Differences in height due to duration of growth were therefore absent. With duration differences excluded, northern trees outgrew the southern trees. When

accelerated trees were placed outdoors, photoperiodic differences in duration of growth became effective, causing southern trees to outgrow the northern ones.

Such a hypothesis has a sound foundation. It has long been known that photoperiod controls the duration of growth for a number of tree species (Waring, 1956). Differences in daylength required for bud set among different geographic races have also been shown for several wood plants, and most commonly trees of milder (southern, coastal, low elevation) habitats require longer nights before setting bud (Vaartaja, 1957 and 1959, and Dormling, 1973).

The objectives of the present study were twofold. The first was to test the validity of the above hypothesis by separating, as much as possible, the effects of continuous light from those of the many other environmental variables that differed in the accelerating and nursery regimes in the previous test. In particular, we were interested in partitioning greenhouse and extended photoperiod effects in comparison to outdoor conditions. The second objective was to determine whether other western conifers would react to accelerating conditions in the same manner as blue spruce.

MATERIALS AND METHODS

Seeds of blue spruce, Engelmann spruce (Picea engelmannii), Douglas-fir (Pseudotsuga menziesii), and white fir (Abies concolor) were obtained through the cooperation of the U.S. Forest Service, the British Columbia Forest Service, and Crown-Zellerbach Corporation. A total of 48 seedlots were used: 18 of Douglas-fir, 14 of blue spruce, 10 of Engelmann spruce, and six of white fir.

All collections were from the Rocky Mountains except for six coastal provenances of Douglas-fir. For purposes of analysis and convenience of presentation, seedlots were grouped by region of origin. The regional groups were based on variation patterns found in Douglas-fir (Wright, et al, 1971), white fir (Wright, Lemmien, et al, 1971) and blue spruce (Chapter 1). They are defined as follows:

Southern Rockies: Arizona, New Mexico and (for blue spruce)
southern Colorado

Central Rockies: Utah and Colorado

Northern Rockies: Central Montana

Inland Empire: Western Montana, northern Idaho,
eastern Washington and Oregon

Coastal: Western Washington and Oregon

Table 11 lists the number of seedlots for each species that were put into each region.

All seeds were weighed and then stratified to promote uniform germination. The period of stratification was six weeks for white fir and three weeks for the other species.

TABLE 11. Number of seedlots in this experiment from each geographic region.

Region	Blue Sp.	Eng. Sp.	Doug.-Fir	White Fir
So. Rocky Mtns.	10	3	3	3
Cen. Rocky Mtns.	4	3	5	3
No. Rocky Mtns.	0	2	2	-
Inland Empire	-(a)	2	2	-
Pacific Coast	-	0	6	0

(a) Species does not natively occur in regions marked by (-).

The seeds were sown in May, 1977, at East Lansing, Michigan, in 2 x 2 x 11 in. polyethylene coated paper bands which were placed in one foot square plastic milk boxes. Each box supported 36 paper bands. The bands were filled with a mix of peat, vermiculite and perlite in a 1:1:1 ratio. Four to six seeds were sown in each band. After the first month of growth the seedlings were thinned to one per band.

The germinating seeds were placed under three growing regimes for the six month experimental period. Two regimes were in a greenhouse and one outdoors. The two greenhouse treatments were separated by a light-proof black cloth, and one was subjected to continuous illumination by fluorescent light at night. In that treatment, the light intensity at night was about 200 ft-c at the soil surface. The regime of continuous light in the greenhouse will be referred to hereafter as the accelerating regime.

Trees in the outdoor treatment were showing signs of severe chlorosis after two months. This was thought to be a result of the high solar radiation. Trees were therefore moved into a lath house for the remainder of the experimental period, whereupon recovery was observed.

All trees were watered as necessary. For the greenhouse grown trees, watering was about once every two weeks. The outdoor trees, which had the benefit of rainfall, were watered less frequently. Half strength 19-19-19 fertilizer was incorporated in each watering.

The experimental design consisted of eight blocks within each of the three regimes. Species were randomized within each block

and seedlots randomized within species. Each plot contained six trees. Analysis was done for each species separately. Degrees of freedom were as follows:

<u>Source</u>	<u>Doug.fir</u>	<u>Blue Sp.</u>	<u>Eng.Sp.</u>	<u>White fir</u>	<u>All</u>
Regime	2	2	2	2	2
Species	-	-	-	-	3
Seedlot/species	17	13	9	5	44
Block/regime	21	21	21	21	21
Seedlot x regime	34	26	18	10	94
Species x regime	-	-	-	-	6
Seedlot x block	357	273	189	105	987
Species x block	-	-	-	-	63

For each species, considered separately, the error terms for regime, seedlot/species, and seedlot x regime were block/regime, seedlot x block, and seedlot x block, respectively. For all species considered together, the error terms for regime, species, and regime x species were block/regime, species x block, and species x block, respectively.

All trees were measured for bud set on a weekly basis and for height at 10 weeks, before trees had set bud, and 26 weeks when the experiment was terminated. For bud set, each tree was determined to have set bud or not, and the plot sum of trees having set bud was recorded. For height, plot means were recorded.

RESULTS AND DISCUSSION

Pattern of growth under the three regimes. Trees grown outdoors set winter buds and ceased height growth in late August or early September, when they were approximately 3 months old. (Table 12). In the greenhouse, Douglas-firs grown without supplemental light responded similarly, but other species given natural daylength indoors set winter buds and ceased growth 1 to 3 weeks later.

Trees given continuous light in the greenhouse did not become dormant during the 6-month test period. Instead, most of them grew intermittently. A tree would grow for a few weeks, set a temporary bud, then start growth again several days later. The number of growth flushes varied among species, being greatest in white fir. Nearly all trees of that species produced four to five growth flushes. Douglas-firs from the Pacific Coast grew continuously, but those from the inland parts of the range grew in spurts. Douglas-firs from the northern Rocky Mountains had more (two to three) growth flushes than those from farther south (one to two). These results contrast with those of Irgens-Moller (1967), who studied geographic variation in growth periodicity under 16-hour photoperiod. In his experiments, southern Rocky Mountain seedlings had the most growth flushes.

In previous trials conducted in the same greenhouse, blue and Englemann spruces given continuous light grew continuously and attained heights of 20-25 cm at the age of 6 months. In the tests described here, they grew in flushes and grew only half as

TABLE 12. Dates when 50% of trees set winter buds for four conifers in three growing regimes.

Regime	Species			
	Blue sp.	Eng. spruce	Doug.-fir	White fir
----- Date of winter bud set -----				
Accelerating	--	--	--	--
Greenhouse, natural daylength	9/5	9/12	8/29	9/18
Outdoors	8/29	8/22	8/29	8/29

much. Because of this poor growth, I had the soil tested and found it to be deficient in all major nutrients. Young and Hanover (in press) found that nutrient stress, but not temperature or water stress, induced bud set of blue spruces grown under continuous light. Their results suggest that the nutrient deficiencies were probably responsible for the growth flushes in my experiment.

Height of trees in the three regimes. Heights of the trees treated to the three growing regimes are given in Table 13, by species and region of origin. At the age of 10 weeks, most of the greenhouse-grown trees were 15-30% taller than the seedlings grown outdoors. Only in white fir were the outdoor and indoor trees the same height. As for the greenhouse-grown trees, those given continuous light were the same height as those given natural daylength. The advantage offered by the greenhouse environment was probably a combination of higher night temperature, lower insolation, and lower wind movement.

The 10 week measurements were made in early August. The trees given natural daylength continued to grow another 1-5 weeks outdoors and another 3-6 weeks indoors before they formed dormant winter buds. During that time they grew another 30-90%. Trees given continuous light continued to grow during the entire period of the experiment, and as a result were 30-180% taller than outdoor-grown trees by the 26th week.

In absolute terms, Douglas-fir responded most to the accelerated, continuous-light conditions. In percentage terms, the blue and Engelmann spruces responded most. Whether stated in ab-

TABLE 13. Height at ages 10 and 26 weeks of four species of trees
grown under three regimes, by region of origin of seed.

Region of origin	Species and Regime (a)											
	Blue spruce			Eng. spruce			Douglas-fir			White fir		
	ACC	GRE	OUT	ACC	GRE	OUT	ACC	GRE	OUT	ACC	GRE	OUT
-----mm-----												
Height at age 12 weeks												
Sou. Rockies	53	58	43	43	48	37	84	91	75	45	47	47
Cen. Rockies	51	53	41	43	48	35	78	75	63	33	37	36
Nor. Rockies	--	--	--	43	45	35	69	60	48	--	--	--
Inland Empire	--	--	--	54	55	40	108	114	86	--	--	--
Pac. Coast	--	--	--	--	--	--	118	130	106	--	--	--
Height at age 26 weeks												
Sou. Rockies	123	96	64	117	97	65	212	160	133	104	91	78
Cen. Rockies	120	77	54	115	78	43	198	118	98	78	66	48
Nor. Rockies	--	--	--	113	70	40	158	85	68	--	--	--
Inland Empire	--	--	--	134	78	47	272	158	128	--	--	--
Pac. Coast	--	--	--	--	--	--	293	225	183	--	--	--

(a)ACC = Accelerated regime; GRE = Greenhouse regime with natural daylength; OUT = Outdoor regime.

solute or percentage terms, white fir responded least to the continuous light.

On five other occasions blue and/or Engelmann spruces have been grown under continuous light in similar greenhouses. In those previous experiments, height at the age of 26 weeks was approximately twice that achieved in the present experiment. My comparatively poor results are probably due to the previously mentioned soil deficiency.

Geographic variation in date of bud set. Seedlings given continuous light did not set dormant winter buds by the 26th week no matter what the origin of the seed. Those given natural day-length set winter buds in late summer, the exact time varying with geographic origin of the seed and with species. Although time of bud set was earlier for the trees grown under the "outdoor" regime, the geographic variation pattern was so similar for the "greenhouse" and "outdoor" regimes that average dates for the two regimes are given in Table 14.

If the Pacific Coast Douglas-firs, with their very late bud set, are excluded, the general trend in all species was for seedlings from southern areas to set buds later than those from farther north. In both Engelmann spruce and Douglas-fir there was almost a month difference in the onset of dormancy between the trees from the Inland Empire and northern Rockies, which set buds in mid-August, and those from the southern Rockies, which maintained active terminal growth for another month.

TABLE 14. Date of 50% budset for trees grown under natural photo-period.

Region	Blue Sp.	Eng. Sp.	Doug.-Fir	White Fir
So. Rocky Mtn.	9/5	9/15	9/12	9/18
Cen. Rocky Mtns.	8/25	8/25	8/22	9/5
No. Rocky Mtns.	--	8/15	8/10	--
Inland Empire	--	8/15	8/15	--
Pacific Coast	--	--	9/25	--

Geographic variation in height growth in the three regimes.

At 10 weeks of age, seedlot rankings for height were similar in all growing regimes. Furthermore, the geographic patterns of height were roughly similar among the species tested. Heights, expressed as percent of species means in each regime, are given in Table 15 to facilitate comparisons among species. Except coastal Douglas-firs, which were tallest, the general pattern was for trees from the Inland Empire to be tallest, followed in decreasing order of height by trees from the southern, central, and northern Rocky Mountains.

Regional differences in height were larger for some species than others, however. Specifically, spruces were less variable than Douglas-firs or white firs. Regional variation was only 7% for blue spruce and 20% for Engelmann spruce. By contrast, differences in white fir were 30%, despite the restricted range of the collections used; and for Douglas-fir from the Rocky Mountains, Inland Empire trees were nearly 100% taller than trees from the northern Rocky Mountain region.

After the 10th week, trees under continuous light increased their heights by 130-170% before the experiment was terminated at 26 weeks. The relative amount of growth was equal in trees from all regions so that trees which were tallest at 10 weeks were also tallest at 26 weeks. This, however, was not the case with trees grown under natural photoperiod, in the greenhouse or outdoors. In these, the amount of new growth after the 10th week depended on the geographic origin, growth being least in trees which set buds earliest. Trees from the northern Rockies and In-

TABLE 15. Relative height of trees from different geographic regions
in three growing regimes.

Region of origin	Species and Regime (a)											
	Blue spruce			Eng. spruce			Douglas-fir			White fir		
	ACC	GRE	OUT	ACC	GRE	OUT	ACC	GRE	OUT	ACC	GRE	OUT
Height at 10 weeks -----% of regime mean for each species-----												
So. Rocky Mtns.	103	105	104	95	99	102	89	92	93	115	112	113
Cen. Rocky Mtns.	98	96	97	95	97	97	83	76	79	85	88	87
No. Rocky Mtns.	--	--	--	94	92	96	73	61	60	--	--	--
Inland Empire	--	--	--	118	112	108	115	115	107	--	--	--
Pacific Coast	--	--	--	--	--	--	125	132	131	--	--	--
Height at 26 weeks												
So. Rockies	101	108	106	98	118	130	92	100	102	115	120	124
Cen. Rockies	98	86	90	96	95	88	84	74	75	85	80	76
No. Rockies	--	--	--	95	85	82	67	53	53	--	--	--
Inland Empire	--	--	--	112	96	95	115	98	91	--	--	--
Pacific Coast	--	--	--	--	--	--	124	140	141	--	--	--

(a)ACC = Accelerated regime; GRE = Greenhouse regime with natural daylength, OUT = Outdoor regime.

land Empire, which set buds earliest, grew an additional 30-40% after the 10th week, depending on species. Trees from the central Rockies grew another 40-60%; those from the southern Rockies, 60-90% more; and coastal Douglas-fir, an additional 75%. As a result, in the regimes having natural photoperiod, trees from the southern Rockies and Pacific coast increased in relative height between the 10th and 26th weeks, while trees from the Central and Northern Rocky Mountain and Inland Empire regions declined (Table 15). For Douglas-fir and Engelmann spruce, changes in seedlot rankings occurred. For blue spruce and white fir, height differences between southern and central Rocky Mountain trees were widened. In general, seedlot differences were less in the accelerating treatment than in treatments having natural photoperiod.

Statistically speaking, seedlot x regime interaction between the accelerating regime and the others was significant for all species but white fir at 26 weeks. Interaction was strongest for Engelmann spruce, weaker in Douglas-fir and weaker yet in blue spruce. The weak interaction in blue spruce contrasts with findings in a much larger study conducted earlier (Chapter 2). In that study with 192 half-sib families, northern trees grew somewhat faster under the accelerating conditions, whereas, in the present study southern trees were faster. Rankings of accelerated trees in the present study were therefore more similar to rankings outdoors than in the previous test.

No statistically significant interaction was detected between the outdoor and greenhouse with natural photoperiod regimes, for any species.

CONCLUSION

For the species tested in the present experiment, photoperiod was shown to influence the period of growth. Formation of winter buds was induced when dark periods of critical lengths were reached. Furthermore, critical night lengths causing bud set were different for trees of different geographic origin. Critical night lengths were longer and, hence, duration of growth longer in southern and coastal trees. Under natural photoperiods, the final heights of trees depended upon their rate of growth and duration of growth. However, under continuous light tree heights depended only on the average rate of growth since no trees were induced to set winter buds. Where fast growth rate and long durations of growth occurred in the same trees, rankings were similar in the accelerated and nonaccelerated treatments and interaction was absent or small. Such was the case with blue spruce and white fir where southern trees were the tallest in all regimes. But, when trees with faster growth rates did not have the longer periods of growth, some differences in height ranking occurred between trees allowed to grow continuously and those which set bud under the control of natural photoperiod. This was the case with Inland Empire trees which were fast growing and well above average in height in the accelerated treatment. In the natural photoperiod treatments they were also fast growing before bud set but grew for a relatively short period so that their final heights were less than average.

CHAPTER IV

GEOGRAPHIC VARIATION IN SHOOT GROWTH COMPONENTS OF BLUE SPRUCE AND INTERIOR DOUGLAS FIR

ABSTRACT

The annual shoot growth of a tree can be divided into two components: the number of leaf nodes and the distance between leaf nodes. The number of needle nodes in the uppermost branches of trees from ten provenances of 8-year-old blue spruce and nine provenances of 15-year-old interior Douglas-fir, grown in southern Michigan, accounted for the majority of variation in yearly growth increment. All needles on the shoots of blue spruce, and most of the needles on Douglas-fir, were present in the bud prior to shoot elongation.

To investigate how rate and duration of needle primordia initiation (NPI) in the bud affect total needle complement, NPI was monitored during 1977 by periodically sampling terminal buds from the topmost branches on trees of all provenances. Although trees from southern sources were the first to begin shoot elongation in the spring, they began NPI at a slower rate than northern trees. Northern trees ceased NPI in August while southern trees continued into late September. As a result of the longer period of NPI, blue spruce from Arizona and New Mexico produced a larger

total complement of needle primordia in the resting bud than blue spruce from farther north. In Douglas-fir both rate and duration of NPI were responsible for geographic differences in needle primordia complement in the winter bud.

INTRODUCTION

Provenance variation in height growth ultimately derives from differential activity of the apical and subapical meristems. The apical meristem determines the number of stem units (defined by Doak (1935) as the needle and its subtending internode) and the subapical meristem determines the degree of elongation for each stem unit internode.

The activity of these meristems is phased and controlled independently (Romberger, 1963; Zimmerman and Brown, 1971; Cannell, 1976). The apical meristem is active during the entire growing season producing needle and bud scale primordia, while the subapical meristem is active for a much briefer time during which elongation occurs. For young Picea, Pseudotsuga, Abies, Tsuga and Larix the apical meristem first produces needles, then bud scales and finally needle primordia which accumulate within the bud. As a tree ages the number of needle primordia produced early in the season, before bud formation, is greatly reduced or absent; only bud scales are produced at the onset of apical activity in the spring. The yearly shoot growth for older trees is said to be determinate, because all stem units have been predetermined the year before during bud development.

The subapical meristem begins activity in spring, elongating internodes between needles. Activity increases acropetally and ceases when bud scales are reached. Trees having a single flush of growth, such as Picea and Pseudotsuga, usually require chilling before resumption of extension growth can continue.

In young trees, some needles are produced and their internodes elongated during the season of their initiation. This has been termed "free growth" (Jablanski, 1971). In older trees such growth is much reduced or absent.

Provenance variation in first year seedling height is primarily due to the duration of free growth which in turn is determined by photoperiod in Pseudotsuga and several species of Picea (Chapter 3; Pollard, 1976, Pollard et al., 1975; Dormling et al., 1968). Southern trees, which tolerate longer nights before bud set, generally grow longer into the season. Beyond three years of age, however, photoperiodic determination of growth ceases in blue spruce, Picea pungens (Young and Hanover, 1976), and many other species of Picea, Abies, and Pseudotsuga as well. Provenance variation in height beyond this young age must be due to other internal and external factors regulating meristematic activity.

Size alone can have substantial effect on subsequent growth because of differences in photosynthetic surface area. Provenance differences established at early ages can therefore be maintained for longer periods. However, juvenile size differences cannot account for growth rates at more mature ages in blue spruce or interior Douglas-fir (Pseudotsuga menziesii, var glauca) growth in Michigan. For example, blue spruce grown under continuous light for six months, which eliminated differences in duration of growth, showed little provenance differentiation for height. Differences did not develop until after age 3, when they had been in the field for two years. Provenance differentiation beyond age 3 years was quite substantial, however, so that trees at age 7 showed a pat-

tern of provenance variation for height similar to those grown under natural conditions in which southern trees were tallest from the first year. In Douglas-fir, southern trees were also tallest from the beginning, but this advantage has diminished in later years, while trees from the Inland Empire have increased in relative height (Wright, Kung *et al.*, 1971).

The purpose of this study was to investigate variability in the different processes of meristem activity which might be responsible for provenance variation in young blue spruce and Douglas-fir. The importance of variability in stem unit number and elongation, presence of free growth, and rate and duration of needle primordia initiation were considered.

MATERIALS AND METHODS

This work consisted of three separate studies conducted over a two year period. Provenance tests of interior Douglas-fir and blue spruce established at Kellogg Experimental Forest in Kalamazoo County in southern Michigan provided the material used in all work. Eight provenances of interior Douglas-fir and ten of blue spruce, chosen from many portions of each species' range, were used. Each provenance of Douglas-fir was planted in 4 tree plots replicated in 10 blocks. Blue spruce half-sib families were also planted in 5 tree plots and replicated in 5 blocks. Each blue spruce provenance had 3-10 half-sib families. The Douglas-fir were 14 years old when work began in fall, 1976, and the blue spruce were 7 years of age.

In the first study, occurrence of free growth was determined by sampling one or two terminal buds from lateral branches in the first whorl beneath the leader in December, 1976. The bud scales were removed and the needle primordia were determined by counting the number of primordia files (contact parastiches), the number of primordia per file, and then taking their product. In August, 1977, elongated terminal shoots from the same whorl on the same trees were collected and the number of needles counted. Where needle numbers on the elongated shoots exceeded primordia counts in the buds, free growth was considered to have occurred. A paired t-test was used to determine the statistical significance of the differences. Eight trees from each of the provenances were used.

In the second study, provenance variation in the number of

needles and distance between needles was measured and related to variation in current shoot length. This study was done twice for blue spruce. In the first case, first order twigs from the second whorl beneath the leader were used. These were the same twigs collected in August, 1976, for determination of free growth. In the second case, branches from the whorl beneath the leader were collected. For Douglas-fir only branches from the whorl beneath the leader were used. Branch lengths were measured and needle numbers were counted in an electronic seed counter. Douglas-fir needles were pulled off when fresh; blue spruce needles were allowed to air dry on the branch and then naturally abscissed. Eight trees from each provenance were used. Analysis of variance were performed for needle number, stem unit length and branch length.

In the third study, provenance variation in rates and times of needle primordia initiation in the bud were investigated. Beginning in May, 1977, just after budbreak, and every 2-4 weeks thereafter through November, terminal buds from the expanding lateral branches in the first whorl beneath the new leader were collected and the number of needle primordia within them were counted as described above. Then trees from each provenance were sampled in each collection. Half were trees used in the collection done two to four weeks before. Paired t-tests were used to test the significance of differences in needle primordia number between dates of collection for each provenance. LSD values calculated from analysis of variance were used to detect differences between provenances on a given date.

Tree heights were measured on all provenances in both species for comparison with the trees sampled. Finally, the leaders on the sampled trees were measured for comparison with the laterials used.

RESULTS

Blue spruce. Differences in distance between needles on a shoot were detected among blue spruce provenances, but they were small and not related to geographic origin (Table 16). Rather, geographic differences in shoot length were due to variation in needle number. Furthermore, overall variation in branch length was primarily a result of differences in needle number, not to differences in distance between needles. Needle number explained 84% of the variation in length of branches taken from the top whorl and 52% in branches from the second whorl beneath the leader. Differences in elongation between needles accounted for 8% and 13% of the variation in length of branches from the top and second-to-the-top whorls, respectively. These statistics are based on the r^2 values for needle number and stem unit length correlated with branch length.

The geographic differences in needle number were not the result of differences in free growth. In all provenances the number of primordia in the buds exceeded the number of needles on the subsequently elongated shoots (Table 17). Not only was there no free growth on these 7-year old blue spruce, but apparently the last formed primordia in the winter bud differentiated into budscales during the development the following spring. More primordia existing in the winter bud developed into budscales in southern trees than northern trees, but the difference was small.

Table 16. Provenance variation in shoot growth traits of blue spruce.

Region and Provenance No.	Shoot length		Needles	
	Leader	Lateral	number of	distance between
Southern				
31	36	20	332	16.5
9	36	20	398	18.4
39	42	20	343	17.5
28	31	17	306	18.5
27	37	21	333	16.2
	Average 31.5	19.2	328	17.4
Northern				
40	31	21	355	17.4
15	30	16	296	18.1
11	28	18	315	17.5
16	31	19	325	17.2
13	36	20	347	17.4
	Average 36.0	19.8	328	17.5
<hr/>				
Statistical significance ^{1/}				
Between				
stands	**	**	**	**
regions	**	*	**	ns

^{1/} ** = significant at $p = .01$;
 * = significant at $p = .05$;
 ns = not significant

Table 17. Number of primordia in buds and needles on shoots derived from comparable buds of blue spruce.

Region and Provenance No.	[A] Primordia in bud	[B] Needles on shoot	[B-A]
Southern			
31	363	343	-20**
9	354	306	-48**
39	436	398	-38**
28	367	332	-35**
27	348	328	-24**
Average	378	343	-35
Northern			
40	340	347	+ 7 ns
15	350	315	-35**
11	325	296	-29**
16	329	325	- 4 ns
13	392	355	-37**
Average	348	328	-20

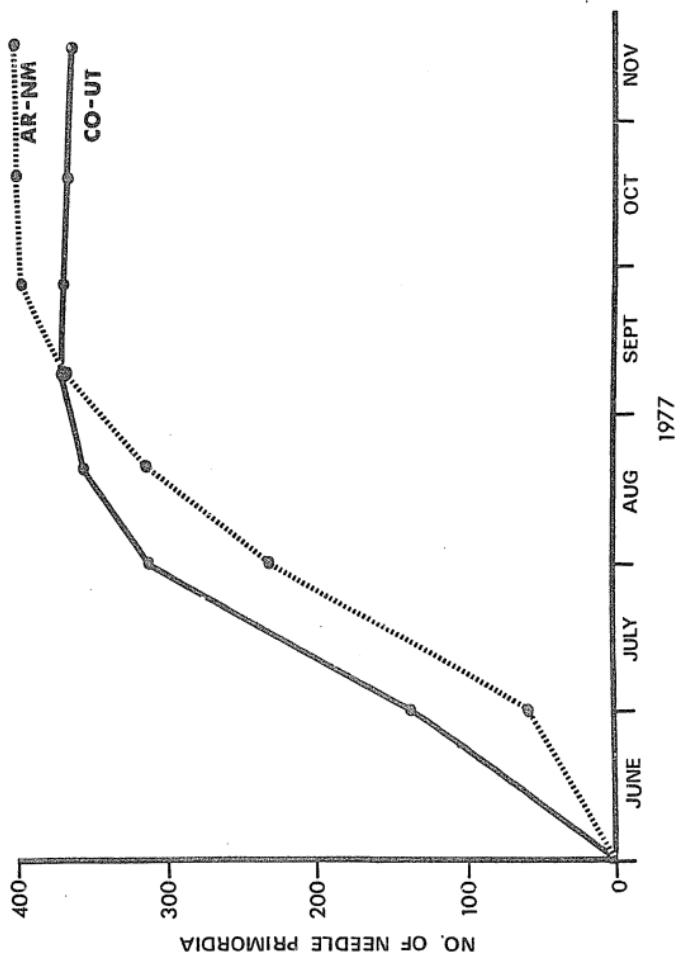
** = significant at $p = .01$

ns = not significant

Because free growth was absent in these blue spruce, all variation in needle number must result from differences in development of the winter bud. In following the development of the 1977-78 winter bud, during May - November, 1977, bud scales were observed at the ends of the 1977 shoots as they emerged from their buds in early May. Bud scales continued to be produced in all provenances through June 7. When the next sample was taken, on July 1, needle primordia were observed in the buds of all provenances, but there was considerable variation in the number of needle primordia accumulated. Southernmost trees had the fewest primordia and northern trees the greatest number. These differences resulted either from differential rate of primordia initiation or differences in the onset of initiation. In other spruces, Cannell and Willett (1975) showed that southern Picea sitchensis began needle initiation after northern trees, but Pollard (1973) found no differences in the date when needle primordia production began for Picea glauca from a narrower geographic range.

The development of the primordia shoot in 1977-78 winter buds is shown in Figure 4. Provenances have been bulked into northern and southern curves to emphasize gross geographic differences. During July there were no geographic differences in rate of development. After July, rates of initiation slowed for all provenances, but decreased most for trees of northern origin. After September 1, there were no further increases in the number of needle primordia through September. No needle primordia were initiated after October 13 in the southern blue spruce.

FIGURE 4. Seasonal accumulation of needle primordia
in terminal buds of lateral branches in the
first whorl beneath the leader of 8-year-
old blue spruce. Curves for the northern
and southern portions of the range are
based on average of 5 stands.



When bud development was completed, southern trees averaged 5% more primordia than northern trees. This difference did not emerge until after September 1, when northern trees had completed initiation and southern trees were still adding to their primordia complement. Before September 1, northern trees had more needle primordia than southern trees because of their more prolific start.

Within each of the two geographic groups in Figure 4, there was considerable variation in total needle primordia complement. Both rate and duration of initiation contributed to within region differences. Phenological events were strongly related to latitude. Northern trees began initiation earlier but southern trees ceased activity later so that more southern trees typically had a smaller portion of their needle primordia complements accumulated at any time than trees from more northerly locations (Table 18). However, differences in rate of primordia production were often large enough to offset differences in duration so that the correlation of total needle primordia number with latitudutde was not strong.

TABLE NO. 18. Seasonal accumulation of needle primordia in the developing buds of trees from 10 blue spruce provenances.

Region and Provenance No.	State ^{1/}	Lat. (°)	Needle primordia complement		
			% of total on 7/1	% of total on 8/18	Total
Southern					
31	AR	33.5	11	72	383
9	NM	33.9	11	72	388
39	NM	36.1	20	88	392
28	CO	37.5	17	84	417
27	CO	37.6	21	87	418
AVG.			15	81	400
Northern					
40	CO	39.3	33	92	402
15	CO	39.6	31	96	351
11	UT	40.0	39	97	353
16	CO	40.1	34	95	370
13	WY	43.3	41	98	398
AVG.			35	96	375

Correlation with lat. (r) +.95**^a +.93** -.17 N.S.

^a** = significant at p = .01; N.S. = not significant.

^{1/}AR = Arizona; NM = New Mexico; CO = Colorado; UT = Utah; WY = Wyoming

Douglas-fir. Unlike blue spruce, there were large geographic differences in the distance between needles as well as in number of needles. The geographic pattern for needle number was similar to the pattern for annual height increment (Table 19). Trees from the Inland Empire had the greatest number, Arizona-New Mexico trees the next greatest, and trees from Colorado, Utah and Montana had the fewest needles. The geographic pattern for distance between needles was different however. Trees from the southern Rockies had long stem units and northern Rocky Mountain trees had short stem units. This was similar to the pattern of frost damage that occurred during spring, 1977, just before the shoots were sampled. We reason that the great elongation between needles in the southern trees was a direct result of the frost damage. Trees that were frost damaged were able to funnel their photosynthetic reserves into the surviving shoots, stimulating greater elongation than normal. Colorado-Utah trees were most severely damaged by frost and responded by producing the longest stem units. The unusually long shoot growth of southern trees, compared to the annual height growth over the previous 3 years, is evident from the data in Table 19.

Needle number was much more important in determining shoot length for Douglas-fir when northern and southern trees are considered separately, however. For northern trees, 80% of shoot length variation was explained by needle number and only 4% by distance between needles. For southern Douglas-fir, 58% of the shoot length was explained by needle number and 7% by elongation

Table 19. Relative geographic differences in shoot growth traits of Douglas-fir.

Region ^{1/}	Annual ^{2/} increment	Shoot length		Needles	
		leader	lateral	number of	distance between
- - - - - % of INEMP - - - - -					
AR-NM	96	111	109	79	130
CO-UT	62	107	104	66	150
C MONT	60	67	69	61	110
INEMP	100	100	100	100	100

^{1/} AR-NM = Arizona-New Mexico; CO-UT = Colorado-Utah
 C MONT = Central Montana; INEMP = Inland Empire

^{2/} Growth from 1974-1976.

between needles.

Also, unlike blue spruce, some needles were initiated and expanded in the same season for most Douglas-fir (Table 20). Only trees from Arizona and New Mexico did not have significantly more needles on elongated shoots than in comparable buds the winter before expansion. Trees from the Inland Empire initiated 20% of their total needle complements as free growth. This was the total difference between these sources and Arizona-New Mexico in needle counts. Trees from Colorado, Utah, and Montana obtained a small part of their needle complements from free growth, but it affected their height ranking very little.

All needles initiated and elongated in the same spring must have initiated before bud break because new bud scales were visible at the tips of the elongating shoots as they emerged from their buds.

Most of the geographic variation in needle number resulted from differences in the number of primordia determined in the bud. Both rate and duration of needle primordia initiation were important in determining the total needle complements.

Inland Empire and Arizona-New Mexico trees had the most pre-determined needles and there was no statistically significant difference between them. They achieved their high counts through different "strategies," however (Figure 5). Inland Empire trees started fast, tapered off, and finished early. Arizona and New Mexico trees started slower, initiated primordia at a constant rate throughout the summer and finished later. Colorado-Utah trees had the same pattern of needle initiation as the Arizona-New Mexico trees, but

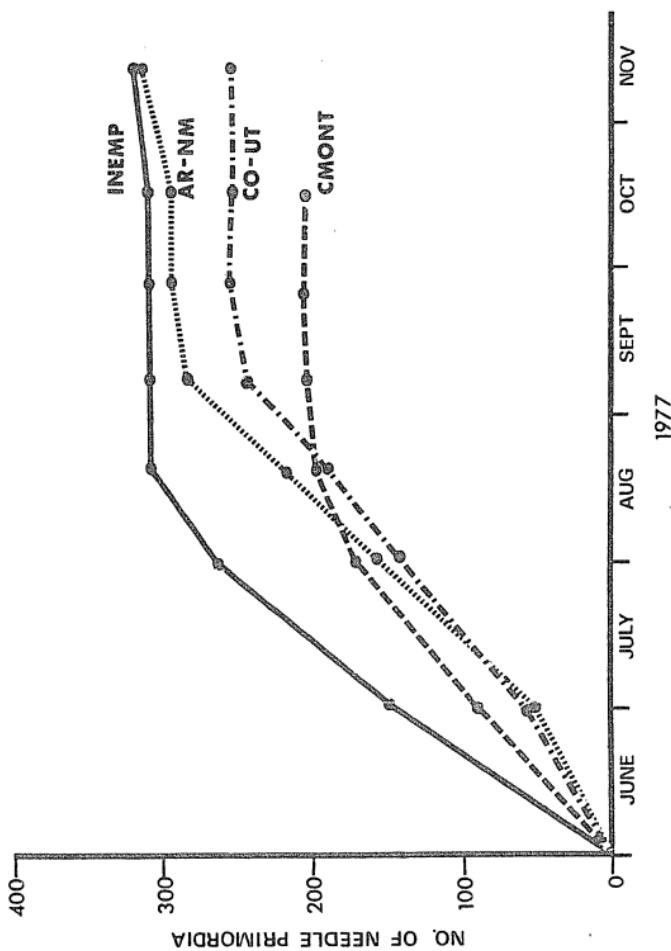
Table 20. Number of primordia in buds and needles on shoots derived from comparable buds of Douglas-fir.

Region and Provenance No.	[A] Primordia in bud	[B] Needles on shoot	[B-A]
AR-NM			
594	322	321	- 1ns
610	272	282	+10ns
Average	297	301	+ 4
CO-UT			
630	251	268	+17**
611	220	256	+36**
605	219	241	+22**
Average	230	255	+25
C MONT			
505	190	238	+48**
648	230	252	+22**
Average	210	245	+35
INEMP			
517	307	392	+85**
563	308	379	+71**
Average	308	386	+78

** = significant at $p = .01$

ns = not significant

FIGURE 5. Seasonal accumulation of needle primordia in terminal buds of lateral branches in the first whorl beneath the leader of 15-year-old Douglas-fir from 4 regions. Curves for each region are based on averages of two or three provenances.



then initiated primordia at a slower rate at any given time. Trees from central Montana had the fewest needle primordia. Their pattern of development was similar to that of the Inland Empire trees, but rates of initiation were much slower.

Trees from the Inland Empire and central Montana had ceased needle primordia production by August 17, while trees from the southern and central Rockies continued initiation a month longer. Differences in needle primordia production within each of these two groups were due to rate of initiation rather than duration.

Similarity of leader and lateral shoots. In the present study, lateral shoots from the top whorls of the trees were used in order to spare the leaders. This has been the common practice for studies of this kind. There must be some assurance that these branches behave similarly to the leaders if this study is to have usefulness. For Picea sitchensis and Pinus contorta Cannell (1974) found that the behavior of laterals at the tree tops resembled that of the leaders. In this study, differences in lateral lengths were similar to differences in leader length, and needle number was well correlated with periodic annual growth (Tables 16 and 19). But stem unit length and occurrence of free growth were not measured on the leaders, so that some caution must still be observed in relating meristem activities of the laterals to that of the leaders.

DISCUSSION

For blue spruce and for northern and southern interior Douglas-fir considered separately, needle number was a good determinant of shoot length. Distance between needles varied little and contributed little to shoot length variation among provenances. For other Picea species and for Pinus contorta needle number has also been closely correlated, and stem length poorly correlated, with shoot growth (Cannell, 1974; Pollard, 1973).

The difference between northern and southern Douglas-fir was probably a result of frost damage on the southern trees causing their shoots to elongate to an abnormal degree. This response has also been observed on frost damaged white and white x blue hybrid spruce grown in southern Michigan where 1 m leaders were observed on 2 m trees after 90% of their shoots were killed. Several consecutive frosts would, of course, lead to greatly diminished growth, but occasional heavy frosts permit the spring photosynthate reserve to be channelled to the surviving shoots, resulting in unusually long, spindly growth.

Most of the difference in needle number was determined in the winter bud, before shoot extension. Eight-year-old blue spruce had entirely passed the juvenile phase in which predetermined growth is augmented by free growth. But, for 15-year-old interior Douglas fir, up to 20% of the total needle complement was derived from free growth. These Douglas-fir (and the long shoots of Larix (Clausen and Kozlowski, 1970) are apparently exceptions to the rule that all

shoot growth of mature individuals in the Pinaceae is predetermined in the winter bud (Jablanski, 1971; Pollard, 1976; Lanner, 1976).

The free growth of Douglas-fir should not be confused with lammas growth. In both free and lammas growth, stem units are initiated and extended in the same season. But, lammas growth is the premature expansion of a developing winter bud. Under favorable conditions the primordial shoot in the developing bud will extend during midsummer without having been chilled. New winter buds form at the ends of lammas shoots and these buds contain fewer needle primordia when completed than comparable shoots which have not produced lammas growth (Bongarten, unpublished). Free growth, on the other hand, is the production and elongation of stem units in the same season prior to bud development. For interior Douglas-fir grown in Michigan, lammas growth is confined to trees from the southern Rockies while free growth is more pronounced on trees from the southern Rockies.

In the developing buds of blue spruce and interior Douglas-fir, there were strong latitudinal trends in the phenology of primordia initiation as there were for Picea sitchensis (Cannell and Willett, 1975). Trees of northern origin began primordia initiation at an earlier date than southern trees, but southern trees continued to initiate needle primordia for up to a month longer into the season. Thus, southern trees initiated needle primordia longer than northern trees. Differences in duration were 2-4 weeks for trees from latitudinal extremes.

The longer duration of needle primordia initiation in southern trees parallels the longer duration of free growth in these trees as seedlings. Duration differences in the free growth of seedlings are determined by photoperiod, and it is possible that photoperiod also regulates the duration of needle primordia initiation in the buds of mature trees.

Interestingly, unlike most temperate zone trees, blue spruce and Douglas-fir from southern origins began shoot extension before northern trees when grown at a common location. But like Sitka spruce, they apparently began needle initiation in the bud at a later date than northern trees. This is further evidence that apical and subapical meristem activity are controlled independently.

For blue spruce, differences in duration of needle primordia initiation wholly accounted for the longer mean shoot lengths of southern trees, but differences in rate of needle primordia initiation resulted in differing needle counts among trees from similar latitudes. For example, provenance 40 from northern Colorado had more needle primordia in the fully developed bud than other nearby provenances although there were no phenological differences.

In interior Douglas-fir there were important regional differences in rates of needle initiation, but they were not latitudinally or longitudinally consistant. Inland Empire trees had the largest number of needle primordia because of their fast rate of initiation, although the duration of initiation was short. Trees from further east in central Montana had the same phenology of needle primordia initiation, but because of their much slower

rates of initiation, they produced the fewest needle primordia. Also, the greater number of needles in Arizona-New Mexico trees compared to Colorado-Utah trees were primarily a result of differences in rate of initiation rather than duration. The greater growth of Arizona-New Mexico and Colorado-Utah trees over central Montana trees, however, resulted from the longer duration of initiation in the former.

In conclusion, phenology of needle primordia initiation was strongly dependent on latitude of origin for both species. However, both rate and duration were important in provenance variation in needle primordia number. The faster growth of southern blue spruce can be attributed to the longer duration of needle primordia initiation. Southern Douglas-fir was fast growing for the same reason. But Inland Empire Douglas-fir had a rapid rate of primordia production and was able to produce free growth. These traits permitted them to the fastest growing trees in the tests.

CHAPTER V

SUMMARY

A rangewide seed collection of 260 half-sib families from 61 native stands of blue spruce (*Picea pungens*, Engl.) was made in 1969. Seeds were grown outdoors in a nursery and also in a greenhouse with continuous light. Trees in the latter group, referred to as "accelerated," were field planted in southern Michigan after 6 months of continuous growth. Trees grown in the outdoor nursery were field planted at the same height after 3 years, adjacent to the "accelerated" trees, and also at eight other locations from Montana to Maine. After 7 years from seed, the tests were compared for genetic variation. This work describes the genetic variation of blue spruce and focuses particularly on factors of shoot growth that have lead to different patterns of height growth in the accelerated and nursery-grown trees. Three other western conifers are compared to blue spruce in their reaction to accelerating conditions and Douglas-fir is compared to blue spruce for several components of shoot growth variation.

For the nursery-grown blue spruce, results were similar at all nine plantation locations. Trees from southern Arizona and New Mexico were the fastest growing, but had mostly green foliage. Trees from northern Arizona and New Mexico and southern Colorado

were also above average in height and were the bluest. Trees from Utah, Wyoming, and northwest Arizona were least susceptible to spring frost damage although even the most susceptible were damaged infrequently. Trees of all origins suffered heavy terminal bud mortality each winter. This was a cause of forking and diminished height growth. Significant variation in height, color, and date of leafing out was found for region, stand and family of origin, although blue spruce showed less total genetic variation than other Rocky Mountain conifers for all traits but color.

At the same age, accelerated trees were taller, had bluer foliage color, later date of leafing out, less frost damage, less winter needle browning, less terminal bud mortality and higher survival than the nursery-started trees. Except for height, differences were small. For height, accelerated trees were 70% taller at age 7. However, if growth is measured from time of field planting, heights were equal at 4 years from planting.

Genotype x plantation interaction for the accelerated and nursery-grown trees in Michigan was pronounced only for height. Much of the interaction was evident in the regional patterns of height. In the first year, accelerated seedlings from northern regions were taller than southern trees, while the reverse was true in the nursery seedlings. After 7 years, southern trees were taller in both tests, although the differences were smaller in the accelerated test.

First year differences resulted directly from the different photoperiods. Blue spruce under natural photoperiods, whether outdoors or in the greenhouse, set buds when the night period reached

a critical length. Trees from southern origins required longer nights before being induced to dormancy, and were taller by virtue of their longer period of growth. Under continuous light, blue spruce were able to grow continuously during the 6-month growing period. The geographic pattern of height in accelerated blue spruce, represents differences in growth rate in the absence of duration differences. Northern trees had a weak tendency for faster rate of growth.

Genotype x seedling treatment interaction was also found in testing Engelmann spruce and Douglas-fir under 24-hour and natural photoperiods. Southern trees, having late bud set, were relatively taller, and northern trees, having early bud set, were relatively shorter in the natural photoperiod regime than under continuous light. For white fir there was no interaction, as southern trees were much faster growing under both conditions.

After field planting, the accelerated trees began a slow reversion to the geographic pattern of the trees grown outdoors. Since the photoperiodic control of shoot growth ceases after the third year, other factors must have been involved in the continued faster growth of southern trees. Such factors must operate through the meristems which give rise to shoot growth. Two meristems are involved: the apical meristem which determines the number of stem units (leaf nodes) and the rib meristem which determines the distance between leaf nodes. For 8-year-old blue spruce, differences in needle numbers accounted for most of the variation in shoot length; internode distance was not variable. Furthermore, all needles were evident in the preformed winter bud.

Inherent variation in the rate and duration of bud development was therefore undertaken. Taken as a group, southern trees had more needle primordia in the buds because their period of initiation was almost a month longer than the northern ones. Rate of needle initiation was not important in regional differences in needle number; however, differences within regions were large and resulted from differences in rate of needle initiation.

In Douglas-fir, like blue spruce, the phenology of bud development was correlated well with latitude, northern trees beginning fast and finishing early compared to the southern trees. However, regional differences in Douglas-fir also depended to some degree on rates of needle initiation. Furthermore, southern trees seemed to have longer distances between needles.

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