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GENETIC VARIATION OF
MORPHOLOGICAL AND PHYSIOLOGICAL TRAITS
IN BLUE AND ENGELMANN SPRUCE

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GENETIC VARIATION OF
MORPHOLOGICAL AND PHYSIOLOGICAL TRAITS
IN BLUE AND ENGELMANN SPRUCE

By

George Philip Buchert

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DEDICATION

To my Father and Mother,
who gave me the opportunity
to achieve my full potential.

ABSTRACT

GENETIC VARIATION OF MORPHOLOGICAL AND PHYSIOLOGICAL TRAITS IN BLUE AND ENGELMANN SPRUCE

By

GEORGE PHILIP BUCHERT

Genetic variation in height growth, susceptibility to frost damage, timing of phenological events, foliage color, needle morphology, and physiological response to water stress was studied in an all-range collection of blue spruce open-pollinated families and selected Engelmann and white spruce seedlots, under southern Michigan growing conditions. Seedlings of 238 blue spruce families from 44 populations in eight climatic regions throughout the natural range were raised under accelerated-growth conditions and under standard nursery conditions. Regional differences in 6-year height were well-expressed in nursery-reared trees, accounting for 19% of total variation, but were nonexistent in trees reared under accelerated conditions. Among-population and between-family components were similar in nursery and accelerated trees, ranging from 17 to 20% of total variation. Utah sources grew slowest, had the least number of blue-needled trees, flushed out latest and

sustained the least frost damage, while southern New Mexico and Arizona sources grew fastest, flushed out earliest and suffered the most frost damage. Expression of blue foliage color increased with age, and was most prevalent on sources from Colorado and northern New Mexico. Western Colorado appears to be an area of extreme variability for all traits measured. Seedlots from this area varied as much as 88% in 6-year height and ranged from 0-78% in number of blue-needed trees. A selection index based on family growth rate and foliage color identified those families to be included in a breeding population which would produce genetically improved blue spruce seed for a variety of horticultural and regeneration purposes.

Although blue spruce may have been derived from Engelmann spruce ancestors, adaptation to warmer, drier habitats resulted in a recognizably different taxon. Blue spruce seedlots were, on average, taller than Engelmann spruce after 6 years. Blue and Engelmann seedlots from a common Arizona origin were tallest at 5 years; however, growth losses due to repeated spring frost damage were a major factor in height growth between species. Because of adaptations to high elevation environments, Engelmann spruce flushed out earlier than blue spruce and was more susceptible to spring frosts. However, Engelmann spruce was quite variable in growth-related traits at regional, population and family levels. It appears that morphological characters are under very different selective pressures for blue and

Engelmann spruce. The ratio of needle length to resin sac length proved to be a reliable diagnostic character for differentiating the two species; however, other morphological characters were more variable. Needle width of blue spruce was highly variable among families within populations, but relatively uniform among populations, whereas Engelmann spruce populations were very different from each other.

Transpiration curves were determined for selected blue, Engelmann and white spruce seedlots by expressing water loss as $\text{g}\cdot\text{dm}^{-2}\cdot\text{h}^{-1}$. Three patterns of transpiration response to diminishing soil moisture were apparent among species. Blue spruce transpiration rates were inhibited at field capacity (18-22% soil moisture), reached maximum rates at 10-14% soil moisture, declined gradually as soil moisture declined to a threshold of 4.5%, then dropped rapidly to a minimum at 3% soil moisture. Although some Engelmann spruce reacted like blue spruce, others simply decreased transpiration gradually as soil moisture decreased. White spruce transpiration rates were highest at field capacity, reached an intermediate level between 8 and 18% and then decreased gradually to a minimum between 3 and 8% soil moisture. Fast-growing blue spruces are evidently capable of maintaining gas exchange at lower soil moisture and more negative xylem pressure potential, thus allowing growth processes to take place in stress conditions. The strong differences in transpiration pattern among and within species indicate

adaptation to very different habitats, and suggest that family selection for this trait may be an effective way to screen for fast growth.

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CHAPTER 1. GEOGRAPHIC VARIATION IN BLUE SPRUCE --
SIX-YEAR RESULTS

INTRODUCTION

Picea pungens Engelm. is known throughout the world's temperate climatic zones as Colorado blue spruce. P. pungens occurs naturally from southern New Mexico and Arizona to southwest Montana, and eastward from central Utah through the Colorado Rocky Mountains (Hanover 1975). In general, blue spruce is found in riparian habitats and the borders of forest openings. Common tree species associated with blue spruce are Populus tremuloides Michx., Pseudotsuga menzesii (Mirb.) Franco, Pinus ponderosa Dougl. ex Laws. in the lower portion of its elevation range and Picea engelmannii Parry ex Engelm. near its upper elevation limits.

Because blue spruce is tolerant of both cold and drought conditions, it has been used very successfully in windbreak plantings in low rainfall areas such as the Great Plains. Since its introduction into the horticultural trade in 1862, the striking steel blue foliage and symmetrical form of blue spruce has ensured a continuous demand for ornamentals derived from the dozen or so recognized cultivars, so it is highly valued by the landscape industry (Rehder 1940). Blue spruce is also characterized by very slow growth, and studies have been initiated to ascertain the amount and pattern of genetic variation in several

economically important characters for use in selection and breeding.

In a 1908 trial of possible coniferous species suitable for Canadian prairie shelterbelts, blue spruce, white spruce (Picea glauca Voss) and Norway spruce (Picea abies L. Karst) proved to be the most successful (Department of Regional Economic Expansion, 1977). However, due to pine needle scale and spider mite mortality of white and Norway spruce during drought years, blue spruce has been found to be the best suited for shelterbelt planting (Cram 1964). Because pest resistance appears to be related to the amount of epicuticular waxes on blue spruce needles, Saskatchewan's Indian Head Nursery has, since 1954, been conducting breeding studies to increase the frequency of blue foliage seedlings by crossing selected blue needled parent trees (Cram and Lindquist 1969). Cram (1957) reported that substantial difference in survival, vigor and foliage color were present among progenies of 25 selected parents 8 years after planting. Cram (1956) also reported that self incompatibility differed between selected parent trees.

The first provenance study of P. pungens, in which seedlings from a total of 12 provenances in four states were outplanted in three Minnesota plantations, was initiated in 1951 by D. P. Duncan of the University of Minnesota. Seedlings from seven of these provenances were outplanted by the U. S. Forest Service in North Dakota, and Dawson and Rudolph (1966) reported on survival, height, susceptibility

to frost damage and crown diameter after five years. Their results indicated that trees from the north side of the Uinta Mountains, in the Ashley National Forest, Utah, were the tallest after five years in the field. This provenance also had the best survival and was least damaged by late spring frosts. The slowest-growing provenance came from the south side of the Uinta Mountains, also in the Ashley National Forest. Scholten¹ observed that the two provenances from Arizona (Kaibab and Apache National Forests) were tallest in three Minnesota plantations after 19 years from seed. In these plantations the shortest provenances were from the Wasatch National Forest, Utah and the Targhee National Forest, Wyoming. Provenances having the bluest or most desirable foliage color were from Chaffee County, Colorado and Apache National Forest, Arizona, with 48% and 44% blue trees, respectively. Although both of the above studies gave some indication of relative adaptability to their planting sites, too few provenances were included to accurately estimate the amount and pattern of genetic variability. The North Dakota planting gave evidence of intra-population variation, as seen in the Ashley National Forest seedlots which included the fastest and slowest growing trees. However, trees from these same two sources were very similar in their resistance to frost damage. The three

1 Scholten, H. unpublished report on file in Forestry Department, Michigan State University.

Minnesota plantings indicated that trees with blue color came mostly from areas in Colorado and Arizona.

In 1969 Dr. J. W. Hanover of Michigan State University initiated a range-wide collection of open-pollinated cones from individual trees as a first step in the genetic improvements of blue spruce. Through the cooperation of the U. S. Forest Service, more than 400 open-pollinated families of blue and Engelmann spruce from 75 populations were collected and sent to Michigan State University. Subsequently, 238 of these families were grown under accelerated growth conditions (Hanover and Reicosky 1972) and also in an East Lansing nursery (Hanover 1975). Seedlings from these families were planted out in permanent genetic test plantations near Battle Creek, Michigan. Patterns of genetic variation for 15 growth and foliage characters are presented in this report, along with a simple selection index for determining seedlots of greatest value in a tree improvement program.

MATERIALS AND METHODS

Seedlings of each of 238 open-pollinated families were raised under the accelerated growth conditions described by Hanover and Reicosky (1972). Four-tree plots of each family were outplanted in three replicates of a randomized complete block design genetic test plantation near Battle Creek, Michigan in September 1970. This experiment is designated the ACCEL plantation in the following report.

Progenies from the same families were raised in an East Lansing nursery (Hanover 1975) and were outplanted adjacent to and in the same design as the ACCEL plantation. The nursery-grown progeny experiment is referred to as the NUR plantation in this report.

ACCEL progenies were measured at 3 and 6 months of age prior to outplanting and at 2, 5 and 6 years of age in the plantation. NUR progenies were measured at 2 years of age in the nursery, and at 5 and 6 years of age in the plantation. All plot trees were measured and the mean plot value was used for analysis.

On May 18, 1973, a severe frost (-3°C) occurred over most of southern Michigan and resulting damage to newly emerged buds in the ACCEL plantation was evaluated on June 9, 1973. By this date undamaged buds had flushed completely, while those buds killed by frost had dried and were quite conspicuous. Damage was estimated visually and graded in the following manner:

<u>Frost Damage Grade</u>	<u>Condition of Tree</u>
1	- less than 1/3 of all new shoots killed
2	- more than 1/3 but less than 2/3 of all new shoots killed
3	- more than 2/3 of all new shoots killed

Individual plot trees were graded and a plot mean was calculated. Since relative damage between seedlots was considered most important, a relative frost damage value was calculated for each plot by distributing the mean plot value

on a relative damage scale from 0 to 100%. A regression was calculated using damage grade as the independent variable and relative frost damage as the dependent variable, as follows:

<u>Independent Variable</u>	<u>Dependent Variable</u>
Damage Grade 1.0	0% Relative Frost Damage
Damage Grade 2.0	50% Relative Frost Damage
Damage Grade 3.0	100% Relative Frost Damage

The resulting linear regression equation was:

$$\hat{Y} = 50X - 50$$

Percent Relative Frost Damage (RFD) was expressed as

$$\hat{Y} \cdot 10^{-2}$$

and RFD was calculated for each mean plot value. For analysis of variance, RFD values were transformed to arcsine $\sqrt{\text{percent}}$ (Steel and Torrie 1960).

In spring 1974, the ACCEL plantations were evaluated for variability in shoot phenology. On May 1, 15, 21 and 29, all seedlots were scored for stage of bud development using six easily recognizable phenophases which correspond closely to Nienstaedt and King's (1970) phenophases for white spruce. Phenophases were recorded as follows:

<u>Bud Stage</u>	<u>Condition of Buds</u>
1	winter resting bud
2	bud beginning to swell
3	bud fully swollen, needles inside
4	needles bursting through scales
5	shoot elongating, needles closely appressed
6	shoot elongated, needles free

Each individual plot tree was scored for bud stage and plot means were calculated and used as observations in subsequent analysis. Concurrent temperature data were recorded near the plantation site and were used to calculate growing-degree-days of heat accumulation by summing up mean daily temperature in degrees above a base temperature of 5.5°C.

Proportions of blue and steel blue trees per plot were recorded in May of the fifth and sixth years of growth in the ACCEL plantation, and transformed to arcsine $\sqrt{\text{percent}}$ for analysis. The assessment was made soon after flushing, to record maximum color expression since environmental weathering of epicuticular waxes had not yet occurred.

A simple selection index (SEI) was developed to identify families which might be included in a blue spruce breeding program. Six-year NUR and ACCEL height and 6-year % blue and % steel blue trees were included in the index because of their obvious economic value. The amount contributed by each character was additive, and those

open-pollinated families with the highest SEI values were considered for selection. Foliage color values which were expressed as percent of blue and steel blue trees were directly additive, while ACCEL and NUR heights were expressed in a percent of the plantation mean and then added, so that:

$$SEI = \frac{a}{62} + \frac{b}{85} + c + d$$

where a = mean family 6-year NUR height
 b = mean family 6-year ACCEL height
 c = mean family % blue trees at 6 years
 d = mean family % steel blue trees at 6 years

With this equation, fast-growing families would be favored regardless of foliage color, while families with predominately blue progeny would also be selected, irrespective of growth rate.

In order to estimate the extent to which regional climatic and topographic patterns influenced genetic variation, populations were grouped into eight climatic regions (Table 1) as suggested by Baker (1944). An analysis of variance was calculated for each character (Table 2), where σ^2 estimates the variance attributable to error, σ_r^2 estimates the variance among climatic regions, σ_p^2 estimates the variance among populations within climatic regions and σ_f^2 estimates the variance among families within populations. Because of unequal subclass numbers in the hierarchal design, expected mean square coefficients were calculated

Table 1. Climatic Summary at Origin of 44 Parental Blue Spruce Populations

Popula- tion Number	Climatic Region	Eleva- tion Meters	North Lat. Degrees	West Long. Degrees	Mean Celsius Temperature		Annual Precipita- tion cm.	Grow- Season Days	Frost Prec Days	Days From January 1 of	
					January	July				Last Spring	Frost
13A	WYO	1830	43.30	110.80	-9	17	43	210	140	130	130
13B	WYO	1860	43.30	110.67	-9	16	43	205	135	130	130
13C	WYO	1890	43.30	110.56	-9	16	43	200	130	130	135
4	UINTA	2130	40.47	111.33	-7	18	36	167	70	167	167
7	UINTA	2590	40.58	110.33	-11	13	61	130	0	360	360
50A	UINTA	2400	40.75	109.75	-10	14	56	145	40	190	190
1	WAS	2360	38.82	111.67	-9	16	51	145	45	180	180
11	WAS	2360	39.65	111.18	-9	16	51	150	45	180	180
12	WAS	2280	40.43	111.57	-8	17	51	155	56	175	175
25	WAS	1980	38.73	111.32	-6	18	41	105	85	160	160
26	WAS	2500	39.27	111.52	-9	14	56	135	0	360	360
32	WAS	2560	39.33	111.50	-10	14	61	130	0	360	360
38	WAS	2560	38.10	111.43	-10	14	61	136	0	360	360
5	WCOL	2340	40.08	106.08	-7	18	36	170	104	157	157
6	WCOL	2320	39.47	107.50	-7	18	48	170	100	160	160
10A	WCOL	2670	39.47	107.00	-9	14	58	155	75	165	165
10B	WCOL	2060	39.47	107.00	-6	19	41	185	120	145	145
10C	WCOL	2210	39.47	107.00	-7	18	46	175	110	155	155
15	WCOL	2390	39.58	106.38	-7	17	53	170	96	165	165
16A	WCOL	2590	40.12	107.07	-8	16	58	158	78	170	170
27B	WCOL	2410	37.75	108.00	-8	17	56	165	95	160	160
27C	WCOL	2470	37.75	108.00	-8	16	61	160	85	165	165
33	WCOL	2560	38.55	107.32	-8	16	58	159	78	170	170
35B	WCOL	2800	38.27	106.18	-9	14	66	145	60	180	180
37A	WCOL	2440	39.53	107.03	-8	17	56	165	90	160	160
37B	WCOL	2490	39.25	107.03	-8	16	56	160	85	165	165
40	WCOL	2510	39.23	106.80	-8	17	56	162	87	165	165
8	ECOL	2510	39.75	105.52	-5	16	46	162	83	160	160
14A	ECOL	2860	38.85	105.68	-8	13	53	135	45	185	185
14B	ECOL	2930	38.88	105.97	-8	13	56	130	35	195	195
24	ECOL	2900	38.97	106.05	-7	13	53	133	46	185	185
29	ECOL	2390	38.18	105.12	-11	17	46	172	98	155	155
28	NNMEX	2440	37.48	106.90	-5	17	53	190	102	105	105
36	NNMEX	2900	36.30	105.42	-8	14	71	150	70	165	165
39A	NNMEX	2560	36.10	106.47	-6	17	56	175	105	155	155
39B	NNMEX	2590	36.00	106.00	-6	16	58	170	100	160	160
48	NNMEX	2340	35.73	105.67	-4	18	48	190	123	140	140
53	NNMEX	2620	36.47	106.50	-6	16	56	175	96	150	150
31A	ARIZ	2490	30.67	109.25	-3	16	69	180	90	160	160
31B	ARIZ	2720	33.65	109.30	-3	14	81	160	75	170	170
31C	ARIZ	2580	33.75	109.35	-2	15	76	170	90	165	165
31D	ARIZ	2600	33.82	109.37	-2	15	76	170	90	165	165
9	SNMEX	2600	33.87	107.50	+2	9	61	248	148	127	127
62	SNMEX	2590	33.28	107.83	+2	9	66	245	150	127	127

WYO = Western Wyoming; UINTA = Uinta Mountains; WAS = Wasatch Mountains; WCOL = Western Colorado; ECOL = Eastern Colorado; NNMEX = Northern New Mexico; ARIZ = Southern Arizona; SNMEX = Southern New Mexico.

Table 2. Analysis of Variance for Blue Spruce Half-sib Progenies

Source of Variation	NUR 5, 6 Year Height		NUR 2 Year Height	
	d.f.	Expected Mean Squares	d.f.	Expected Mean Squares
Blocks	2		3	
Regions	7	$\sigma^2 + 3\sigma_f^2 + 12.98\sigma_p^2 + 59.80\sigma_r^2$	7	$\sigma^2 + 4\sigma_f^2 + 19.04\sigma_p^2 + 92.80\sigma_r^2$
Populations	35	$\sigma^2 + 3\sigma_f^2 + 11.50\sigma_p^2$	37	$\sigma^2 + 4\sigma_f^2 + 16.83\sigma_p^2$
Families	126	$\sigma^2 + 3\sigma_f^2$	149	$\sigma^2 + 4\sigma_f^2$
Error	336	σ^2	582	σ^2

Source of Variation	ACCEL 2, 5, 6 Year Height		Bud Phenology		Selection Index	
	d.f.	Expected Mean Squares	d.f.	Expected Mean Squares	d.f.	Expected Mean Squares
Blocks	2		3			
Regions	7	$\sigma^2 + 3\sigma_f^2 + 14.80\sigma_p^2 + 71.57\sigma_r^2$	7	$\sigma^2 + 4\sigma_f^2 + 19.77\sigma_p^2 + 95.43\sigma_r^2$	7	$\sigma^2 + 4.28\sigma_p^2 + 19.43\sigma_r^2$
Populations	36	$\sigma^2 + 3\sigma_f^2 + 13.44\sigma_p^2$	36	$\sigma^2 + 4\sigma_f^2 + 17.91\sigma_p^2$	35	$\sigma^2 + 3.73\sigma_p^2$
Families	157	$\sigma^2 + 3\sigma_f^2$	157	$\sigma^2 + 4\sigma_f^2$	122	σ^2
Error	400	σ^2	600	σ^2		

after the manner of Kempthorne (1957). An F-test was made for each component by dividing by the appropriate mean square. An approximate F-test was made for climatic region mean squares by reconstructing the error mean square from the estimated variance components and expected mean square coefficients to provide a clean F-ratio, as suggested by Namkoong et al. (1972). Estimated variance components were then calculated as a percent of total variance so that relative differences would be more meaningful. Significant differences among mean character values were determined by the LSD method (Steel and Torrie 1960).

In order to ascertain relationships between measured characters and environmental variables, simple correlations were calculated between characters and elevation, latitude and longitude of parental populations. Additionally, general climatic parameters were estimated for each population by interpolation from Baker's (1944) climatic charts. In this way, mean January temperature, mean July temperature, annual precipitation, length of growing season, number of frost-free days and length of spring frost season were correlated with measured characters.

RESULTS

Height Growth

Analyses of variance for all measured characters are summarized in Table 3, while individual variance components are presented in Table 4. Most characters showed highly significant differences ($F \geq 0.01$) within the three levels of classification. Significant differences among climatic regions were present in NUR trees at 2, 5 and 6 years of age. However, percent of total variance due to differences among climatic regions ($\sigma^2_{r \text{ NUR}}$) decreased with increasing plantation age so that by age 6 years $\sigma^2_{r \text{ NUR}}$ was only two-thirds that at age 2 years. As seen in Table 5, trees from the Uinta Mountains (UINTA) were generally the slowest growing at age 6, while trees from southern New Mexico (SNMEX) were generally tallest. Significant changes in ranking occurred among climatic regions with age; western Wyoming materials were shortest in the nursery, but at age 6 were not significantly different from the fastest-growing climatic region, SNMEX. In marked contrast to NUR materials, differences among climatic regions were absent in ACCEL height data at all ages.

Differences among populations within climatic regions (σ^2_p) were highly significant for 2, 5 and 6 year NUR heights. When expressed as a percent of total variance, $\sigma^2_{p \text{ NUR}}$ fluctuated with age. At 5 years, $\sigma^2_{p \text{ NUR}}$ was about

Table 3. Mean Squares for Measured Characters of Blue Spruce Half-sib Progenies

Source of Variation	d.f.	6 Yr. NUR Height	5 Yr. NUR Height	d.f.	2 Yr. NUR Height	6 Yr. Color % Blue Trees	Relative Frost Damage	6 Yr. Color % Blue Trees	6 Yr. Color % Steel Blue Trees	5 Yr. Color % Blue Trees	5 Yr. Color % Steel Blue Trees	d.f.	Selection Index
Blocks	2	90.92	3.20	3	66.55			153.83	166.54	2931.54	139.82		
Regions	7	996.29 **	857.52 **	7	442.94 **		7710.32 **	23583.07 **	4261.60 **	9205.55 **	1434.26 **		
Populations	35	206.92 **	121.12 **	37	54.57 **		686.65 **	3586.05 **	1291.23 **	2013.04 **	348.97 **		
Families	126	72.38 **	44.16 **	149	9.91 **		265.94 n.s.	857.05 **	346.69 **	490.45 **	136.36 **		
Error	336	31.07	17.41	580	5.97		230.50	378.13	166.90	260.27	86.75		
Source of Variation	d.f.	6 Yr. AOCEL Height	5 Yr. AOCEL Height	2 Yr. AOCEL Height	Bud Phenology 5/21/74	Bud Phenology 5/29/74	Bud Phenology 5/15/74	Bud Phenology 5/1/74					
Blocks	2	115.11	18.22	6.38	135.42	4.25							
Regions	7	593.80 n.s.	248.05 n.s.	81.07 n.s.	340.62 **	737.69 **						7	20759.41 **
Populations	36	511.63 **	272.74 **	54.64 **	77.16 **	37.98 **						35	4365.39 **
Families	157	167.96 **	85.76 **	22.72 **	25.71 **	12.02 **						122	1194.63
Error	400	91.64	52.83	7.98	10.94	6.82							

n.s. = F-value not significant
 ** = F-value significant at 0.01 level

Table 4. Components of Variance for 16 Blue Spruce Characters.

CHARACTER DESCRIPTION	VARIANCE COMPONENT ¹				PERCENT OF TOTAL VARIANCE			
	σ_r^2	σ_p^2	σ_f^2	σ_e^2	$\frac{\sigma_r^2}{\sigma^2}$	$\frac{\sigma_p^2}{\sigma^2}$	$\frac{\sigma_f^2}{\sigma^2}$	$\frac{\sigma_e^2}{\sigma^2}$
2 year height, NUR	4.29	2.65	1.31	5.97	19	17	20	44
5 year height, NUR	12.31	6.69	8.95	17.32	27	15	20	38
6 year height, NUR	13.08	11.70	13.77	31.07	30	19	9	42
2 year height, ACCEL	0.37	2.38	4.91	7.98	2	15	32	51
5 year height, ACCEL	0	13.91	11.03	52.66	0	18	14	68
6 year height, ACCEL	1.13	25.57	25.44	91.64	1	18	18	63
Relative Frost Damage	93.14	31.30	11.81	230.50	27	8	3	62
Bud Phenology, May 1	5.34	1.60	1.83	7.02	34	10	12	44
Bud Phenology, May 15	2.30	2.71	3.71	7.90	14	16	22	48
Bud Phenology, May 21	2.87	2.76	3.69	10.94	14	14	18	54
Bud Phenology, May 29	7.33	1.45	1.30	6.81	43	9	8	40
5 year color & blue trees	100.50	113.29	76.73	260.27	18	21	14	47
5 year color & steel blue trees	15.16	15.82	16.45	86.75	11	12	12	65
6 year color & blue trees	279.40	203.05	159.64	378.13	27	20	16	37
6 year color & steel blue trees	41.50	70.27	70.91	166.96	12	20	20	48
Selection Index	790.13	984.25		1194.63	27	33		40

- 1 σ_r^2 = variance among climatic regions
 σ_p^2 = variance among populations within climatic regions
 σ_f^2 = variance among families within populations
 σ_e^2 = error variance

Table 5. Mean Values of 16 Blue Spruce Characters for 8 Climatic Regions.

Climatic Region	CHARACTER															
	NUR Height, cm		ACCEL Height, cm		Relative Frost Damage	Bud Phenology		5 year Color		6 year Color						
	2 Yr	5 Yr	2 Yr	5 Yr		May 1	May 15	May 21	May 29	blue	steel	blue	steel			
WYO	9	33	47	29	64	83	17	21	31	44	51	1	0	7	1	
UINTA	13	24	35	28	60	80	18	22	34	47	54	2	0	8	0	
WAS	13	29	42	29	62	83	11	21	33	47	53	11	1	13	2	
WOOL	14	31	44	29	60	79	31	25	35	49	58	17	3	35	10	
BCOL	14	28	41	27	57	76	33	24	35	48	58	25	8	39	17	
NNMEX	16	34	47	27	62	83	35	26	36	50	59	37	12	58	20	
ARIZ	17	36	49	27	61	83	38	28	36	49	59	5	0	16	0	
SNMEX	16	40	54	28	60	84	38	28	37	50	59	20	6	51	13	
Plantation Mean	14	32	44	28	61	81	27	24	35	48	56	16	4	29	8	

20% lower than σ^2_p NUR at 2 years. However at age 6, σ^2_p NUR accounted for 17% of total variance. This fluctuation may be the result of a fairly uniform post-planting response among populations which served to minimize population differences immediately after planting, the effects of which are decreasing with age from planting. In the ACCEL materials, variation attributable to populations within climatic regions (σ^2_p ACCEL) was in the same range as described for NUR materials (18% of total variation at age 6 years), and had increased somewhat since outplanting.

In NUR height measurements, differences among populations were detected in 5 out of 7 climatic regions at age 2 years; but at 6 years of age only western Colorado (WCOL) had significant variability among populations (Table 6). The two tallest populations (27B, 27C) in the NUR plantations as well as some of the shortest (16A, 35B 37A) were from this area. Based on 6-year heights, the fastest-growing population was 55% taller than the slowest-growing population. WCOL was also the most variable in ACCEL height measurements. At 6 years of age, one of the tallest (27B) and the shortest (5) populations in the ACCEL plantation were from this area, indicating that selection of proper source populations could increase height growth by 48%. Six-year ACCEL heights for seedlots from the Wasatch Mountains of Utah (WAS) and northern New Mexico (NNMEX) indicated significant differences among populations from

Table 6. Summary of Population Character Means Grouped by Climatic Region

Climatic Region	Population	NUR Height, cm.			ACCEL Height, cm.			Bud Phenology, 1974			Relative Frost Damage	Blue Trees		Steel Blue Trees	
		2 Yr	5 Yr	6 Yr	2 Yr	5 Yr	6 Yr	5/1	5/15	5/21		5/29	5 Yr	6 Yr	5 Yr
WYO	13A	10	31	47	30	64	83	22	32	44	52	2	7	0	2
	13B	9	34	47	29	67	87	20	30	42	52	2	11	0	0
	13C	8	-	-	28	61	80	21	32	45	52	0	3	0	0
UINTA	4	14	-	-	29	62	81	21	31	44	51	3	8	0	0
	7	15	26	36	26	55	75	24	35	49	54	3	6	0	0
	50A	12	23	34	28	62	80	23	36	48	56	2	9	0	0
WAS	1	12	31	46	29	58	81	23	35	48	51	3	1	3	3
	11	13	28	38	29	60	80	22	34	48	54	11	17	4	3
	12	12	32	46	29	59	77	21	31	45	53	6	3	0	0
WCOL	25	12	30	46	29	65	87	22	35	48	55	16	22	0	5
	26	16	34	46	33	68	95	20	31	47	52	8	0	0	0
	32	13	28	40	29	67	82	20	32	46	51	7	0	0	0
ECOL	38	12	24	36	26	63	84	20	30	40	50	11	12	6	0
	5	10	27	39	26	53	64	25	34	51	59	14	79	14	38
	6	15	32	44	31	66	87	22	34	47	56	15	14	4	6
NNMEX	10A	12	29	39	32	66	84	23	35	50	58	18	35	2	12
	10B	14	29	40	25	54	69	25	34	47	57	40	25	7	25
	10C	16	32	47	30	59	85	23	34	47	56	22	6	0	0
ARIZ	15	14	32	47	32	66	83	26	36	49	58	24	12	0	2
	16A	13	28	36	29	56	73	24	34	49	58	32	5	0	0
	16B	18	40	56	33	72	94	29	40	52	60	45	50	72	12
SNMEX	27C	20	43	56	33	69	92	29	41	53	60	31	28	64	5
	33	16	36	48	26	57	76	27	37	51	59	34	13	27	0
	35B	11	26	36	24	52	71	23	34	46	55	33	23	45	2
WYOM	37A	14	24	37	25	51	72	25	38	52	60	46	13	46	0
	37B	16	28	42	30	63	87	22	33	47	57	24	20	25	3
	40	15	34	48	28	61	81	25	36	49	58	35	6	27	2
ECOL	8	13	27	39	28	61	79	22	34	48	57	35	34	9	16
	14A	12	30	42	27	54	74	26	36	48	59	32	6	18	0
	14B	12	27	41	25	56	74	26	36	50	58	37	20	33	0
NNMEX	24	15	30	41	26	57	74	24	34	48	58	29	27	48	8
	29	15	30	41	27	57	77	22	33	47	58	30	56	65	28
	28	17	37	49	28	64	87	26	35	50	50	29	34	64	8
ARIZ	36	16	34	43	24	53	71	28	38	51	59	47	26	50	0
	39A	15	35	46	27	65	87	25	32	48	59	22	46	69	16
	39B	15	33	43	28	60	80	26	37	49	57	35	27	39	9
SNMEX	48	16	32	50	26	65	88	27	35	46	58	38	19	41	0
	53	16	32	45	26	62	81	28	38	53	60	45	56	73	21
	31A	17	37	50	28	61	83	29	38	52	60	45	2	14	0
SNMEX	31B	17	35	47	27	61	85	26	33	46	57	31	6	6	0
	31C	18	36	48	25	57	78	27	37	49	58	40	2	14	0
	31D	18	40	51	28	62	86	28	38	51	60	39	9	29	0
SNMEX	9	16	39	52	28	62	88	30	37	50	59	32	29	74	10
	62	16	42	56	28	55	78	28	38	49	59	32	29	74	10
					28	55	78	28	38	49	59	5	15	5	5

these regions also, with height differences of 23% and 25% between the tallest and shortest populations in each region, respectively.

In NUR materials, variance due to families within populations ($\sigma^2_{f \text{ NUR}}$) doubled from age 2 to age 5 and remained at 20% of total variance through age 6 years. This change may be age-related but also may reflect a differential family response to planting effects and test environment. In ACCEL materials, family-within-population variance ($\sigma^2_{f \text{ ACCEL}}$) decreased by 1/2 between 2 and 5 years of age and then increased again from 5 to 6 years. At 6 years of age, error variance was much higher for the ACCEL than for the NUR plantation.

Significant differences among families were observed in 11 of the 44 populations represented in the NUR plantation. Difference in height of the tallest family in relation to the shortest family ranged from 32% to 88% among populations. The tallest family in the experiment was seedlot #8162 from population 27C (Table 7), in WCOL. Two families were included in this population sample; selection of the taller instead of the shorter family would give a growth differential of 26%. The shortest family was seedlot #8034 from population 8 in eastern Colorado (ECOL), and was little more than 50% as tall as the tallest seedlot in that population. The 15 tallest families constitute about 10% of the total number of families, and are derived from 12 different populations in 5 different climatic regions.

Table 7. Simple Correlations Among Growth and Environmental Factors for 44 Blue Spruce Populations.

	ACCEL Height			NUR Height			Relative Frost Damage	Bud Phenology, 1974			Foliage Color	
	2 Yr	5 Yr	6 Yr	2 Yr	5 Yr	6 Yr		5/1	5/15	5/21	5/29	& Blue
ACCEL Height, 2 yrs.	.5											
5 yrs.	.4	.9										
6 yrs.	.1	.1	.2									
NUR Height, 2 yrs.	.1	.2	.2	.6								
5 yrs.	.1	.1	.3	.5	.9							
6 yrs.	.1	.1	.3	.5	.9							
Relative Frost Damage	-.4	-.4	-.4	.4	.3	.2						
Bud Phenology 5/1	-.2	-.2	-.2	.6	.4	.4	.7					
5/15	-.2	-.3	-.2	.4	.2	.2	.6	.7				
5/21	-.1	-.3	-.3	.4	.1	.1	.6	.7	.8			
5/29	-.2	-.2	-.1	.5	.3	.2	.7	.7	.7	.7		
6 Year Color, & Blue	-.2	0	-.1	.3	.2	0	.5	.2	.1	.1	0	
6 Year Color, & Steel Blue	-.1	0	-.2	-.1	.9	.1	.4	.1	.1	.1	0	
Latitude	.2	.1	.1	-.7	-.5	-.4	-.5	-.6	-.4	-.4	-.6	-.1
Longitude	.2	.2	.2	-.3	0	.2	-.7	-.4	-.3	-.3	-.4	-.4
Elevation	-.2	-.2	-.1	.4	-.1	-.1	.4	.4	.3	.4	.4	.1
Growing Season	.1	.1	.1	.1	.5	.5	.3	.2	0	-.1	.1	.2
Frost Free Days	.1	.2	.1	0	.4	.1	.3	.3	.1	-.1	.2	.2
Days to Last Frost	-.1	-.2	-.3	-.1	-.5	-.4	-.1	-.2	.1	.1	.1	-.2
January Temperature	-.1	0	.2	.1	.6	.6	.4	.6	.2	.2	.3	.1
July Temperature	.2	.2	.1	-.1	-.2	0	-.2	-.2	-.2	-.1	-.1	-.2
Precipitation	-.2	-.1	.1	-.5	-.1	.2	.4	.4	-.4	.3	.2	-.1

Fourteen of these seedlots originated in the climatic regions of WCOL, NNMEX, SNMEX and ARIZ. The remaining seedlot, #8088 came from population 13B in western Wyoming.

Correlations between NUR height measurements and environmental variables at seed origin were low, (Table 7) although several factors correlated significantly with 5- and 6-year height. Latitude of seed source origin was significantly correlated with 5- and 6-year NUR height, while mean January temperature was significantly correlated with NUR height at all three measurement ages. ACCEL height was negatively and significantly correlated with relative frost damage and length of frost season.

When 6-year height measurements were correlated with the same parameters within a given climatic region, a somewhat different pattern emerged (Table 8). Highly significant relationships between 6 year NUR and 6 year ACCEL height were present in western Colorado, but not in other regions. Although correlation coefficients were relatively high in eastern Colorado and northern New Mexico, small sample sizes precluded statistical significance at these levels. Environmental variables conditioned by elevation were highly correlated with 6-year NUR and ACCEL height in ECOL and NNMEX and with both latitude and longitude in WCOL (Table 9).

Table 8. Correlation Coefficient Between 6-Year
NUR Height and Climatic Parameters

<u>Trait or Climatic Parameter</u>	<u>Climatic Region¹</u>				
	<u>WAS</u> 6 df	<u>WCOL</u> 13 df	<u>ECOL</u> 4 df	<u>NNMEX</u> 5 df	<u>ARIZ</u> 3 df
6-year ACCEL height	.26	.75*	-.78	.62	.36
Relative frost damage	-.59	-.05	-.36	-.66	.52
Bud stage 5/1	.30	.75*	.64	-.33	.78
Bud stage 5/29	.29	.43	.80	.16	.87
Elevation	-.54	.13	.44	-.80*	-.51
Latitude	.31	-.67*	-.79*	.08	-.11
Longitude	.49	-.22	.11	.38	.33
Mean January temperature	.58	.07	-.74	.82*	.62
Mean July temperature	.57	.17	-.43	.84*	.50
Annual precipitation	.58	.10	.57	-.78*	.43
Growing season length	-.17	.14	-.43	.81*	.51
Frost free days	.47	.19	-.43	.78*	.68
Days from January 1 to last spring frost	-.40	-.11	.48	-.60	-.51

*significant at P = 0.01

1 WASatch, Western COLorado, Eastern COLorado, Northern New MEXico,
ARIZona.

Table 9. Correlation Coefficient Between 6-Year ACCEL Height and Climatic Parameters.

Trait or Climatic Parameter	Climatic Region ¹									
	WYO 2 df	UINTA 2 df	WAS 6 df	WCOL 13 df	ECOL 4 df	NNMEX 5 df	ARIZ 3 df			
Relative frost damage	-.94	-.98**	-.48	-.37	.13	-.73	-.41			
Bud stage 5/1	-.36	.94	-.34	.29	-.91**	-.48	.00			
Bud stage 5/29	.99**	-.22	-.12	.17	-.81*	.03	.30			
Elevation	-.45	-.87	.07	.46	-.89**	-.99**	.36			
Latitude	.00	.00	-.40	-.52*	.35	.08	.04			
Longitude	.41	.27	-.03	.71**	-.71	.56	-.05			
Mean January temperature	-.06	.78	-.06	.72**	.29	.92**	-.42			
Mean July temperature	.45	.83	-.15	-.08	.87**	.95**	-.29			
Annual precipitation	.00	-.74	.03	.34	-.94**	-.93**	.24			
Growing season, length	.45	.87	-.56	-.08	.89**	.93**	-.29			
Frost free days	.45	.95*	-.32	-.03	.88**	.92**	-.43			
Days from January 1 to last spring frost	-.84	-.99**	.50	.04	.91**	-.61	.29			

*significant at P = 0.05

**significant at P = 0.01

1 WYoming, UINTA, WASatch, Western Colorado, Eastern Colorado, Northern New Mexico, ARIZONA

Foliage Color

Foliage color, a function of the amount of epicuticular waxes on needle surfaces, was highly variable, and changed over the two years of observations. Highly significant differences were detected at all levels of classification and during both 1974 and 1975 (Table 3).

When blue plus steel blue trees were considered together in the fifth year, σ^2_r contributed 18%, σ^2_p contributed 21% and σ^2_f accounted for 14% of total variance (Table 4). However, one year later, these components had changed to 27%, 20% and 16% for σ^2_r , σ^2_p and σ^2_f , respectively. When steel blue trees were considered alone, σ^2_r remained fairly constant at about 12%, while σ^2_p and σ^2_f both increased from 12% to 20% of total variation from the fifth to the sixth year. Generally, longitude was negatively correlated with amount of foliar waxes at 6 years. As Table 5 indicates, northern New Mexico and eastern Colorado respectively, had the greatest percent of blue and steel blue trees for both years. With the exception of seedlots #8065 and #8150 from Utah populations 11 and 25 respectively, the percentage of progeny with steel blue foliage was very low for Wyoming and the Uinta and Wasatch Mountains of Utah. Also, seedlots from Arizona showed almost no steel blue progenies at age 6 years. However, the relative importance of σ^2_r in steel blue foliage color is little better than 1/2 that of σ^2_p and σ^2_f at 6 years of age. As Table 6 shows, population 29 from eastern

Colorado had the highest percent of steel blue trees, 46% at age 6 years, while population 5 from western Colorado was next with 38% steel blue trees at age 6. Variation among families within these populations is extreme (Appendix A). In population 29, family values for percent steel blue progenies range from 5% for seedlot #8173 to 85% for seedlot #8176. Similar extremes are found in population 5 (range 0-78% steel blue trees) and population 39A (7-75% steel blue progenies) from northern New Mexico.

Appendix A demonstrates the magnitude of change in foliage color between the fifth and sixth year after outplanting. Although a few seedlots remained constant or even decreased in percent of blue-needled progeny, most showed an increase in expression of blue foliage color. Even in the climatic regions with little expression of foliage color, that which was expressed was mostly in the sixth year after outplanting.

Besides longitude, the only significant correlation involving foliage color was between percent blue trees and relative frost damage ($r = 0.48$, significant at 0.01 level). The available climatic data proved to be of little value in determining which environmental variables might act as a selective force for or against foliage color. When color data for each population for a given climatic region was correlated with extrapolated climatic data for that region, there were no significant relationships between foliage color or any environmental factor.



Relative Frost Damage

Differences in relative frost damage (RFD) were highly significant among climatic regions (Table 3) with σ^2_r accounting for 26% of total variance (Table 4). The areas of western Wyoming and the Wasatch and Uinta Mountains of Utah in general exhibited significantly less RFD than did those climatic regions to the east (Table 5). Uinta populations were the least damaged while southern New Mexico populations suffered the most damage.

Highly significant differences between populations within climatic regions accounted for 8% of total variance; differences were limited to populations within climatic regions of western Colorado and northern New Mexico (Table 6). Values ranged from 15 to 45 percent RFD for populations 6 and 37A respectively, in western Colorado and from 29 to 47 percent for populations 28 and 36 respectively, in northern New Mexico.

Analysis indicated that within a given population, relative frost damage sustained by individual families was fairly uniform, and accounted for a mere 3% of the total variance (Tables 3, 4). However, significant differences between families were identified in three different populations (population 10C, 29 and 31C from western and eastern Colorado and southern New Mexico, respectively). Other populations included families with mean RFD values which, although widely separated, were not significantly different at the 0.01 level.

Rangewide, RFD was generally highly positively correlated with elevation of source population, mean January temperature and mean annual precipitation, both of which are strongly influenced by elevation, although in opposite ways. Height of ACCEL trees was significantly negatively correlated with RFD at all three measurement ages; while 2 year NUR height was significantly positively correlated with RFD, but not 5- or 6-year NUR height.

Bud Phenology

Differences in bud phenology were highly significant at all levels of classification and on all dates that phenological development was assessed (Table 3). As indicated by Table 4, σ^2_r was relatively high at the beginning of bud flush (May 1, 1974), then dropped by more than 50 percent at the two intermediate dates of assessment, and then tripled again at the last assessment date. Conversely, σ^2_p increased by about 50 percent and σ^2_f just about doubled between the first and second phenological assessments, remained rather high during the third, and then dropped to less than 10 percent of total variance by the time of the last assessment. The relative phenological stage at the beginning and ending of phenological development was highly influenced by climatic region of seed source, while population and family effects were of lesser importance. However, in the middle of active bud flush, population and family effects were more strongly expressed.

Seedlots from the more northerly and westerly climatic regions were the most retarded in phenology all during the period of assessment, while seedlots from the most southerly region (Arizona) were the most advanced (Table 5).

Populations from western Colorado (climatic region 23) were highly variable throughout the period of bud flush. Indeed, population 27C was most advanced of all populations included in the test at all assessment dates, while population 37B had phenological scores similar to materials from Utah and Wyoming (Table 6). Significant differences among populations from UINTA, WAS, ECOL, NNMEX and ARIZ were detectable only during the May 15 and May 21 assessment dates, although generally those populations which had lower initial phenological scores tended to remain behind the others from the same climatic region.

Differences among families within populations were present, not only in initial or final stage of phenological development but also in the pattern of development (Appendix A). In general, those seedlots which were more phenologically advanced on May 1 were more advanced on May 29. However, some families seemed to accelerate phenological development and, although they were retarded at the beginning, equalled or surpassed other families which were further along in development in the early assessment dates. Examples include seedlot #8305 in population 50A from the Uinta Mountains. Although retarded in early development

relative to seedlot #8309 from the same population, by the last assessment date, the slower seedlot had overtaken the faster seedlot in stage of development. Relative rates of phenological development among families in population 10A from western Colorado were also very different, where the most retarded family at the initial assessment (#8047) was the most developed at the last assessment.

Rangewide, bud stage increased with increasing elevation but decreased with increasing latitude and longitude (Table 7). Furthermore, these trends were present at all four phenological assessment dates. However, of the environmental variables which are conditioned by elevation, only mean January temperature and mean annual precipitation were significantly correlated with phenological development. In general, the more advanced a seedlot was phenologically, the more relative frost damage it incurred.

Selection Index

Analysis of variance of family selection index values indicated highly significant differences among climatic regions (Table 3), which accounted for about 27% of the total variance (Table 4). The pattern of regional ranking (Table 5) indicated that, in general, blue spruce from the western part of its range had lower SEI values than material from the east. The climatic regions of

northern and southern New Mexico had the highest SEI values.

Highly significant differences among populations within climatic regions accounted for about one-third of the total variation. As in most other characters, western Colorado exhibited the most variability among populations, with SEI values ranging from the lowest (SEI = 135, population 16A) to the highest (SEI = 334, population 27B). As well, population 27C, with the second-highest SEI value also came from western Colorado. As Table 6 indicates, significant among-population SEI differences were also found in eastern Colorado, northern New Mexico and southern New Mexico.

Selection index values for individual families were quite variable and ranged from SEI = 117 (seedlot #8120, population 16A, WCOL) to SEI = 353 (seedlot #8176, population 29, ECOL). Variation within populations accounted for 40% of the total variance, and was concentrated in 13 populations (Appendix A), where differences between family SEI values exceeded 74 (lsd 0.01). The greatest variation occurred in population 39B, NNMEX, between seedlots #8268 and #8265, where the difference was 162 SEI units. The most promising open-pollinated families were chosen by SEI value. Arbitrarily, all families with SEI values exceeding 250 were chosen as outstanding phenotypes suitable for inclusion in future breeding work.

These 30 families from 14 populations in 4 climatic regions are summarized in Table 10. It is interesting to note that two-thirds of these selected families come from western Colorado and adjacent northern New Mexico.

DISCUSSION

Genetic variation in blue spruce is complex. Results revealed geographic differentiation which corresponded to regional topographic and climatic patterns in the central and southern Rocky Mountains. Analysis of 15 growth and foliage color characters indicated that for 12 of these, Utah and Wyoming populations were different from populations to the east and south. In addition, materials from populations in western Colorado exhibited extreme variability, indicating strong selection pressures over relatively short distances. However, estimates of variance components for individual traits indicated that significant genetic variation exists not only among climatic regions, but also among populations within several of these regions, as well as among individual open-pollinated families within many populations. In addition, the relative importance of individual components changed over time for growth characters.

Differences in expression of geographic variation were found between ACCEL materials raised under optimal greenhouse conditions, which included long photoperiods, and NUR materials raised in nursery beds under natural

Table 10. Selection Index Values of Selected
Blue Spruce Families

Climatic Region ¹	Popu- lation	Seedlot	Selection Index	6-Year Height cm.		6-Year Foliage Color -- %	
				NUR	ACCEL	Blue	Steel Blue
WCOL	5	8016	262	36	53	83	58
		8019	271	39	72	74	53
		8021	329	43	68	100	78
	10A	8051	258	43	94	65	25
	10B	8053	286	44	72	90	45
	15	8111	251	49	85	75	10
	27B	8160	291	58	98	70	25
		8161	337	54	91	100	50
	27C	8162	311	62	90	69	44
		8163	262	51	93	67	17
	ECOL	8	8035	267	38	89	78
24		8145	259	42	85	67	33
29		8172	286	32	78	80	65
		8176	353	46	79	100	85
		8177	279	37	72	79	58
NNMEX	28	8166	325	49	86	95	55
		8167	268	48	69	84	32
		8169	267	50	94	74	16
		8170	301	48	91	89	37
	39A	8258	343	44	84	100	75
		8261	298	53	95	68	42
		8262	313	57	87	100	33
	39B	8266	259	41	88	72	28
		8268	287	54	94	68	32
	53	8326	333	38	88	100	71
		8329	289	40	86	89	42
		8331	289	44	74	89	47
	SNMEX	9	8044	289	56	90	85
8045			266	53	88	74	16
8046			291	48	86	89	33

¹ Western COLorado, Eastern COLorado, Northern New MEXico,
Southern New MEXico.

photoperiod and temperature regimes. In the ACCEL treatment, growth differences among broad climatic regions were not discernable. Furthermore, growth differences among families became attenuated after outplanting. In NUR materials, regional effects decreased over the first 6 years while population differences remained fairly constant, whereas ACCEL materials did not indicate any age trends in regional or population differences.

Genetic variation among populations within climatic regions (σ^2_p) remained fairly constant between 2 and 6 years of age in both NUR and ACCEL plantations. This is in contrast to the increase in variance among populations of ponderosa pine (Namkoong and Conkle 1976; Wang and Patee 1976) and Douglas-fir (Namkoong et al. 1972) during early growth. However, in the ponderosa pine and Douglas-fir studies, seed sources from only a portion of the species range were compared within the general climatic region of the collections, while the Michigan blue spruce plantations were quite different from environmental conditions at the seed source origins. Considerable genotype x environmental interaction among populations can be expected when trees are grown outside their natural ranges (Morgenstern and Teich 1960; Morgenstern 1976), and since genetic variances for climatic regions, populations within regions and families within populations indicated substantial selective forces acting at each level, such interactions could be expressed for climatic regions also.

It is possible that blue spruce could have a unique pattern of time-mediated genetic variation which is unlike ponderosa pine or Douglas fir. Namkoong et al. (1972) observed that high variances within populations of Douglas fir seemed to be limited to that period in the life cycle when competition for moisture and nutrients with grasses and brush was at a maximum, and once the trees achieved dominance over plant competition, differences among families were reduced. This expression of ecological dominance is illustrated in the silvical characteristics of Douglas fir and ponderosa pine. Both are intolerant of competition and require mineral soil and direct sunlight for seedling survival and stand establishment (Fowells 1965). In comparison, blue spruce is a more tolerant species, which can become established and survive in an understory position (Baker 1949). Perhaps time-mediated changes in components of genetic variance in blue spruce reflect growth patterns at different stages of its life cycle. Further data will determine whether blue spruce conforms to this model.

The sharp contrast between time trends in variance components for NUR and ACCEL plantations gives evidence of disequilibrium of natural growth processes due to early ACCEL growth conditions. In the ACCEL plantation, variance among populations (σ^2_p) increased steadily over time like ponderosa pine and Douglas fir. Family response of ACCEL materials was likewise more representative of time

trends for family variance in ponderosa pine, Douglas fir and eastern white pine (Kriebel et al. 1972). It seems likely that NUR time trends more accurately reflect the true pattern of variation in blue spruce, while ACCEL patterns are unnatural and result from early growth differences conditioned by long photoperiods in the ACCEL treatment. Early differences were pointed out by Hanover and Reicosky (1972) and Hanover (1975), where many of the same blue spruce populations included in this study were ranked after six months in the greenhouses and two years in the nursery. Although many of the tallest trees in the greenhouses were from Utah sources, Colorado and Arizona trees were tallest in the nursery. The clinal pattern of early ACCEL height growth variation differs from growth trends of other, nursery-grown Rocky Mountain tree species, where latitude was negatively correlated with height growth (Kung and Wright 1972; Wright 1976). Upon germination, blue spruce seedlings from Utah and Wyoming grow very rapidly under long photoperiods. The mechanism responsible for this is probably the ability of these sources to differentiate needle primordia at least as fast as southern sources when day length is not limiting. Such a mechanism was described in Sitka spruce by Pollard et al. (1975), where, for a short period after budset, northern provenances underwent more rapid bud morphogenesis than did southern provenances. However, as photoperiod became more limiting, southern provenances produced more needle primordia than

northern ones. Lanner (1976) has suggested that this short period of rapid bud morphogenesis is an adaptation to harsh climates with short growing season, a description which fits Utah blue spruce habitats. This would be facilitated by a large apical dome capable of producing needle primordia rapidly (Cannell et al. 1976). A biological feedback mechanism is then responsible for subsequent growth performance of the ACCEL seedlings. Larger seedlings tend to produce larger apical buds with more primordial stem units, which in turn produce more photosynthetic tissue for subsequent bud development (Pollard 1974). When out-planted under natural photoperiods, the relative advantage of northern sources should disappear and southern sources, with the ability to produce stem units at photoperiods when northern ones stop, will in time exhibit faster growth. In contrast, NUR seedlings of southern sources will have had the advantage of prolonged primordial production after cessation of initiation by more northerly sources, with the result being that northern sources will always be shorter. However, other factors such as differential physiological response to temperature, nutrient levels and water stress are also important in growth performance. Young and Hanover (1978) have shown that nitrogen levels and moisture stress may induce dormancy in blue spruce seedlings, even under continuous light. Pollard and Logan (1977) found that temperature strongly affected the rate of needle primordia initiation in white spruce. Perhaps a combination of

factors might explain why seedlots from populations 27B and 27C from western Colorado performed so well in both NUR and ACCEL experiments. Results of water stress studies (Chapter 3) indicate that trees from these populations may be able to carry on essential gas exchange (and presumably photosynthesis) at soil moisture levels prohibitive to trees of other populations. Thermal efficiency, or the threshold temperatures at which different seed sources can actively undergo cell division may also vary geographically, as well as within populations. Boyer (1976) reported that such variation existed within stands of loblolly pine, and could account for height growth differences in progeny tests. Such factors may explain why Wyoming and Utah populations were similar in phenological and foliage color traits, but differed in growth rate in the NUR experiment. Also, eastern Colorado populations exhibited phenological and foliage color characters like western Colorado, New Mexico and Arizona populations, but grew as slowly as Utah populations. Such regional trends are reflections of adaptations to selection pressures conditioned by broad regional climatic regimes.

Strong east-west differences were apparent in phenology-related traits. Utah and Wyoming populations flushed late and were less susceptible to late spring frosts than populations to the east. However, in contrast to white spruce (Nienstaedt and King 1970; Nienstaedt 1973), the tallest families were also the early flushing ones, and

were most damaged by late spring frosts. This fundamental difference between closely-related species is probably due to very basic differences in adaptation to regional climatic patterns. After mean daily temperatures exceed freezing in the Lake States and adjacent Canada, there is a period of 6 to 10 weeks when arctic airmasses may bring cold air to the region (Hare and Thomas 1974). A combination of advective and radiative frost, in the form of long-wave re-radiation of energy from the earth's surface then may cause below-freezing temperatures in the region as the cold airmass passes (Findlay 1970). Provenance variation in time of budburst and spring frost damage has been reported in white spruce (Logan and Pollard 1975) and balsam fir (Lester et al. 1977). Further study of Ontario white spruce has indicated that most of the genetic variance in spring phenology occurred among families within stands, rather than among stands (Pollard and Ying 1979) and was interpreted to mean that long-term population fitness to unpredictable spring temperature regimes was maintained by much individual tree variability within a given climatic region. However, Morgenstern (1969) indicated that in a rangewide collection of black spruce, differences in spring growth were expressed clinally, with very large differences among forest regions, but very little among or within stand variability.

Blue spruce, which apparently has adapted to quite different climatic patterns than white or black spruce,

reacted much differently when planted in Michigan. The arbitrary division of the entire blue spruce range into regions based upon broad climatic patterns proved useful, and results suggest very real regional differences. Large regional variance components in several characters indicated that such regional differences do exist, especially with respect to early NUR height growth, foliage color and phenology-related traits. In contrast to the general pattern reported in white spruce (Nienstaedt and King 1970), height growth at age 6 was significantly correlated with relative frost damage and phenology. The influence of regional climate on frost damage and phenology may be explained in part by broad-scale patterns of spring airmass movement. The Utah and Wyoming populations break bud dormancy later, and subsequently suffer less spring frost damage in Michigan than trees from other areas because they are adapted to a much slower spring warming rate at the seed origin. Utah and Wyoming are subject to spring air-masses of predominately Pacific origin (Trewartha 1966), and average temperatures increase slowly as the airmass source areas (the north and central Pacific Ocean) accumulate heat proportional to seasonal changes in solar radiation intensity. Furthermore, occasional incursions of arctic air may bring spring frosts to these areas, resulting in selection for a higher threshold temperature to initiate growth. These airmasses may be substantially altered, both in temperature and trajectory as they pass

over the Utah and Wyoming mountains, with a subsequently different effect in the Colorado and New Mexico mountains (Colson 1949).

In contrast, airmasses moving into the southern and central Rocky Mountains during the spring originate in the Gulf of Mexico, and are warmer and more moist than Pacific air (Trewartha 1966; Wardle 1968). Such airmass differences may be at least partly responsible for the "Early Ridge" observed by Caprio (1966), where at a given elevation, phenological events were consistently in advance of similar responses in areas to the east and west of the Continental Divide area in Colorado and New Mexico. Caprio (1966, 1967) reported other anomolous areas in the lee of mountain ranges, where foehn or chinook patterns modify temperatures, and in areas of high solar radiation intensity, which tends to advance phenological activity by heating up plant tissue above ambient temperatures.

Because of intensive selection pressures in the mountainous west, differentiation of local populations has been suggested in Douglas fir (Irgens-Moller 1967; Namkoong et al. 1972; Rehfeldt 1974a, 1978; White et al. 1978), white fir (Wright et al. 1971; Hamrick and Libby 1972; Hamrick 1976) and ponderosa pine (Wang and Patee 1974, 1976; Madsen and Blake 1977; Mitton et al. 1977). This indicates that, although gene flow between populations is facilitated by pollen dispersal, natural selection, conditioned by local climatic regimes, is the overriding factor

which determines changes in gene frequencies. In all of the above species, variation is also strongly expressed on a regional (ecotypic) level as well as on an individual family level. This variation must be taken into account in any tree improvement program. The one species which does not fit this pattern is western white pine, although early results seemed to indicate strong local differentiation into discrete populations (Squillace and Bingham 1958). However, subsequent studies by Townsend et al. (1975) and Steinhoff (1979) showed no evidence of population differentiation, although the latter work indicated much genetic variability among trees within any given stand. Rehfeldt (1979) suggested that phenotypic plasticity could account for western white pine's adaptability to the wide range of environments in which it grows.

Partitioning the variance into component parts in blue spruce gave values which seem quite reasonable when compared with results from studies in other species. It is quite possible that the variances are somewhat inflated, and had other plantations been established, genotype X environment interactions might have reduced the variance due to genetic components significantly (Rehfeldt 1974b). However, Wright (1973) summarized the genotype X environmental interactions in a number of studies involving Rocky Mountain tree species in the north-central United States and concluded that, although some winter-hardiness traits indicated north-south interactions, variances due to

genotype and plantation were stronger than interactions. Furthermore, King (1965a, b) reported that genotype X plantation interactions in Scotch pine were small when compared to genetic variance. At present there is no reason to suspect that blue spruce is any different in this respect.

Results of this study indicate that blue spruce from western Colorado is genetically the most variable over the range of the species. Significant differences among populations were present in all sixteen measured characters, as well as in the composite selection index (SEI). Populations from northern New Mexico exhibited variability in 10 of the measured characters; however, NUR height differences were not apparent among populations from this region. Populations from the Front Range in Colorado showed variability in many of the same traits as the northern New Mexico populations suggesting, perhaps, the same selective forces acting in the eastern part of the Colorado Rockies as in northern New Mexico.

The reason for greater differentiation in western Colorado may lie in the large topographical variation throughout the region. Baker (1944) suggested that the area could be subdivided into several climatic provinces, but in spite of a number of sampling stations, he found that data were still too limited to accurately delineate separate entities. However, the diverse physiographical elements suggest the possibility of significant microclimatic

variation over relatively short geographical distances. For example, there are high mountain ranges in several ranks near the continental crest, interspersed with high valleys. The western part of the area is composed of high plateaus and deep canyons of the Colorado and Grand River drainages. In contrast, the Wasatch Mountains of Utah are a rather narrow range and present a fairly uniform barrier to airmasses approaching from the west. Likewise, the eastern ranges of the Rockies which comprise eastern Colorado are similarly more uniform in that they are made up of one or two narrow north-south ranges with a single crest. The large physiographic diversity of western Colorado increases environmental complexity, where changes in aspect, elevation, moisture regime and soil type interact to vary habitats in neighboring areas (Geiger 1966).

It is possible, of course, that differences within other climatic regions would have been more strongly expressed if more populations had been sampled. The area of western Colorado was the most intensively sampled, with 14 populations of two or more trees included. In contrast, the Wasatch Mountains of Utah provided only 7 populations.

Although foliage color was not significantly correlated with environmental variables, it is interesting that the proposed physiological functions of and the developmental changes in the amounts of epicuticular waxes is compatible with a scheme of ecological adaptability which reflects the time-mediated changes in genetic control

of height growth.

Jeffree et al. (1971) postulated that the increase in foliar transpiration commonly observed when surface waxes were removed from plant leaves was due to the increased cross-sectional area in the stomatal antechamber available for diffusion of water vapor, and to the decrease in diffusive resistance once these waxes were removed. They calculated that in Sitka spruce, wax in the stomatal antechambers reduced transpiration to one-third the rate possible had no wax been plugging up the orifice. They also postulated that there was a 32% reduction in photosynthesis due to obstruction to the CO₂ diffusion pathway. However, as Reicosky and Hanover (1976) observed, wax plugs are present in the stomatal antechamber of both glaucous and nonglaucous trees (Reicosky 1974) giving evidence that in blue spruce, surface waxes are not an adaptation primarily for control of water loss. Instead, the function of blue spruce epicuticular waxes seems to be one of protection against certain wavelengths of solar radiation. Reicosky and Hanover (1978) showed that glaucous foliage reflected a significantly higher percentage of radiation from the UV and blue portions of the electromagnetic spectrum than did nonglaucous foliage. They suggested that this feature might be advantageous in environments where trees are subject to high levels or long periods of solar radiation. However, results of this study support the general observation that the amount of

epicuticular wax produced on new needles increases with age (Hanover 1976; Hanover and Reicosky 1978). If foliage color is truly an adaptive trait, why does maximum expression occur years after the very critical period of seedling establishment is past? If, however, seedlings are adapted to spend the earliest part of their life as somewhat tolerant understory, and are afforded partial protection by the older, existing stand whose production of surface waxes are fully expressed, then there is no immediate need for protection from solar radiation. Engelmann spruce is probably closely related to blue spruce (Wright 1955; Daubenmire 1972) but, in the southern and central Rocky Mountains generally grows at higher elevations than blue spruce (Jones and Bernard 1977). Ronco (1970) reported that high seedling mortality in Engelmann spruce plantations above 10,000 feet elevation in the Rocky Mountains was probably due to solarization by high light intensities. Ronco found that seedlings of Englemann spruce responded to increasing light intensities like other shade-tolerant species -- i.e., light saturation of photosynthesis occurred at about one-third the level of full sunlight, whereas photosynthesis in lodgepole pine was not light-saturated even at full sunlight. In the southern Rocky Mountains where both Engelmann and blue spruce reach their maximum altitudinal distributions, Engelmann spruce commonly has blue foliage color, while blue spruce may or may not (Jones and Bernard 1977). When Engelmann spruce seedlings were

growing in the nursery in East Lansing, they could be easily recognized by their intense blue foliage even at 2 years of age. Perhaps this is an adaptation to the high levels of solar radiation this species experiences in the southern Rocky Mountains at the elevations where it is found, even though it is a very tolerant species and naturally regenerates under a forest canopy. Blue spruce, however, is not generally found at elevations over 10,000 feet and may not have had the same selective pressure to develop foliage waxes at such an early stage in its life cycle. Indeed, the level of variability of foliage color among families within populations indicates that this trait may not be under as intensive selection pressure as phenological traits. However, the frequency of occurrence of blue foliage in the central Rocky Mountains as compared to Utah and Wyoming suggests adaptative significance between climatic regions.

The selection index used here to determine which blue spruce families are the most desirable for inclusion in a breeding program is necessarily quite arbitrary, and certainly will not be adequate for selecting materials for the various special uses for which genetically improved strains of blue spruce might be needed. Height growth was considered an important character, and both NUR and ACCEL heights were equally weighted. However, for ornamental horticultural use, growth rate may be of little importance. It is conceivable that foliage color, crown shape and pest

resistance may be important, and slow growth may be desirable. Slow-growing trees will take much longer to dominate the aesthetic landscape, and may have a longer useful life-span as a component part in landscape design, both reducing maintenance costs (trimming, pruning) and removal/replacement costs. If, however, trees are to be selected for their performance in wind protection, then aesthetic values such as color will necessarily become secondary to height growth, resistance to dessication and tolerance to pesticides, road salts, etc. The level of variability contained within populations for selection index values is encouraging, and suggests that progeny testing and family selection is the most efficient method of exploiting this variability.

CHAPTER 2. SPECIES DIFFERENCES BETWEEN BLUE AND ENGELMANN SPRUCE

INTRODUCTION

Engelmann spruce (*Picea engelmannii* Parry) is a wide-ranging species commonly found in the Rocky Mountains at higher elevations in cold, humid habitats (Pearson 1920; Bates 1924; Alexander 1958; Fowler and Roche 1975). In contrast, blue spruce (*P. pungens* Engelm.), a very closely related species (Wright 1955) generally inhabits a lower elevational zone in the southern and central Rocky Mountains than Engelmann spruce (Pearson 1931). However, occasional areas of range overlap do occur (Daubenmire 1972; Hanover 1975), and because of close morphological similarity, blue and Engelmann spruce are commonly misidentified (Marco 1931; Reed and Freytag 1949; Jones and Bernard 1977). Despite the sympatry of ranges and presumably close phylogenetic relationships, the two species are quite distinct in physiological response to environmental factors when planted outside their natural habitats (Pearson 1920, 1931).

Taxonomic keys have commonly used such characters as cone length, needle sharpness and number of resin canals in needle cross-section to differentiate between the two species (Jones and Bernard 1977). Marco (1931) found that needle cross-sections gave misleading results when used to estimate resin sac numbers because resin sacs were discontinuous over the length of the needle. Reed and Freytag

(1949) reported that blue spruce from southwestern Wyoming had three times the number of resin sacs per needle as Engelmann spruce. Furthermore, blue spruce resin sacs were three times as long as those of Engelmann spruce. Habeck and Weaver (1969) attempted to characterize suspected blue-Engelmann hybrid populations by analysis of cortical oleoresins. Daubenmire (1972) and Hanover (1975) used cone morphological characters to distinguish populations which were of intermediate and pure blue and Engelmann spruce composition. Daubenmire (1972) concluded from his evidence that blue and Engelmann spruce could occupy the same site at higher elevations in the blue spruce range and still retain their species identity. Evidence of strong incompatibility between blue and Engelmann spruce was reported by Fechner and Clark (1969) and Kossuth and Fechner (1973). Taylor, et al. (1975) analyzed phenolic compounds of blue and Engelmann spruce foliage from several sympatric populations and concluded that although natural hybridization does occur, it is infrequent.

Recently, Jones and Bernard (1977) presented aids to distinguish the two species in the southwest by means of gross morphological characters, which, when used in conjunction with one another, make field identification of mature trees easier. However, in the seedling stage of development, species identification can be difficult. Marco (1931) and Jones and Bernard (1977) suggested that seedlings could be differentiated by the bristly appearance

of blue spruce as opposed to the soft, drooping look of Engelmann spruce. Marco concluded that the angle of growth of the twigs and arching of needles gave Engelmann spruce a "flattened spray" effect, while in blue spruce the needles "bristle from all sides of the twig".

When a rangewide study of geographic variation in blue spruce was initiated at Michigan State University in 1969 (Hanover and Reicosky 1972; Hanover 1975) the inclusion of several Engelmann spruce seedlots gave the opportunity to study in more detail materials of both species from different geographic origins. Since the seedlots were growing in uniform environments (i.e., genetic test plantations, common nursery beds and greenhouse) species differences in physiology and morphology could be investigated. The following report is a compilation of several studies on genetically similar plant materials which have been grown and outplanted under uniform environmental conditions, thus allowing maximum expression of species and seedlot characters.

MATERIALS AND METHODS

Eleven open-pollinated seedlots of Engelmann spruce from five populations were identified from collection records and morphological appearance in Michigan nursery beds. These were characterized by their drooping branches and soft foliage appearance, in contrast to the straight planar branching and stiff, bristly appearance of blue

spruce seedlots. Six Engelmann and three blue spruce seedlots came from population 36 in northern New Mexico (Table 11). One blue and one Engelmann seedlot were collected from population 57 in southeastern Arizona, and three seedlots from two populations (47, 58) represented Engelmann spruce from southern New Mexico. The remaining Engelmann seedlot represents population 41 from southeastern Utah.

Height Growth

Seedlings of blue and Engelmann seedlots were grown under accelerated growth conditions described by Hanover and Reicosky (1972). Four-tree plots of each seedlot were outplanted in three replicates of a randomized complete block design genetic test plantation near Battle Creek, Michigan in September 1970. This experiment is designated the ACCEL plantation in the following report. Progenies from the same seedlots were raised in an East Lansing nursery (Hanover 1975) and were outplanted adjacent to and in the same design as the ACCEL plantation. The nursery-grown experiment is referred to as the NUR plantation in this report.

ACCEL seedlings were measured at 3 and 6 months of age prior to outplanting (Hanover and Reicosky 1972) and at 2, 5 and 6 years of age in the plantation. NUR seedlings were measured at 2 years of age in the plantation. All plot trees were measured and the mean seedlot height was used for comparison.

Table 11. Origins of Engelmann Spruce Seedlots Included in Rangewide Blue Spruce Seed Source Collection.

<u>Seedlot</u>	<u>Population</u>	<u>Species</u>	<u>State</u>	<u>Elevation Meters</u>	<u>Latitude Degrees</u>	<u>Longitude Degrees</u>
8232	36	Engelmann	Colorado	2896	36.30 N	105.42 W
8233	36	Engelmann	Colorado	2896	36.30 N	105.42 W
8234	36	Engelmann	Colorado	2896	36.30 N	105.42 W
8235	36	Engelmann	Colorado	2896	36.30 N	105.42 W
8236	36	Engelmann	Colorado	2896	36.30 N	105.42 W
8238	36	Engelmann	Colorado	2896	36.30 N	105.42 W
8282	41	Engelmann	Utah	2591	37.88 N	109.50 W
8297	47	Engelmann	New Mexico	3048	33.13 N	107.92 W
8347	57	Blue	Arizona	2804	33.67 N	109.33 W
8348	57	Engelmann	Arizona	2804	33.67 N	109.33 W
8352	58	Engelmann	New Mexico	3170	33.97 N	107.18 W
8354	58	Engelmann	New Mexico	3170	33.97 N	107.18 W

Terminal Shoot Elongation

In spring 1973, 16 blue and 6 Engelmann seedlots (Table 12) were selected from the nursery materials and transplanted in an adjacent bed in a replicated complete block design, with four trees per plot in each of four replicates. Prior to the 1975 growing season, a straight pin was inserted in the twig of each tree below the terminal bud for an index mark. Shoot extension was measured to the nearest millimeter at approximately weekly intervals until elongation ceased. Mean plot values were used to determine seedlot cumulative height growth, and a cumulative height growth curve was plotted from the data. Concurrent temperature data were used to calculate accumulation of growing-degree-days above a base temperature of 5.6C (42F) in an effort to discern critical heat units required for leader elongation.

Frost Damage

On May 18, 1973 the ACCEL plantation at Kellogg Forest was subjected to a killing frost (minimum temperature, -3C). Indications of widespread differences among blue and Engelmann seedlots in frost damage to new growth led to a general damage assessment on June 9, 1973. By this date undamaged buds had flushed completely; those buds killed by the cold had dried and were quite conspicuous. Damage was estimated visually and graded in the following manner:

Table 12. Origins of Blue and Engelmann Spruce Seedlots Included in Nursery Shoot Elongation Experiment.

<u>Seedlot</u>	<u>Popu- lation</u>	<u>State</u>	<u>Elevation Meters</u>	<u>Latitude Degrees</u>	<u>Longitude Degrees</u>	<u>Cumulative Leader Elongation 1975, mm</u>
<u>Blue Spruce</u>						
8022	6	Colorado	2316	39.47 N	107.50 W	207
8024	6	Colorado	2316	39.47 N	107.50 W	192
8038	8	Colorado	2514	39.75 N	105.52 W	186
8081	13A	Wyoming	1829	43.30 N	110.80 W	173
8082	13A	Wyoming	1829	43.30 N	110.80 W	199
8128	19	Wyoming	1957	43.65 N	110.73 W	168
8147	24	Colorado	2896	38.97 N	106.05 W	209
8148	25	Utah	1981	38.73 N	111.32 W	155
8161	27B	Colorado	2408	37.75 N	108.00 W	221
8163	27C	Colorado	2469	37.75 N	108.00 W	215
8240	36	New Mexico	2896	36.30 N	105.42 W	207
8258	39A	New Mexico	2560	36.00 N	106.00 W	223
8261	39A	New Mexico	2560	36.00 N	106.00 W	212
8347	57	Arizona	2804	33.67 N	109.33 W	230
8375	75	Colorado	2469	40.60 N	105.53 W	144
8377	75	Colorado	2469	40.60 N	105.53 W	176
<u>Engelmann Spruce</u>						
8233	36	New Mexico	2896	36.30 N	105.42 W	101
8235	36	New Mexico	2896	36.30 N	105.42 W	104
8236	36	New Mexico	2896	36.30 N	105.42 W	102
8297	47	New Mexico	3048	33.13 N	107.92 W	99
8348	57	Arizona	2804	33.67 N	109.33 W	142
8354	58	New Mexico	3170	33.97 N	107.18 W	123

<u>Frost Damage Grade</u>	<u>Condition of Tree</u>
1	- less than 1/3 of all new shoots killed
2	- more than 1/3 but less than 2/3 of all new shoots killed
3	- more than 2/3 of all new shoots killed

Individual plot trees were graded for frost damage and a plot mean was calculated. To make average damage values more meaningful, mean seedlot values were distributed from 0 to 100, giving a relative frost damage index which was continuous over the range of data. A regression was calculated using damage value as the independent variable and relative frost damage (RFD) as the dependent variable, as follows:

<u>Independent Variable</u>	<u>Dependent Variable</u>
frost damage 1.0	0% relative frost damage
frost damage 2.0	50% relative frost damage
frost damage 3.0	100% relative frost damage

The resulting linear regression equation was:

$$\hat{Y} = 50X - 50$$

Phenology

At four different dates in May 1974 the ACCEL plantation was assessed for stage of phenological development, or phenophase. For convenience and accuracy, six easily recognizable bud stages were scored, corresponding closely to Nienstaedt and King's (1970) phenophases for

white spruce (P. glauca Moench Voss):

<u>Bud Stage</u>	<u>Condition of Buds</u>
1	winter resting bud
2	bud beginning to swell
3	bud fully swollen, needles inside
4	needles bursting through scales
5	shoot elongating, needles closely appressed
6	shoot elongated, needles free

Each individual plot tree was scored and seedlot means were calculated by averaging plot values over all replications. Temperature data were used to calculate growing-degree-days above a base temperature of 5.6C (42F).

Needle Morphology

Twenty-three blue spruce and nine Engelmann spruce seedlots were selected for study from the rangewide collection of open-pollinated families and bulk seedlots. Sample trees were 2/1 nursery stock from unreplicated transplant beds. Seedlot numbers and origins are summarized in Table 13. Blue spruce seedlots consisted of two open-pollinated families from each of 11 populations and one bulk lot from a twelfth population. For Engelmann spruce, in addition to seven bulk seedlots, two open-pollinated families from a single population were analyzed. Each family was represented by two trees, while all bulk populations included four trees. In this way, population comparisons were based on equal numbers of trees. A lateral branch from

Table 13. Blue and Engelmann Spruce Seed Sources
Used in Needle Morphology Study.

<u>POPULATION</u>	<u>ORIGIN</u>
<u>Blue Spruce</u>	
1	Roosevelt N F, Utah
10	Eagle County, Colorado
11	Manti-LaSal N F, Utah
13	Sublette County, Utah
26	Sanpete County, Utah
30	Pitkin County, Colorado
31	Greenlee County, Arizona
39	Rio Arriba County, New Mexico
<u>Engelmann Spruce</u>	
36	Carson N F, New Mexico
47	Gila N F, New Mexico
75	Madison County, Montana
70-55	Kaniksu N F, Idaho
70-90	Beaverhead N F, Montana
70-109	Kootenai N F, Montana
3255	Cache N F, Idaho
3259	Wenatchee N F, Washington

the south side of each tree was removed and four needles from the previous year's growth were taken from the mid-portion. Using a binocular dissecting microscope with calibrated eyepiece, nine characters were assessed on each needle. Included were total needle length, width of four needle sides, number of stomates along a 1.1 mm center portion of each needle surface, number of resin sacs in upper, middle and lower one-third of needle, individual resin sac length. From this data stomates $\cdot \text{mm}^{-2}$ and percent of twice needle length covered by resin sacs were calculated. Analysis of variance for each character was calculated after Kempthorne's (1957) method for hierarchal classification with unequal subclasses; percent of total variance contributed by levels of classification were calculated and when possible, tests of significance between levels were made.

RESULTS

Generally blue spruce seedlots grew taller than Engelmann spruce in the ACCEL plantation. Although meaningful statistical analysis is frustrated by large subclass differences, blue spruce mean six-year height was about 25 percent greater than that of Engelmann spruce (Table 14).

Table 14. Mean Heights of Blue and Engelmann Spruce Seedlots from Greenhouse, Nursery and Subsequent Field Plantings.

<u>Age, Treatment</u>	<u>Blue Spruce Height, cm.</u>	<u>Engelmann Spruce Height, cm.</u>
3-month, ACCEL	3.4	2.4
6-month, ACCEL	22.5	17.2
2-year, ACCEL	26.3	22.3
5-year, ACCEL	58.5	40.6
6-year, ACCEL	77.0	52.1
2-year, NUR	13.9	15.0
5-year, NUR	31.4	32.0
6-year, NUR	43.7	41.1

However, there was substantial variation among Engelmann seedlots included in the progeny test. Seedlots 8236 and 8348 were the tallest Engelmann progenies, with mean heights equal to the mean blue spruce height (Table 15). Species differences accentuated following outplanting.

Table 15. Mean Height Growth for Blue (B) and Engelmann (E) Spruce Seedlots
From Five Natural Populations.

Seedlot	Popu- lation	Species	ACCEL Plantation						NUR Plantation									
			3 Months		6 Months		2 Years		5 Years		6 Years		2 Years		5 Years		6 Years	
			Height in Centimeters															
8232	36	E	2	12	22	34	47	16	--	--	--	16	--	--	--	--		
8233	36	E	2	20	25	29	38	14	--	--	--	14	--	--	--	--		
8234	36	E	3	21	23	43	51	17	29	36	51	17	29	36	51	36		
8235	36	E	4	18	22	43	51	15	26	33	51	15	26	33	51	33		
8236	36	E	2	18	25	39	58	15	--	--	39	15	--	--	--	--		
8237	36	B	3	18	20	56	74	17	39	52	74	17	39	52	74	52		
8238	36	E	2	20	21	35	42	14	33	41	42	14	33	41	42	41		
8239	36	B	3	18	25	52	71	17	28	39	71	17	28	39	71	39		
8240	36	B	3	20	24	59	62	14	35	39	62	14	35	39	62	39		
8282	41	E	2	11	21	28	36	13	--	--	28	13	--	--	--	--		
8297	47	E	2	10	17	40	49	16	29	38	49	16	29	38	49	38		
8347	57	B	3	19	24	61	83	18	55	66	83	18	55	66	83	66		
8348	57	E	2	17	23	45	58	19	49	56	58	19	49	56	58	56		
8352	58	E	2	20	22	40	50	13	--	--	40	13	--	--	--	--		
8354	58	E	2	16	19	34	43	13	23	33	43	13	23	33	43	33		
MEAN	Engelmann		2	17	22	37	47	15	31	40	47	15	31	40	47	40		
MEAN	Blue		3	19	23	57	74	17	40	49	74	17	40	49	74	49		

Whereas early seedling growth in the greenhouse was similar for each species, blue spruce seedlots were substantially taller than Engelmann spruce after the fifth and sixth growing season. This development was strikingly evident in the growth response of seedlots 8347 and 8348, blue and Engelmann progenies from population 57 in eastern Arizona. Although nearly equal in height after the first season in the field, the blue spruce seedlot was about 30 percent taller than the Engelmann seedlot after the fifth growing season. Blue and Engelmann seedlots from population 36 responded similarly, although the blue spruce from this population were not as tall as seedlot 8347.

Five of the 11 Engelmann progenies represented in the ACCEL plantation were also included in the NUR plantation. In contrast to performance of ACCEL materials, mean Engelmann spruce height was somewhat greater than blue spruce height after two years' growth in the nursery. This height difference persisted up through five years of age in the NUR plantation. By the end of the sixth year, however, blue spruce seedlot mean height had exceeded that of Engelmann spruce. Seedlot 8348 grew extremely well in this plantation, ranking second tallest of all seedlots after five years. However, by the end of the sixth year it had dropped to sixth rank overall, still quite good in the light of other Engelmann spruce performance. Significantly, blue spruce seedlot 8347, from the same 2-tree population, was tallest in the entire experiment after the fifth and

Figure 1. Cumulative terminal shoot growth of blue (B) and Engelmann (E) spruce seedlots from bud flush to bud set.

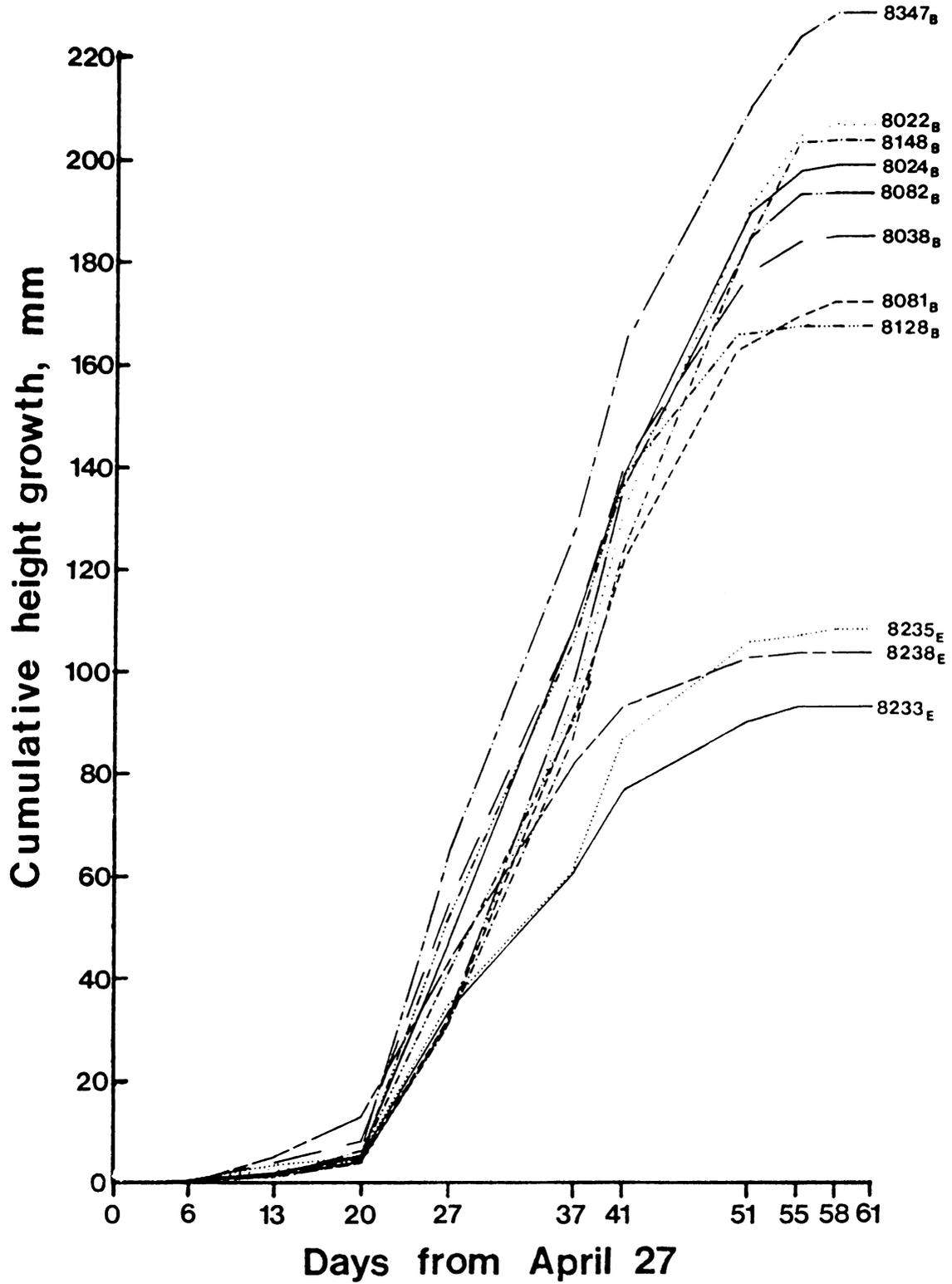


Figure 1.

Figure 2. Cumulative terminal shoot growth of blue (B) and Engelmann (E) spruce seedlots from bud flush to bud set.

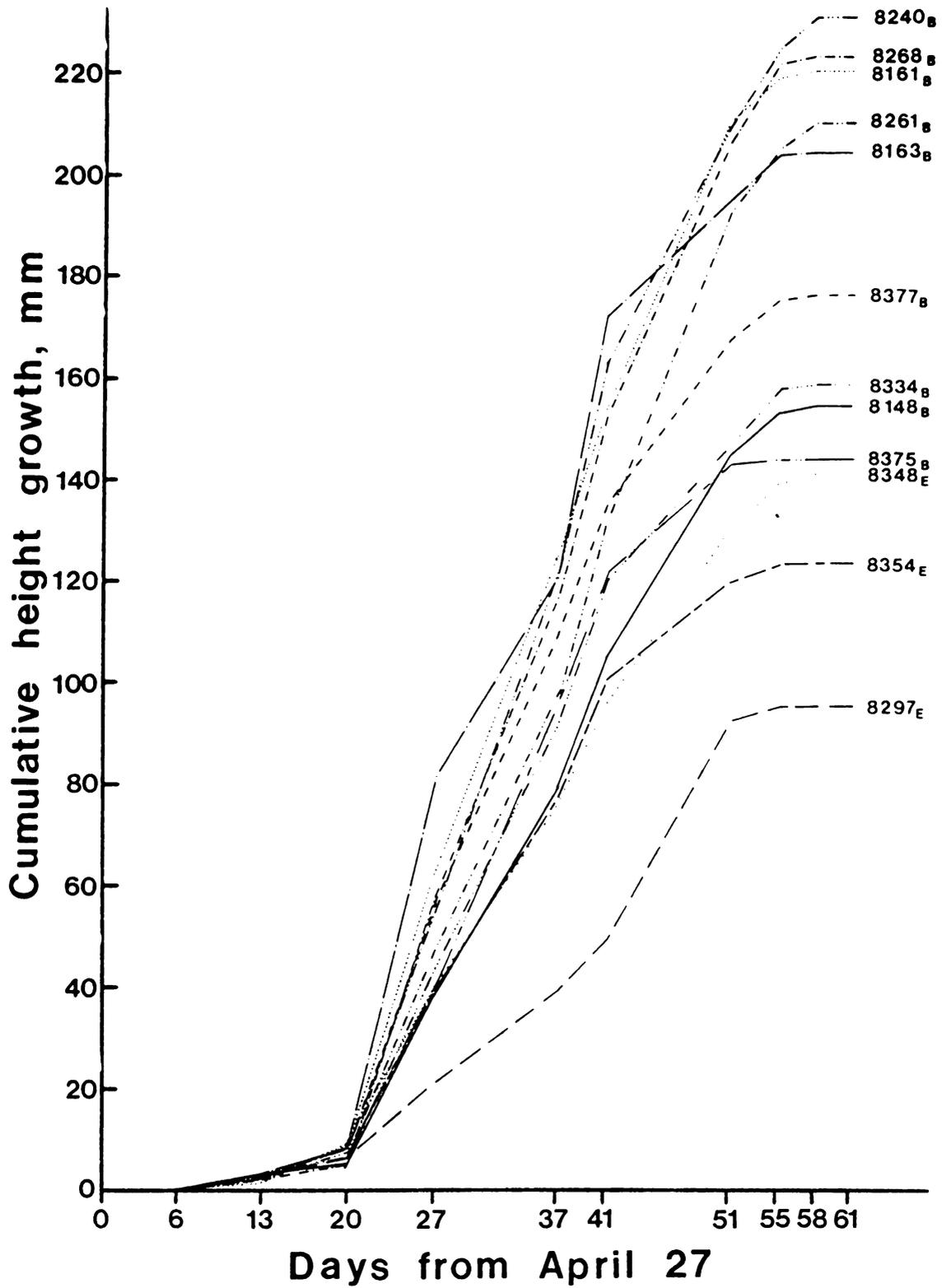


Figure 2.

sixth growing seasons. The remaining Engelmann spruce progenies grew very slowly, obviously poorly adapted to the test environment.

Of the six Engelmann progenies from population 36 included in the ACCEL plantation, only three were outplanted in the NUR test. Growth of these was below average to average for Engelmann spruce, and substantially below average for blue spruce. The three blue spruce progenies included in this population (8237, 8239 and 8240) all grew better than average in the ACCEL plantation. However, in the nursery and the subsequent NUR plantation, 8237 and 8239 were taller than the mean blue spruce height, while 8240 was substantially shorter.

Terminal Shoot Elongation

Seedlots of both species began terminal growth almost simultaneously, and ceased growth about the same time, some 49-52 days later (Figures 1, 2). Mean terminal shoot elongation was much greater for blue spruce than for Engelmann spruce, although that of the tallest Engelmann seedlot exceeded the shortest blue spruce seedlot. In addition to total elongation, the cumulative growth curve of most blue spruce seedlots was strikingly different from that of Engelmann spruce. The log phase of shoot extension in most blue seedlots was prominent in the cumulative growth curves from the fourteenth up to the fifty-first day of growth, while most Engelmann seedlots began to slow

down at least ten days earlier. Engelmann seedlot 8348 was an exception to this trend. In contrast to other Engelmann seedlots, 8348 responded similarly to blue spruce seedlots, and only began to slow down around the fifty-first day of growth. Mean shoot elongation of Engelmann spruce from population 36 was almost uniformly less than one-half the length of the tallest blue spruce seedlot, 8347, and about one-half the length of blue spruce seedlot 8240 from the same population. Seedlot 8297 had the shortest terminal shoot growth, while seedlot 8348 grew about 30 percent taller than the remaining Engelmann spruce.

Frost Damage

Frost damage was much more severe on Engelmann spruce seedlots than on blue spruce (Figure 3). Whereas the blue spruce seedlots generally had less than 50 percent RFD, nine of eleven Engelmann progenies were severely damaged. Of the Engelmann spruce represented, population 36 from northern New Mexico alone included enough seedlots to describe intrapopulation variation. Four of the six Engelmann progenies sustained 75 to 100 percent RFD. Seedlot 8232 showed surprisingly little damage, less than 25 percent, and less than the three blue spruce progenies included in that population. Of the two seedlots from central Arizona (population 57), blue spruce seedlot 8347 suffered less than one-half the RFD that Engelmann seedlot 8348 did. The remaining Engelmann spruce incurred 65 to 90 percent

Figure 3. Relative frost damage of blue (striped) and Engelmann (solid) spruce seedlots from common populations.

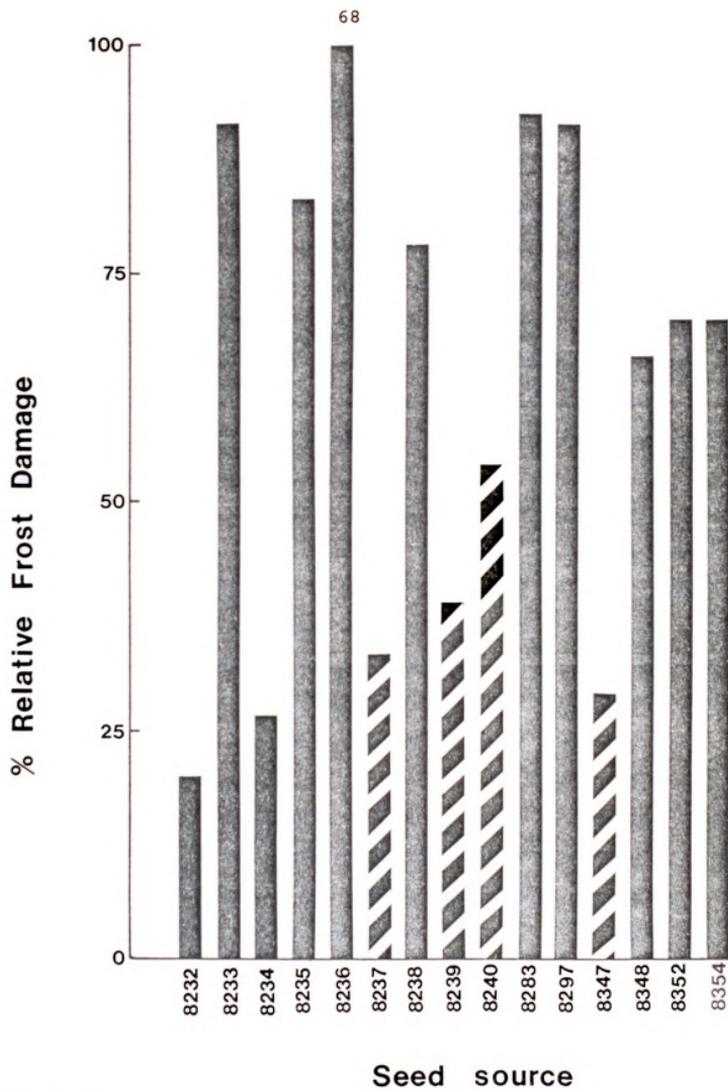


Figure 3.

RFD to their shoots.

Phenology

Blue and Engelmann spruce seedlots were most easily discerned by their differences in spring phenological development. In the spring of 1974, Engelmann spruce reached bud stage 6 (shoot elongated, needles free from each other) at least one week before blue spruce seedlots from common populations (Figure 4). This striking difference in both nursery and plantation in combination with the drooping foliar appearance, was most useful in distinguishing Engelmann from blue seedlots. Unfailingly, Engelmann seedlots were already completely flushed and shoots were elongated while most blue spruce buds were just bursting. Although some early variation was apparent among the representative Engelmann seedlots, by the third week in April differences had disappeared and all seedlots had reached bud stage 6. Meanwhile, blue spruce seedlots common to the same populations were conspicuously less developed.

Figure 5 illustrates the relationship of yearly variation in onset of warming spring temperatures to phenological development and subsequent susceptibility to frost damage. The spring warm-up in 1975 occurred later than during the previous two years, so that March and April mean monthly temperatures were 3°C to 5°C cooler than during the same period in 1973 and 1974. However, once warming

Figure 4. Differences in bud phenology between blue (striped) and Engelmann (solid) spruce seedlots at four assessment dates.

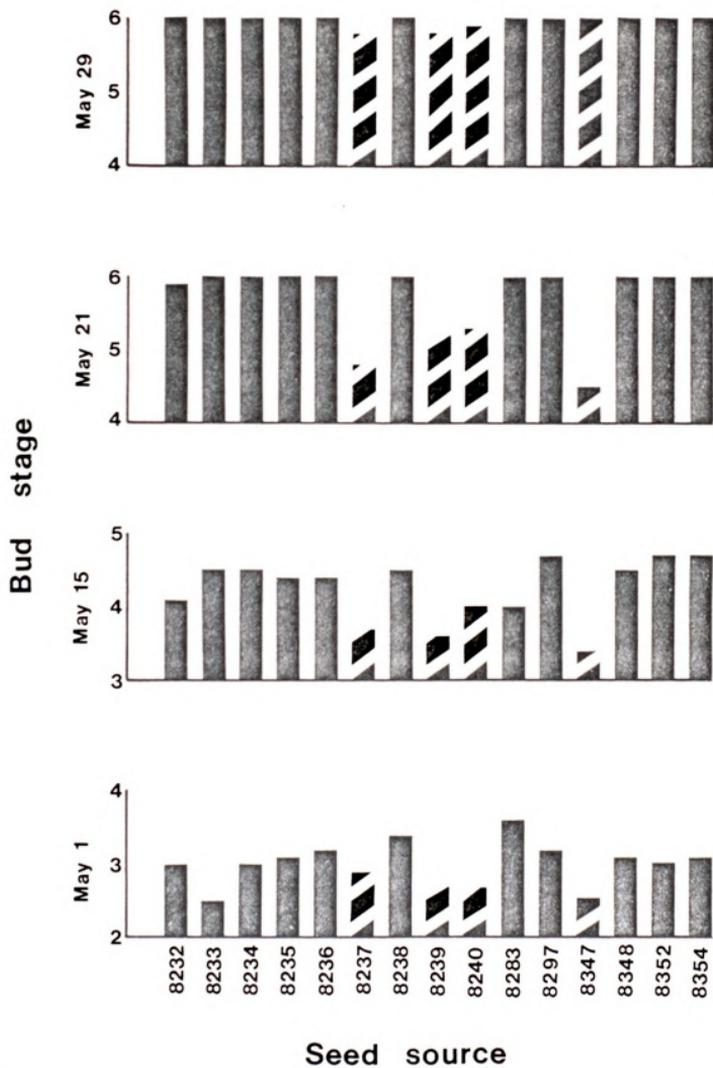


Figure 4.

Figure 5. Pattern of growing-degree day accumulation over three consecutive growing seasons.

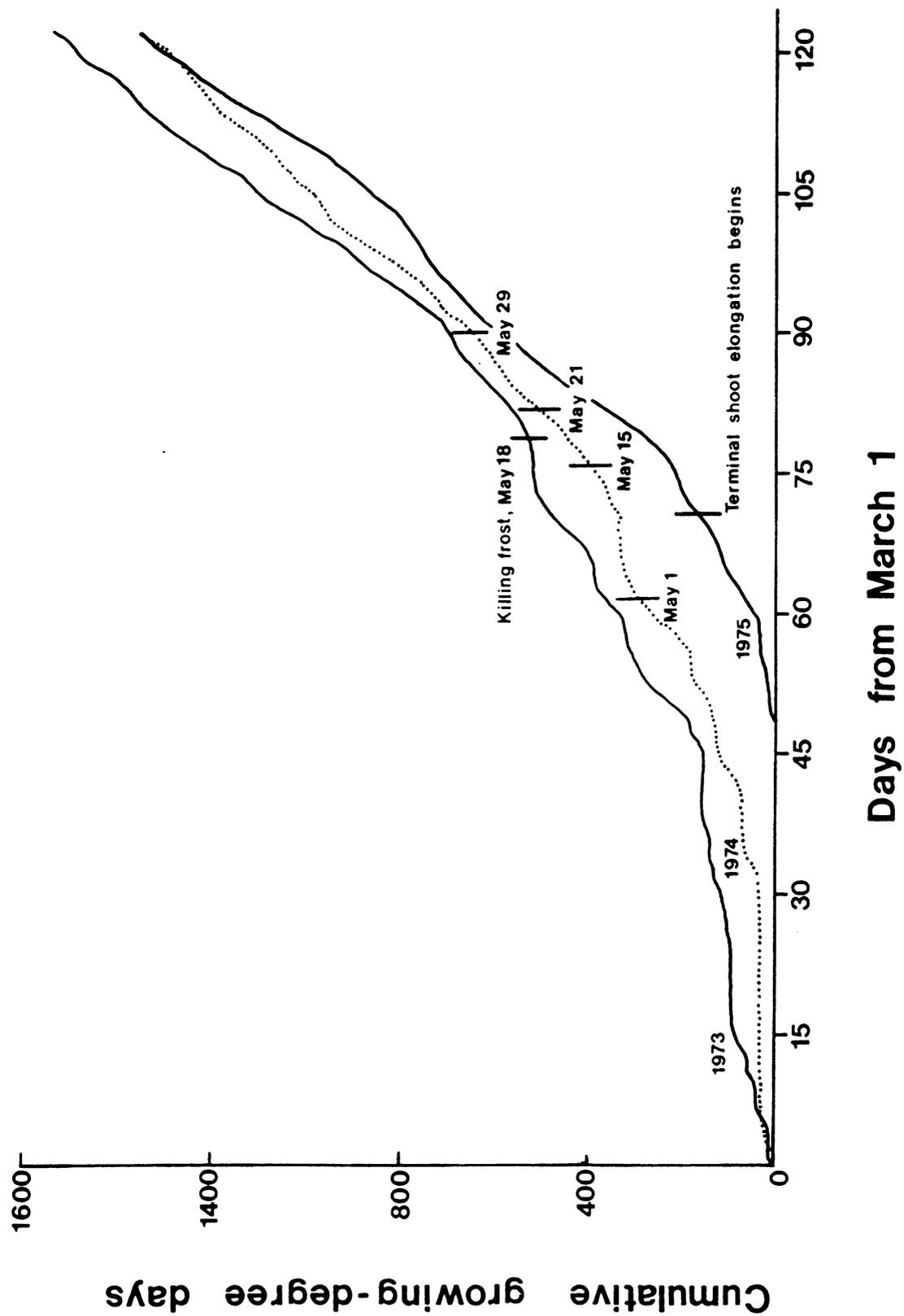


Figure 5.

began, temperature increased very rapidly. As a result, the time interval between stages of phenological development, defined by cumulative growing-degree-days required to reach a given developmental stage, was shortened by almost one-third in 1975 as compared to the previous years. This time compression masked phenological differences, and explains why growth began almost simultaneously for both blue and Engelmann spruce in 1975. The need for several seasons of phenological observations is apparent, as well as the vulnerability of both blue and Engelmann spruce to random year-to-year fluctuations in meteorological events. General climatic parameters, such as the probable date of last spring frost are only relevant in the context of current season's phenological processes which are conditioned by the current season's weather.

Variation in Needle Morphology

Percent of twice needle length covered by resin sacs was strikingly different between blue and Engelmann spruce. Between-species differences accounted for 73 percent of total variance (Table 16). In all populations examined, this ratio always exceeded 40 percent for blue spruce but was always less than 30 percent for those Engelmann spruce seedlots included (Table 17). This character, which is actually a composite of needle length, number of resin sacs per needle and resin sac length, is of more diagnostic value than any of the component

Table 16. Variance Components of Needle Characters Among Blue and Engelmann Spruce Expressed as Percent of Total Variance.

Character	Between Species			Among Blue			Among Engelmann			
	σ^2_s	σ^2_p	σ^2_t	σ^2_p	σ^2_f	σ^2_l	σ^2_p	σ^2_t	σ^2	
Needle length	14	34	38	14	7	45	9	15	48	37
Needle width	65	8	22	5	9	31	14	46	41	13
Stomates . mm^{-2}	9	31	27	33	26	24	38	39	27	34
# Resin sacs	19	29	16	35	25	3	60	31	56	13
Resin sac length	35	29	24	21	28	0	32	15	58	27
% Needle Covered by resin sacs	73	9	10	8	32	0	29	36	43	21
# Resin sacs on lower third of needle	4	0	30	66	0	17	57	1	14	85
# Resin sacs on middle third of needle	23	3	16	58	1	12	75	3	22	75
# Resin sacs on upper third of needle	39	22	6	33	12	2	85	56	17	27

σ^2_s = between species component

σ^2 = error (or among needles/within tree) component

σ^2_p = among populations/within species component

σ^2_f = between families/within population component

σ^2_t = among tree/within population component

Table 17. Mean Values for Needle Morphological Characters of Nine Blue and Eight Engelmann Spruce Populations.

State	Popu- lation	Needle Length mm	Needle Width mm	Stomates . mm-2	# Resin Sacs Per Needle	Resin Sac Length, mm	% of Needle Covered By Resin Sac	# of Resin Sacs on Needle		
								Lower Third	Middle Third	Upper Third
<u>Blue Spruce</u>										
Colorado	10	13.9	0.62	36	4.7	2.78	46	1.2	1.9	1.9
	14	13.6	0.65	37	4.4	2.66	41	1.1	2.0	1.8
	30	17.1	0.61	28	3.8	5.46	56	1.5	1.7	1.5
Wyoming	13	15.1	0.62	29	4.2	4.23	56	1.7	2.1	1.4
Utah	1	20.8	0.65	33	5.6	4.58	60	1.5	2.1	2.3
	11	15.5	0.62	35	4.9	3.35	51	1.8	1.9	1.5
	26	17.1	0.65	30	5.0	3.98	56	1.5	1.9	2.3
New Mexico	39	16.1	0.60	33	4.7	3.00	43	1.4	1.4	1.9
Arizona	31	15.8	0.62	33	4.7	2.82	41	1.3	1.6	2.0
MEAN		16.1	0.63	33	4.7	3.65	50	1.4	1.8	1.8
<u>Engelmann Spruce</u>										
Montana	70-90	17.4	0.52	32	3.8	2.53	28	1.9	1.2	0.8
	70-109	19.0	0.58	24	4.6	2.39	29	1.8	1.2	1.8
	75	19.1	0.50	24	5.1	2.07	27	1.6	1.5	2.1
Washington	3259	17.3	0.48	26	4.0	2.15	24	2.0	0.2	1.8
Idaho	70-55	16.2	0.46	35	3.1	1.67	15	1.3	1.1	0.5
	3255	13.3	0.67	34	4.0	1.40	21	1.8	1.2	1.0
New Mexico	36	19.2	0.53	32	3.4	2.02	18	1.8	1.6	0.0
	47	18.2	0.55	32	3.1	2.33	19	1.4	1.2	0.4
MEAN		17.5	0.54	30	3.9	2.07	23	1.7	1.2	1.0

characters taken separately. Of the three main component characters, the between-species component of resin sac length accounted for the greatest percentage of total variation, 35 percent. Between-species components for needle length and number of resin sacs per needle contributed more modestly to the total variation (14 and 19 percent, respectively).

Species differences in needle width were very pronounced, accounting for 65 percent of the total variance in this trait. More interesting, however, were the variance components for needle width within each species. Blue spruce data showed no differences among populations, but over one-half of the total variance could be explained by differences between-families-within-populations. Conversely, Engelmann spruce population differences accounted for almost one-half of the total variance, while trees-within-populations (which included any family differences) accounted for another 41 percent. Similarly, variance components of resin sac number in upper one-third of needle showed substantial between-species variation (39 percent of total variation). However, distribution of within-species variation was different for each species. In blue spruce, error accounted for 85 percent of the total variation, while in Engelmann spruce, over one-half of the total variation was accounted for by differences between populations. Apparently needle morphological characters are or have been under very different selective pressures for each species.

This knowledge may be useful in attempting to incorporate such traits into a breeding program.

Other measured traits exhibited little or no appreciable between-species variation. In general, these results confirm Reed and Freytag's (1949) findings. However, when the composite character, percent of twice needle length covered by resin sacs, is calculated, species differences are much more pronounced in needle characters.

DISCUSSION

Timing of phenological events have been shown to be under strong genetic control in temperate zone conifers (Nienstaedt 1973, 1975; Nienstaedt and King 1970; Lester, et al. 1977). Growth differences between blue and Engelmann spruce in southern Michigan plantations can be explained in part by differential frost damage sustained by each species. Engelmann spruce susceptibility to late spring frost damage resulted from its ability to break bud dormancy at a relatively lower temperature threshold than blue spruce. Pearson (1931) gave an explanation for this phenomenon from his and Bates' (1924) climatic studies of Rocky Mountain forest types. At higher elevations, temperatures begin to warm up much later than at the intermediate elevations where blue spruce occurs. Spring growth is retarded by the cooling effect of substantial snow cover lasting through late spring. When temperatures finally begin to warm, they do so rapidly, with little danger from advective

frost. Blue spruce, however, is able to avoid most severe late spring frost damage due to its general tendency of flushing only after a greater number of heat units had been accumulated than required for Engelmann, by which time frost danger had passed. The climate of the Lake States region is characterized by late spring anticyclonic disturbances of Arctic origin, the controlling mechanisms of which are not well understood. Hare and Thomas (1975) have attributed this climatic phenomenon to regular anticyclonic tracks which are conditioned by broad seasonal-geographic controls, including ice-covered Hudson Bay, which has a directional effect upon late spring airmasses. Presumably similar conditions are present in the seasonal climatic regimes of blue spruce habitats. Wardle (1968) reported similar situations in the western United States involving airmasses of Pacific origin as opposed to those of Gulf of Mexico origin. Southern airmasses are much warmer than those from the Pacific, even in winter. Generally, threshold temperatures for growth are reached after danger from such cold airmasses is past, although occasionally Engelmann spruce at high elevations are damaged by late spring frosts. Another phenomenon which may help to explain earlier flushing times of the higher elevation Engelmann spruce is the radiant energy heating of needles even though ambient temperatures may be low (Pearson 1931). Such a response has been reported in elevational studies of purple lilac (Syringa vulgaris Linn.;

Caprio 1967, 1971). At higher elevations, lilacs flowered at a lower threshold temperature than required at lower elevations. Caprio suggested that because of radiant heating, a given phenological stage of development, or plant wave, progresses toward higher elevations more rapidly than a given mean temperature, or thermal wave.

The apparent variation in frost damage among Engelmann spruce seedlots from population 36 is interesting in that it illustrates the importance of bud stage of development in relation to freezing injury. Seedlot 8232 was relatively undamaged by the late frost, and also was slightly behind the other Engelmann seedlots in phenological development during the first three weeks of the phenological measurement period. Perhaps this time lag was just enough for it to miss the full effect of the frost. However, as Clements, et al. (1972) pointed out, damage to unopened buds may have occurred, causing them to remain unopened, thus giving an erroneous frost damage grade.

The exceptional performance of both Engelmann and blue spruce seedlots from population 57 indicates inherently high growth potential from this area. These two seedlots were tallest in the NUR plantation until the sixth growing season. Clearly, population differences in height growth are present in Engelmann spruce. One explanation for the different growth rates may be the differential ability for populations to tolerate water stresses which curtail physiological activities. Seedlot 8348 was more

drought tolerant than seedlots from population 36; transpiration rates were higher in 8348 even when soil moisture became limiting (Chapter 3). The implication here is that selective pressures at the seed origin were favorable for development of a more drought tolerant population in Arizona (population 57) than in northern New Mexico (population 36). Pearson (1920, 1931) attributed Engelmann's high elevation distribution to lack of sufficient soil moisture at lower elevations. His climatic and soil moisture data show that in the Engelmann spruce type, the snow pack did not melt until late June, thus the summer dry period experienced at lower altitudes was not noticeable, due to the groundwater charging by late snowmelt. The soil moisture regime at the Michigan planting site may more closely approximate blue spruce habitats than Engelmann spruce, thus inhibiting most Engelmann spruce seedlots from expressing full growth potential.

Speculation on the adaptive value of needle morphology characters is intriguing. Resin sac coverage of needles seems to imply some past or present selective pressure on blue spruce that is not exerted on Engelmann spruce. If, as Daubenmire (1972) suggests, blue spruce is a recent derivation of Engelmann spruce, then range distribution must have been very small at one time. Selection in the form of insect defoliation may have resulted in those trees with resistance due to more resin sacs per needle, perhaps a deterrent to intensive feeding. Lack of

variation between-seedlots-within-populations may have resulted from such a situation. If such an occurrence was climate-related, Engelmann spruce, due to its cooler habitat adaptation, may have been ecologically isolated from such a selective force.

CHAPTER 3. DIFFERENTIAL RESPONSE TO DROUGHT STRESS BY
BLUE, ENGELMANN AND WHITE SPRUCE

INTRODUCTION

Tree species differ in their ability to survive conditions of high water stress. Shirley and Meuli (1939) and Pharis (1966) demonstrated differences in drought resistance among western conifers, while Glerum and Pierpoint (1968) reported differences among three eastern coniferous species. Evidence of genetic variation for drought resistance within tree species has been presented by Meuli and Shirley (1937) for green ash and Squillace and Bingham (1958) for western white pine. Pharis and Ferrel (1966) reported that coastal sources of Douglas fir were less drought resistance than inland sources, but that there was substantial variation in the trait among inland seedlots. Ferrel and Woodard (1966), also studying Douglas fir, concluded that selection for drought resistance may occur on a local level as well as on a regional level. They suggested that transpiration control played an important role in drought resistance.

Differences in transpiration rates have been reported in western conifers by Bates (1923), Sperry (1936) and Lopuskinsky (1969, 1975), with pines and spruces having higher transpiration rates than the firs. Lopuskinsky also reported a more sensitive stomatal control mechanism to water stress, and Pereira and Kozlowski (1976) observed

differential stomatal control between two eucalypt species. Helkvist and Parsby (1976) reported that growth of four clones of scotch pine was related to the xylem pressure potential of each clone, and surmised that this in turn was regulated by the rate of transpiration. Beasley and Klemmedson (1976) postulated that due in part to its lower xylem pressure potential at a given soil water potential, bristlecone pine was better able to withstand high water stress, and therefore able to live to a much greater age than limber pine, it's most common associate.

The following study was initiated to determine whether or not inter- and intraspecific differences in certain plant-water relationships were present among blue, Engelmann and white spruce seedlings. These three species form a complex in the Rocky Mountains, with each species occupying a particular geographical and edaphic habitat. Blue spruce especially is widely recognized for its drought-tolerant characteristics, and is widely planted in the American and Canadian praries for windbreaks and amenity plantings. Meaningful differences among the species would help to explain patterns of distribution and information on intraspecific variation would enable tree breeders to formulate strategies for improving yield through selection for maximum water efficiency. This study was comprised of two separate but related experiments.

First, seedlings at various levels of water stress were sampled in order to determine the levels of xylem

pressure potentials for each species and family. This was done by the pressure chamber method of Scholander, et al. (1965), using the apparatus described by Waring and Cleary (1967). This method, as pointed out by Kaufmann (1968), does not always reflect the exact leaf water potential, but instead, the dimensional deformation caused by xylem tension. Kaufmann suggests the term "xylem pressure potential", and this terminology is used in this report. Although most other authors refer to uncorrected pressure chamber readings as "leaf/plant water potential", Kaufmann (1968) reported that xylem pressure potential of Engelmann spruce was somewhat higher than leaf water potential over most of the range of water potential.

The second experiment was designed to identify differences in pattern of transpiration as soil moisture deficits increased. Potted seedlings were subjected to a drying cycle and water loss was monitored. Transpiration rates were expressed in three different units to ascertain differences in plant control over water loss.

Materials and Methods

For Experiment 1, forty 2/0 trees from each of three Engelmann and three blue spruce seedlots were potted in six-inch diameter polyethylene rose pots. The soil medium was a Foxe loamy sand. Origins of seedlots are listed in Table 18.

Table 18. Origins of Blue and Engelmann Spruce Seedlots Used in Drought Tolerance Studies.

<u>Species</u>	<u>Seedlot</u>	<u>Popu- lation</u>	<u>County</u>	<u>State</u>
Blue spruce	8082	13	Sublette	Wyoming
	8161	27	Mineral	Colorado
	8375	65	Larimer	Colorado
Engelmann spruce	8233	36	Taos	New Mexico
	8238	36	Taos	New Mexico
	8348	57	Greenlee	Arizona

One hundred and twenty 2/0 white spruce trees from a bulk seed collection from the Huron-Manistee National Forest in Michigan were potted in the same manner as the blue and Engelmann seed sources. All potted seedlings were moved into a greenhouse in the fall following potting, and placed in plastic-lined beds. Prior to the start of the experiment the beds were flooded and the pots containing the seedlings were saturated. Water was withheld for a period of two weeks and each day during the drying period one tree from each seedlot was selected for determination of plant water potential. Potted trees were first weighed, and then four branches from each tree were used to determine the plant water potential by the pressure chamber technique (Scholander, et al., 1965). The roots were washed and all soil collected in large galvanized buckets. Percent moisture was indirectly determined gravimetrically by subtracting net dry soil weight from net fresh soil

weight and dividing the remainder by fresh soil weight. Percent soil moisture of soil samples were determined at specific soil water potentials in a pressure plate and pressure membrane apparatus (Richards, 1947, 1948), and a soil moisture curve was constructed which is expressed by the following equation:

$$\log \hat{Y} = 0.671 + 0.231 \log 1/X$$

Given the percent soil moisture of any pot, the soil water potential in bars could be estimated from the curve.

In Experiment 2, a total of 36 potted trees were grouped into a randomized complete block design of four replications. Each replication consisted of one tree from each seedlot used in experiment 1 plus three white spruce seedlings from the bulk Huron-Manistee National Forest collection. Prior to the drying cycle these pots were placed in a laboratory sink and allowed to saturate. After draining excess water, each individual pot was placed inside a clear polyethylene bag, and the top was sealed tightly around the stem of the seedling with a wire twister. The four replicates were arranged in a growth cabinet under continuous light, with temperature and relative humidity held constant at 74°F and 70%, respectively. Each individual pot was weighed every 24 hours, and the net water loss was calculated. Samples of eight needles from each tree were taken and frozen in distilled water for further examination. When an individual tree began dropping

needles, the top was cut at soil level and the roots were washed free of soil in a galvanized bucket. Percent soil moisture was subsequently determined indirectly from gravimetric measurements. Fresh and dry root and shoot weights were recorded for each tree as was net dry foliage weight. Transpiration rate per unit dry foliage was then calculated for each individual tree.

Needle samples were measured microscopically. Total length was measured, as was width of all four sides at the midpoint of the needle. Total number of stomates were counted along a 1.1 mm line on all four sides of each needle. From these measurements total needle surface area, stomatal density and total number of stomates per needle were estimated. The needles were oven dried and then weighed. Estimates of total surface area and number of stomata were then calculated for each individual tree.¹

Results

Experiment 1. Xylem pressure potential response to soil moisture stress.

Xylem pressure potential response to decreasing soil moisture is presented in Figure 6. Because soil moisture exceeded the operating parameters of the pressure plate apparatus over much of the experimental ranges, the soil moisture variable is expressed as percent soil

1 Data on file, Forestry Department, Michigan State University.

Figure 6. Response of blue, white and Engelmann spruce xylem pressure potential to changing soil moisture.

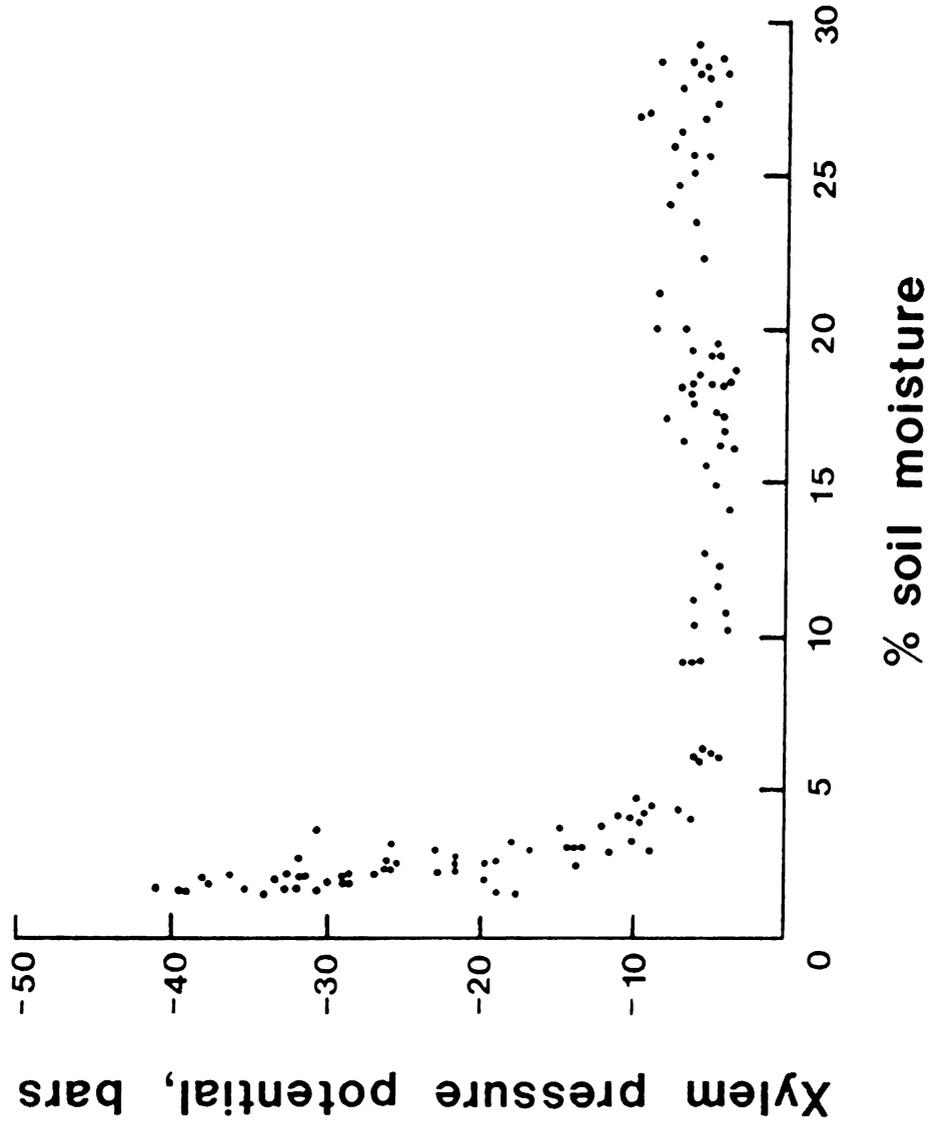


Figure 6.

moisture, rather than negative bars soil water potential. Attempts at curve fitting indicated a marked change in response at about five percent soil moisture (-0.7 bar soil water potential). When soil moisture dropped below five percent, seedlings of blue, white and Engelmann spruce began to exhibit symptoms of water stress. For the purpose of statistical comparison the response curve in Figure 6 was divided into two segments, that part which was less than eight percent soil moisture and that part which was greater than five percent. Inclusion of common terminal values at the interface of each segment allowed comparison over the whole range of the curve.

That portion of the curve between zero and five percent soil moisture was best fitted by using the log of the inverse of percent soil moisture as the X variate. Linear regressions were then calculated for each seedlot and species by the equation

$$\hat{Y} = a + b \log 1/X$$

A comparison of regression lines (Snedecor and Cochran 1969) showed no significant differences in xylem pressure potential among the three Engelmann spruce seedlots or among the three blue spruce seedlots at lower (less than five percent) soil moisture levels. When seedlot values were pooled over each species and specific regression lines were compared in the manner above, no significant differences could be detected between the two southern Rocky

Mountain species, but both differed significantly from the Michigan white spruce population. In this case, the slopes of the regression lines were similar among species, but the line elevations were different, indicating somewhat higher (less negative) xylem pressure potential values in white spruce than either Engelmann or blue spruce. F-values of these comparisons are summarized in Table 19 (Figure 7).

Table 19. Comparison of Regression of Xylem Pressure Potential on Percent Soil Moisture Among and Within Engelmann, Blue and White Spruce Seedlots when Soil Moisture is Less Than Eight Percent.

<u>Species</u>	<u>Seedlot</u>	<u>b^{1/}</u>	<u>r² ^{2/}</u>	<u>F-Value Among Slopes</u>	<u>F-Value Among Elevations</u>
Engelmann	8348	-75.56	0.93		
	8233	-78.29	0.85		
	8238	-77.44	0.88	0.12 n.s.	1.34 n.s.
Blue	8082	-75.46	0.88		
	8161	-47.52	0.63		
	8375	-58.84	0.96	0.88 n.s.	0.30 n.s.
Pooled	Engelmann	-75.52	0.91		
	Blue	-66.33	0.82	0.59 n.s.	1.44 n.s.
	Engelmann	-75.52	0.91		
	White	-66.59	0.84	3.26 n.s.	6.42*
	Blue	-66.33	0.83		
	White	-66.59	0.84	0.80 n.s.	4.75*

^{1/} b = regression coefficient

^{2/} r² = coefficient of determination

* significant at P = 0.05

Figure 7. Response of blue, white and Engelmann spruce xylem pressure potential to soil water changes below 8% soil moisture.

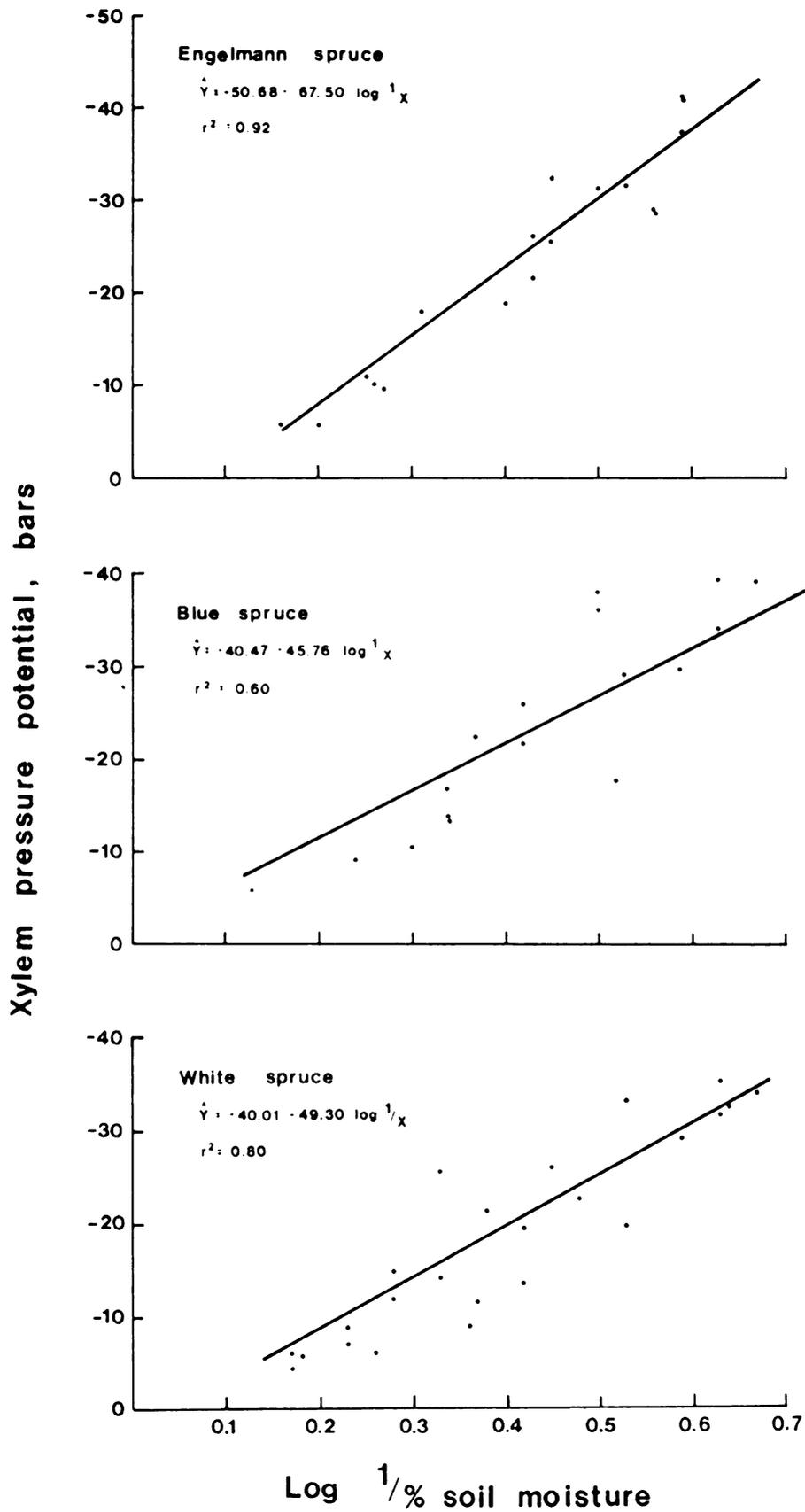


Figure 7.

When soil moisture was greater than five percent, the xylem pressure potential in all three tended to increase (become more negative), indicating that at saturated soil conditions the trees incurred some water stress. There were no intraspecific differences in xylem pressure potential response to increasing soil moisture. However, comparison of pooled regression lines among species indicated significantly higher xylem pressure potential values for blue spruce than for white or Engelmann spruce at soil moisture levels greater than five percent (Table 20).

From these results it seems that xylem pressure potential begins to increase rapidly at some point between five and six percent soil moisture (-0.7 to -0.3 bar); relatively small decreases in soil water availability may greatly affect the plant water status.

Table 20. Comparison of Xylem Pressure Potential on Percent Soil Moisture Among and Within Engelmann, Blue and White Spruce Seedlots When Soil Moisture is Greater Than Five Percent.

<u>Species</u>	<u>b^{1/}</u>	<u>r² 2/</u>	<u>F-Value Between Slopes</u>	<u>F-Value Between Elevations</u>
Blue Engelmann	-0.14 -0.03	0.36 0.03	0.59	6.24*
Blue White	-0.14 -0.11	0.36 0.19	0.78	10.81**

1/ regression coefficient

2/ coefficient of determination

* significant at 0.05 level

** significant at 0.01 level

Experiment 2. Transpiration Response to Changes in Soil Moisture.

Although mean transpiration rates ($\text{g}\cdot\text{h}^{-1}\cdot\text{dm}^{-2}$) did not differ among species (Table 21), analysis of variance indicated that among blue spruce seedlots, transpiration was significantly greater in seedlot 8161 than seedlots 8082 and 8375. However, no differences were detected among Engelmann spruce seedlots. A very marked "block" or "position" effect was evident from the analysis of variance. Transpiration rates were generally much greater for trees in replicate 1 in the growth cabinet than for the other replicates, probably due to the presence of air circulation vents over this area. For this reason data

from replicate 1 was not included in regression lines fitted to each seedlot.

Table 21. Mean Transpiration Rates ($\text{g.h}^{-1}.\text{dm}^{-2}$) for Blue, Engelmann and White Spruce Seedlots, When Soil Moisture is Not Limiting.

<u>Species</u>	<u>Seedlot</u>	<u>Mean Transpiration Rate</u>
Blue	8082	0.1471 \pm 0.0268
	8161	0.2344 \pm 0.0487
	8375	0.1429 \pm 0.0246
Engelmann	8348	0.1797 \pm 0.0454
	8233	0.1428 \pm 0.0309
	8238	0.1255 \pm 0.0543
White	bulk	0.1447 \pm 0.0586

Three distinct patterns of transpiration response to changing soil moisture were evident (Figures 8-10). Blue spruce seedlots 8082 and 8161 followed a curvilinear response over most of the range of soil moisture, best described by the general quadratic equation:

$$\hat{Y} = a + bx + cx^2$$

Transpiration rates reached maximum values somewhere between 11 and 14 percent soil moisture. Very waterlogged soils tended to inhibit transpiration -- as soil moisture dropped from saturated levels transpiration increased. When soil moisture dropped to between three and five percent, transpiration began to decrease exponentially,

Figure 8. Transpiration curves for three blue spruce seedlots.

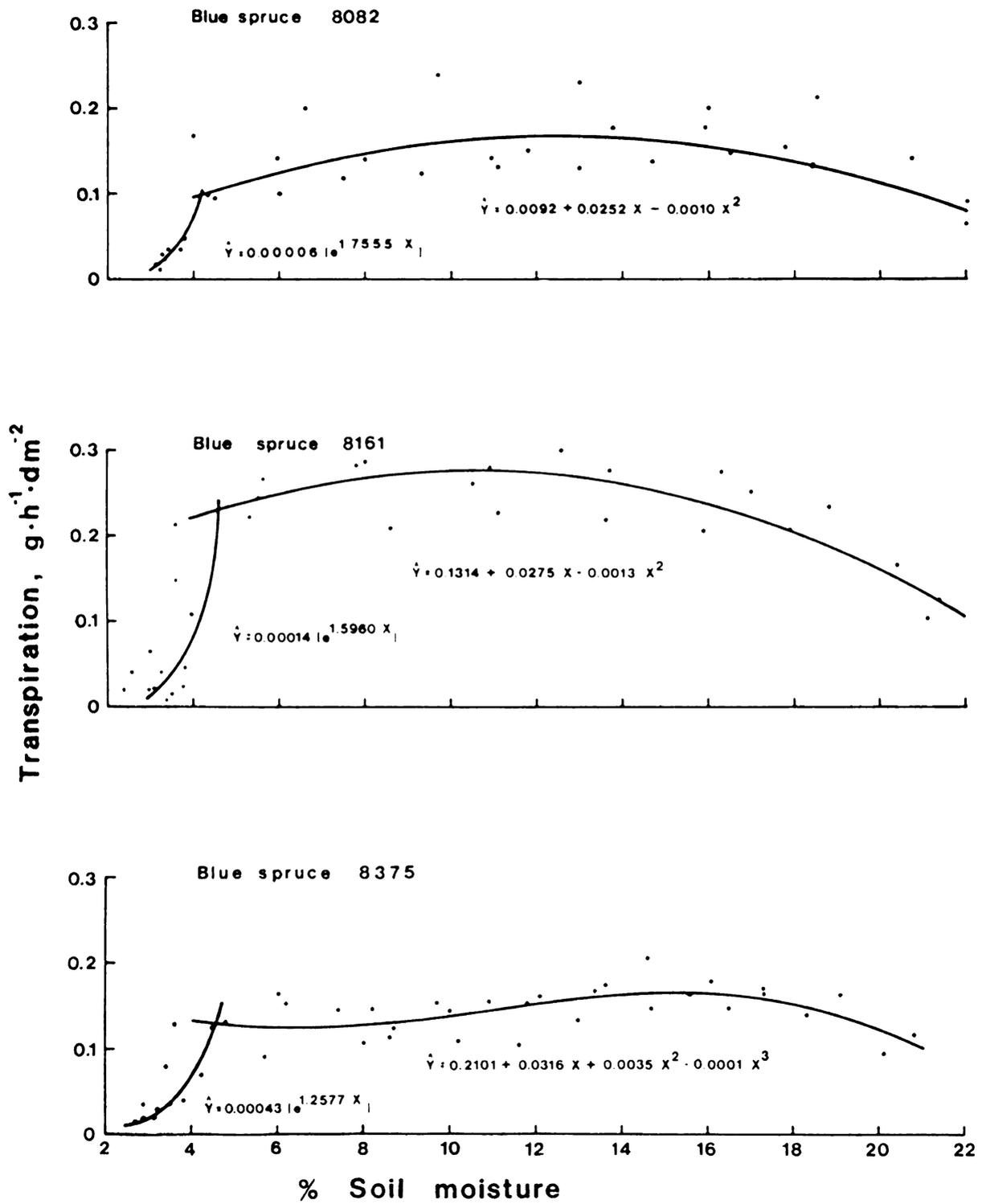


Figure 8.

following the general equation:

$$\hat{Y} = ae^{bx}$$

Although a quadratic regression line did not accurately describe transpiration response for blue spruce seedlot 8375, the inhibiting effect of saturated soil was evident. Regression equations and F-values for significance of departure from linear regression are present in Table 22.

Transpiration in Engelmann spruce seedlot 8348 responded quite similarly to blue spruce seedlots 8082 and 8161, characterized by a quadratic equation over most of the soil moisture range, then dropping exponentially to a minimum value around 4.5 percent soil moisture. Inhibition in waterlogged soils was evident in this seedlot also (Figure 9). Seedlots 8233 and 8238 from northern New Mexico could be characterized by individual quadratic regression lines extending along the entire range of soil moisture. However, there was no sharp drop in transpiration rate when a critical soil moisture deficit was reached. Seedlot 8233 also showed an inhibition of transpiration rate at saturated levels, but not seedlot 8238.

The third general pattern of transpiration response to decreasing soil moisture is unique to the bulk white spruce seedlot from Michigan (Figure 10). In contrast to both blue and Engelmann spruce, white spruce transpiration rates were not depressed at very high soil moisture levels. Instead, most seedlings included in the experiment had high

Table 22. Regression Equations for Transpiration Rate ($\text{g}\cdot\text{h}^{-1}\cdot\text{dm}^{-2}$) on Percent Soil Moisture, and F-Values for Significance of Departure from Linear Regression.

<u>Seedlot</u>	<u>Equation</u>	<u>F-Value</u>
Blue 8082	$\hat{Y} = 0.0092 + 0.0252 X - 0.0010 X^2$	14.54** 2,23 df
8161	$\hat{Y} = 0.1314 + 0.0275 X - 0.0013 X^2$	27.67** 2,18 df
8375	$\hat{Y} = 0.2101 + 0.0316 X + 0.0035 X^2 - 0.0001 X^3$	5.88** 3,28 df
Engelmann 8348	$\hat{Y} = -0.06412 + 0.04096 X - 0.0016 X^2$	23.26** 2,21 df
8233	$\hat{Y} = -0.0830 + 0.0386 X - 0.0014 X^2$	52.80** 2,48 df
8238	$\hat{Y} = -0.0342 + 0.0178 X - 0.0003 X^2$	13.74** 2,34 df
White Bulk	$\hat{Y} = -0.2359 + 0.0932 X - 0.0075 X^2 + 0.0002 X^3$	66.93** 3,119 df

** significant at P = 0.01

Figure 9. Transpiration curves for three Engelmann spruce seedlots.

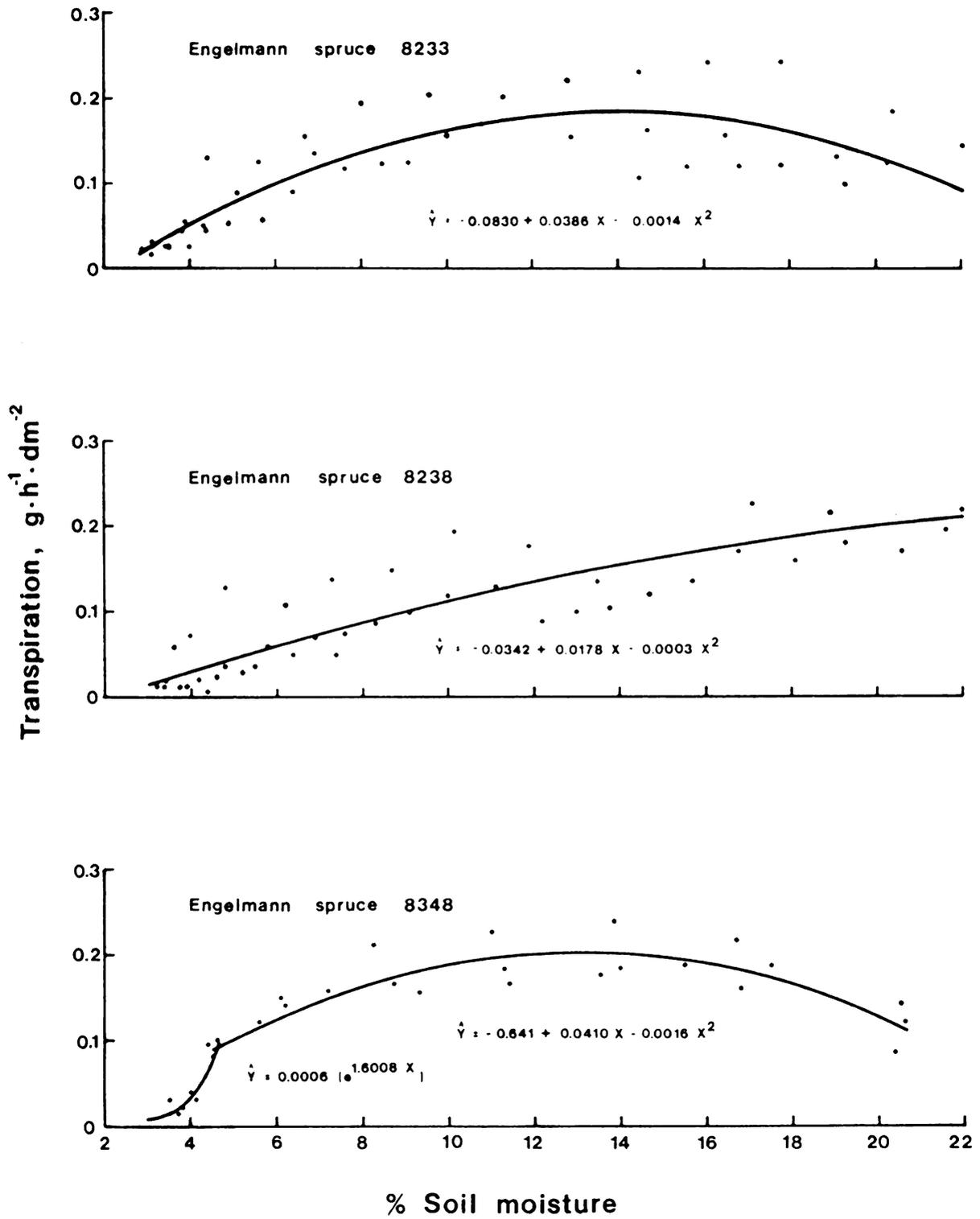
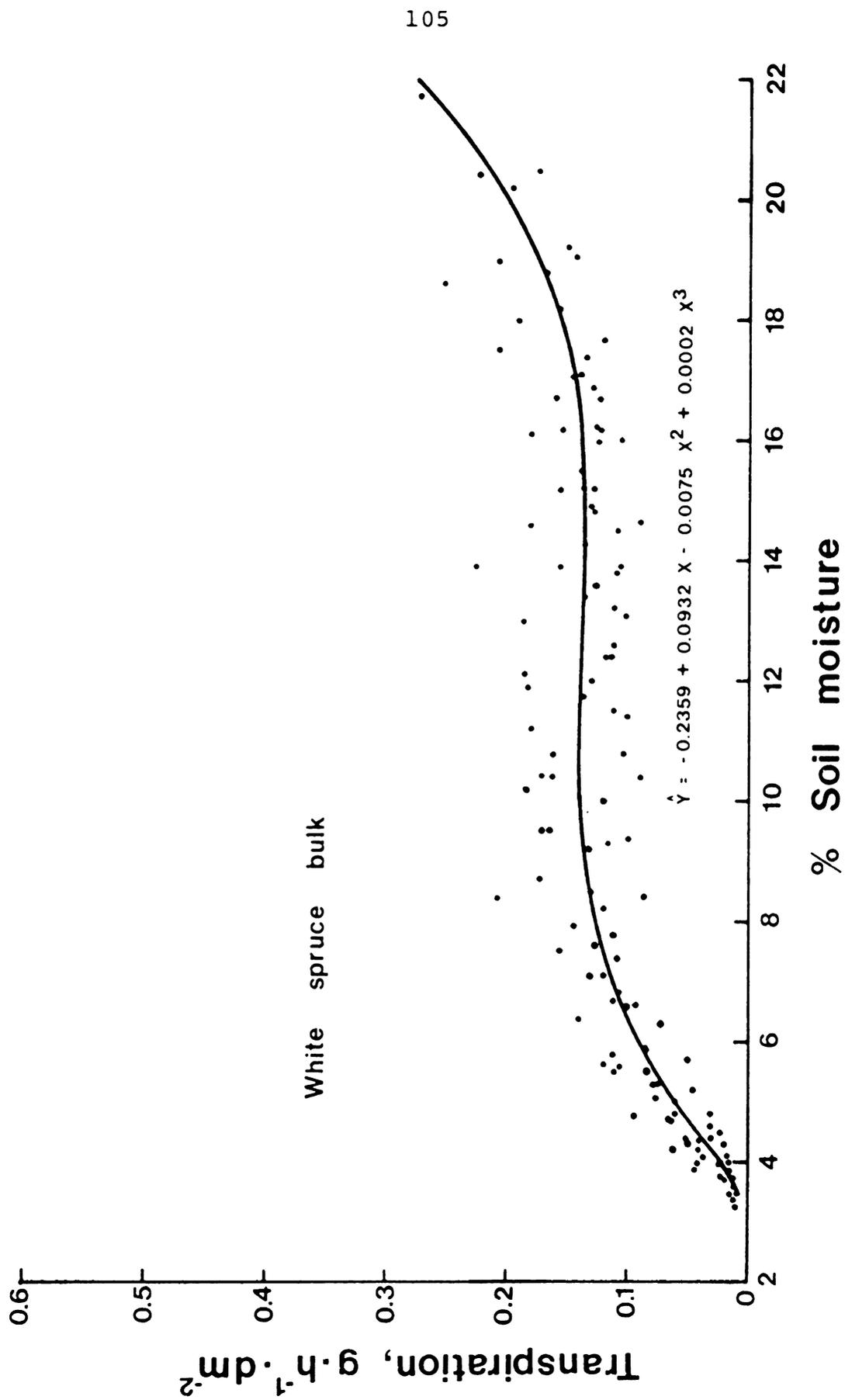


Figure 9.

Figure 10. Transpiration curve for bulk Michigan white spruce seedlot.

Figure 10.



transpiration rates under high soil moisture conditions. Reduction in transpiration was relatively gradual, beginning around eight percent soil moisture. The cyclic fluctuation of transpiration rate in white spruce was most unusual. Daily fluctuations in the other species were apparent, but much more moderate than those of the white spruce seedlings. The most marked fluctuations occurred before transpiration rate began to decline rapidly.

Xylem pressure potentials were calculated for each tree using regression equations obtained from Experiment 1. These were plotted against transpiration rate and regression equations for each seedlot computed. Covariance analysis of regression lines indicated significant differences among blue spruce progenies, as well as among the three species (Table 23). Trees of blue spruce seedlot 8161 had significantly greater transpiration rates at a given xylem pressure potential than did either seedlot 8082 or 8375. White spruce seedlots had significantly lower transpiration rates at a given xylem pressure potential than either blue or Engelmann spruce. Among Engelmann spruce seedlots only 8348 and 8233 had meaningful regression equations (variability in results of 8238 did not allow a good regression line "fit" -- $r^2 = 0.17$ -- so no comparison was attempted). No differences were detected between these seedlots, but when pooled and compared with blue spruce seedlots 8082 and 8375, transpiration rates of the blue spruce seedlots were significantly higher at a

Table 23. Comparison of Transpiration Rates ($g \cdot h^{-1} \cdot dm^{-2}$) Upon Xylem Pressure Potentials Among and Within Engelmann, Blue and White Spruce Seedlots.

Species	Seedlot	Regression Equation	r^2 (1)	F-Value Among Slopes	F-Value Among Elevations
Engelmann	8348	$\hat{Y} = 0.1612 - (9.7636 \times 10^{-3})X$	0.79		
	8233	$\hat{Y} = 0.1292 - (7.2662 \times 10^{-3})X$	0.63	2.00 n.s.	0.250 n.s.
Blue	8082	$\hat{Y} = 0.1907 - (-1.0331 \times 10^{-2})X$	0.65		
	8161	$\hat{Y} = 0.3940 - (2.2835 \times 10^{-2})X$	0.70		
	8375	$\hat{Y} = 0.1995 - (1.1547 \times 10^{-2})X$	0.72	5.625**	5.400**
Pooled	8082			0.222 n.s.	0.3575 n.s.
	8375				
Engelmann	8082			7.095*	4.779*
	8161				
Pooled	8161			6.579*	9.364**
	8375				
Engelmann	Blue (2)			2.833 n.s.	11.500**
	White	$\hat{Y} = 0.0947 - (6.0245 \times 10^{-3})X$	0.64	18.750**	97.750**
Engelmann	Blue (2)				
	White			6.333*	36.000**

* significant at 0.05 level (1) coefficient of determination

** significant at 0.01 level (2) pooled blue spruce including seedlots 8082 and 8375

given xylem pressure potential.

Discussion

Differences in pattern of transpiration response to soil water availability seems to reflect the important extremes in the seasonal water cycle at the place of origin. Blue spruce, native to a rather dry climate is subjected to periods of high water stress during the normal growing season. Undoubtedly, as Major (1967) has pointed out, local seasonal and annual climatic regimes are most important in maintaining selective pressure on a population of trees. Ground water levels are influenced by several variables, aspect, soil type, snow depth and drift levels, summer moisture regime and potential evapotranspiration demand being a few of the most obvious. Characteristics observed in these studies which seem to confer a measure of drought tolerance to blue spruce are:

1. rapid stomatal closure at a critical threshold soil moisture level;
2. ability to carry on gas exchange at levels of low plant water potential.

Sensitivity to a certain threshold soil moisture level and subsequent curtailment of transpiration by rapid stomatal closure is quite evident in blue spruce seedlots 8082 and 8161 and Engelmann spruce seedlot 8348. Additionally, Lopushinsky (1969, 1975) and Lopushinsky and Klock (1974) reported that drought-tolerant ponderosa and lodgepole

pine, as well as Engelmann spruce, followed a similar pattern, while transpiration rates for the drought-susceptible grand-fir and Douglas fir were reduced more gradually. Drought-tolerant seedlots of loblolly pine reacted in a similar manner to blue spruce, while drought-susceptible seedlots displayed a more gradual stomatal response at higher soil moisture levels (van Buijtenen et al. 1976). In contrast, white spruce is a species adapted to more moist soil conditions that are not subject to such frequent depletions of soil water. Intuitively, it does not seem so important for white spruce to be able to carry on gas exchange at low soil moisture levels, therefore early and gradual stomatal closure would be adequate for survival in the more mesic environment where white spruce occurs. A general parallel to this idea is apparent in regard to Douglas fir and grand fir (Lopushinsky, 1969, 1975; Lopushinsky and Klock, 1974). They are found in more mesic habitats than ponderosa and lodgepole pine. Hence, stomatal closure occurs more gradually than in the pines and Engelmann spruce.

Transpiration response at very high soil moisture levels may also reflect soil moisture regimes at seed source origins. All three blue spruce seedlots exhibited reduced transpiration rates under saturated conditions, while at the same time exhibiting an increase in xylem pressure potential indicating that plant water stresses were beginning to develop. Oxygen deficiency (anoxia), in

roots is a result of waterlogging, and seems to reduce root permeability in many species. Anoxia can affect transpiration rates, as well as many other physiological processes (Gill 1970). It may be that soil moisture patterns in the natural blue spruce habitats do not reach such high levels, at least during the periods of greatest transpiration demand. Well-drained soils may facilitate quick runoff of excess moisture before the growth season is underway. The white spruce bulk seedlot included in the experiment exhibited just the opposite characteristics, with very high transpiration rates at high soil moisture levels; these dropped to a lower level at intermediate soil moistures. At the same time, however, xylem pressure potentials increased with increasing soil moisture levels. Results of Experiment 1 indicate that these plant water deficits were significantly lower in white (and Engelmann) spruce than in blue spruce. Clearly, white spruce is somehow able to endure excessive amounts of water more effectively than blue spruce, an adaptation presumably made necessary by the water regimes of the boreal forest environments.

The anatomical and physiological characteristics which allow white spruce to do this are not clear. Perhaps, as Coutts and Armstrong (1976) suggest, white spruce may have more efficient internal gas pathways which allow oxygen transport to the roots under waterlogged soil conditions. High transpiration rates at these waterlogged conditions may have the effect of drying out the soil, and

at the same time allowing foliar gas exchange to take place at a maximum rate, presumably early in the growing season, when high water tables are most prevalent. Obviously, it would be of great interest to compare soil water regimes on sites of each species, and see how these moisture levels coincide with (1) changes in transpiration and plant water potential; and (2) changes in water demand as dormancy is broken and active growth continues.

Experimental results give some evidence for expecting distinct population differences in response to water stress in blue and Engelmann spruce, as well as direction for further comparative work both among and between species. Pharis and Ferrell (1966) indicated variability in tolerance to drought among inland Douglas fir, as did Ferrell and Woodard (1966). The significance of Ferrell and Woodard's report, however, was in the evidence for very localized adaptation to very localized conditions. The results of the blue and Engelmann spruce drought studies also contribute evidence to this hypothesis, although due to inclusion of limited numbers of seedlots from sites with no supporting climatic or edaphic data, only broad hypotheses can be formed, and must await further testing.

Among the blue spruce seedlots tested, 8161 had a significantly greater transpiration rate than either 8082 or 8375. Furthermore, 8161 exhibited the ability to carry on more gas exchange (as evidenced by higher transpiration rates) at lower xylem pressure potentials (and presumably

at lower plant water potentials). This ability, according to Tyree (1976), should permit the plant to maintain longer periods of net CO_2 assimilation, as the hydroactive closure of stomates is postponed until both lower plant and soil water potentials are reached. Perhaps not so coincidentally, seedlot 8161 is one of the fastest growing seedlots in experimental plantations in Michigan, and is from the fastest-growing population in the Michigan State University range-wide progeny test. If Tyree's hypothesis is correct, then seedlot 8161 is best adapted to carry on photosynthesis under situations where soil moisture becomes limiting. Of great interest in this respect would be more comparative water relations studies to determine whether other seedlots from population 27 (which includes 8161) have similar physiological responses to changes in soil moisture levels. One handicap to correlative studies between environmental variables and physiological parameters is the absolute lack of onsite climatic and edaphic records for blue and Engelmann stands of interest. Although general climatic descriptions are available, the variations due to topography and elevation alone make them very inaccurate for describing specific sites.

Engelmann spruce results indicate that considerable selection pressure exists among populations -- perhaps more so than in blue spruce due to the much greater latitudinal and elevational range of Engelmann spruce, and the differences in climatic regimes due to these extremes. The

seedlots included in the drought experiments exemplify this to some extent. Seedlots 8233 and 8238 came from population 38 in north-central New Mexico, while seedlot 8348 of population 57 originated near the middle of the Arizona-New Mexico border. Other than elevation, no environmental parameters are available. However, it seems likely that the southern seed source was subjected to more frequent and severe drought stress than the northern one, and as a result, the pattern of transpiration response to soil moisture is similar to the drought-tolerant blue spruce. Additionally, seedlot 8348 grew surprisingly well for an Engelmann spruce seedlot in the southern Michigan plantations. On the other hand, the northern New Mexico seedlots exhibited a more gradual reduction in transpiration rate, an indication, perhaps, that drought resistance is less important at the point of origin.

Recognizing and defining water use patterns may help to explain the importance and adaptive advantages of other processes influential in growth and dry matter production. Of prime importance is bud initiation and morphogenesis -- the processes by which the next year's growth is in large part determined. Presumably selection for prolonged photosynthetic capacity during the time of initiation and differentiation would positively affect these processes.

CHAPTER 4. CONCLUSIONS AND RECOMMENDATIONS

Rate of wood production is of prime importance in domesticating forest trees, and although relatively easy to measure, it is genetically and physiologically complex. Natural populations must optimize environmental fitness, and in the process of adapting to harsh environments, those component traits which contribute to duration of growth or differentiation period may be affected differently from those component traits which contribute to rate of growth or differentiation process. Maximum environmental fitness "wins out" over maximum growth in natural populations because of environmental constraints on either duration period or rate of process. However, the resulting variability in both duration and rate can be utilized through selective breeding to create new combinations of genotypes which are adapted to a range of habitats, and which maximize growth by optimizing duration and rate through complementation of traits.

Some of this variability has been defined in blue spruce, and to a lesser extent Engelmann spruce, in previous studies, in this study and in subsequent studies. Growth components, environmental fitness traits and some physiological and morphological traits are highly variable, with

substantial portions of that variance attributable to broad regional selection pressures, to much more localized selection pressures, and to random segregation within panmictic populations. However, before practical tree improvement techniques can capitalize on the existing natural variation, it must be more clearly defined. Adaptive significance of these and other component traits is logically deduced, but largely speculative, and needs to be clarified. As well, inheritance mechanisms and phenotypic plasticity must be better understood through selective breeding and extensive progeny testing.

The results I report here have, I feel, answered some basic questions in the physiological genetics of blue and Engelmann spruce, but have, to my mind, stimulated many more. To provide answers to some of these, I offer the following recommendations for future study:

1. That elevational transect collections through the blue and Engelmann spruce zones in the Uinta, Wasatch, Western Colorado and Arizona climatic regions be made to more clearly elucidate elevational effects within and among climatic regions.
2. That blue and Engelmann spruce population collections be made from several diverse sites where detailed site information is available, for correlation with component traits important in growth and fitness.

3. That the role of transpiration control in growth rate be examined in fast and slow growing populations of blue and Engelmann spruce, utilizing rooted cuttings to estimate clonal effects, to determine adaptive significance, and to evaluate this trait's usefulness in early selection.
4. That population diversity in western Colorado be investigated by comparing gene frequencies of endosperm isoenzyme genetic systems.
5. That a systematic study of genetic variation in Engelmann spruce be undertaken to provide basic information for tree improvement strategies in this important western conifer.
6. That comparative studies of populations from very different environments be designed and executed to elucidate whether or not rate and duration component traits of growth will be complementary when recombined through selective breeding.

APPENDIX

APPENDIX A. Open-Pollinated Blue Spruce Family Values for Growth and Foliage Characters.

Climatic Region	Popu- lation Number	Family, MSFG 6000+	NUR Height in cm.			AOCEL Height in cm.			Relative Frost Damage	Bark Phenology, 1974						Blue Trees At Age		Steel Blue Trees At Age		Selection Index
			2	5	6	2	5	6		5/1	5/15	5/21	5/29	5	6	5	6			
WYO	13A	78	10	33	51	27	66	78	27	25	35	49	54	0	0	0	0	0	160	
		79	10	25	41	31	65	92	15	21	31	42	51	0	0	0	0	0	158	
		80	10	-	-	26	60	79	15	22	29	43	52	6	0	0	5	0	-	
		81	14	38	51	32	67	87	10	21	30	43	51	0	0	0	33	7	210	
		82	11	-	-	30	62	80	10	22	32	43	52	0	0	0	0	0	-	
	13B	83	9	28	44	31	61	82	25	21	33	43	52	5	0	0	0	0	153	
		84	9	28	41	30	73	96	20	21	28	41	50	0	0	0	6	0	168	
		85	11	32	44	28	65	86	8	20	31	40	50	0	0	0	6	0	163	
		86	9	33	48	29	69	86	8	20	30	41	50	7	0	0	11	0	174	
		87	9	-	-	28	63	81	13	20	28	44	51	0	0	0	18	0	-	
13C	88	10	43	54	28	64	82	8	20	30	43	50	0	0	0	0	0	169		
	89	10	-	-	29	70	92	23	20	34	46	51	0	0	0	0	0	-		
	90	9	35	50	28	56	70	21	22	32	48	52	0	0	0	0	0	151		
	91	9	-	-	27	66	90	35	20	30	40	48	0	0	0	5	0	-		
	92	9	-	-	28	58	79	15	21	31	42	49	6	6	6	0	0	-		
UINTA	4	93	7	-	-	29	56	76	27	22	35	47	55	0	0	0	0	-		
		94	8	-	-	30	65	87	8	20	31	47	54	0	0	0	0	0	-	
		95	7	-	-	26	64	78	18	21	33	46	53	5	0	0	5	0	-	
		10	14	-	-	26	65	83	20	24	34	50	52	0	0	0	11	6	-	
		11	-	-	-	30	57	78	24	20	30	44	51	0	0	0	7	0	-	
	7	12	13	-	-	27	58	71	8	20	31	42	50	5	0	0	7	0	-	
		13	16	-	-	28	59	78	15	20	30	39	51	11	0	0	5	0	-	
		14	-	-	-	36	70	96	0	21	28	43	51	0	0	0	6	0	-	
		29	15	26	38	26	55	78	35	22	31	48	54	0	0	0	0	0	139	
		31	17	27	38	26	55	82	18	24	37	50	56	5	0	0	5	0	148	
50A	32	14	24	31	26	54	66	28	26	36	48	53	6	0	0	24	0	140		
	304	14	25	37	28	64	86	28	22	33	48	57	0	0	0	20	0	166		
	305	12	23	35	32	63	80	10	24	34	47	59	10	0	0	30	0	166		
	307	11	20	30	24	58	74	26	22	35	48	55	10	0	0	10	0	132		
	308	12	25	37	31	64	83	15	20	36	48	52	0	0	0	0	0	143		
	309	12	23	34	32	69	91	8	27	38	49	58	11	0	0	5	0	151		
	310	11	21	32	20	52	68	18	22	38	50	58	0	0	0	16	0	136		
	1	1	15	37	53	33	66	90	0	22	32	45	54	16	0	0	16	0	191	
		2	12	24	34	27	53	72	8	21	37	49	53	21	0	0	43	0	170	
		3	8	-	-	24	44	66	8	27	37	50	57	16	0	0	11	11	-	
4		12	32	50	30	70	97	0	20	34	47	54	63	5	42	5	226			
11	60	12	29	40	29	56	78	8	22	32	46	52	6	0	0	19	0	162		
	61	-	-	-	26	58	75	13	22	31	50	53	20	10	0	30	0	-		
	63	12	-	-	27	63	81	15	25	38	50	58	0	0	0	19	0	-		
	64	12	30	40	27	61	78	15	22	32	46	56	0	0	0	0	0	143		
	65	11	26	32	28	62	85	0	20	33	50	53	26	0	0	53	17	210		
	66	11	24	37	25	58	75	28	22	37	51	56	21	5	16	0	151			
	67	15	26	36	32	55	74	0	24	34	50	54	13	0	7	0	139			
	68	15	31	42	34	65	89	23	21	33	46	54	21	5	42	0	199			
	69	15	27	39	30	68	86	8	24	36	48	50	24	0	0	0	0	149		

APPENDIX A. (continued)

Climatic Region	Popu- lation Number	Family, MSEG 8000+	NJR Height in cm.			ACCEL Height in cm.			Relative Frost Damage	Bud Phenology, 1974			Blue Trees At Age		Steel Blue Trees At Age		Selection Index	
			2	5	6	2	5	6		5/1	5/15	5/21	5/29	5	6	5		6
WAS	12	70	10	-	-	33	64	83	12	21	29	43	52	0	0	0	0	-
		72	16	32	48	30	60	81	25	20	29	46	53	11	0	16	0	174
		73	14	35	47	26	58	79	15	20	32	48	52	21	0	5	0	160
		75	11	-	-	33	60	79	18	21	30	43	54	9	0	0	0	-
		76	10	30	43	26	54	65	20	22	35	48	56	5	0	0	0	134
		77	9	-	-	28	59	73	23	20	31	48	52	0	0	10	0	-
	25	149	12	33	48	27	63	86	18	24	40	49	56	0	0	9	0	172
		150	12	27	45	31	68	90	0	20	30	46	54	53	5	58	16	239
		151	-	-	-	29	63	86	8	22	34	48	54	0	0	5	0	-
	26	152	16	38	48	34	76	100	8	20	32	46	52	0	0	0	0	177
		153	16	31	45	32	59	90	8	20	31	48	51	0	0	0	0	163
	32	204	14	28	40	27	61	81	25	18	32	48	51	0	0	0	0	146
	205	14	27	39	30	70	86	0	20	31	45	50	5	0	15	0	164	
	206	13	26	37	30	73	100	10	20	34	46	54	0	0	0	0	160	
	207	14	31	44	29	65	84	0	20	34	43	50	0	0	0	0	155	
	208	12	-	-	31	68	91	0	20	31	48	51	0	0	6	0	-	
38	250	13	30	41	28	65	85	15	20	30	40	51	10	0	10	0	161	
	251	12	19	30	25	61	82	0	20	30	40	49	30	0	56	0	186	
WCOL	5	16	9	26	36	21	51	53	35	30	35	48	57	53	26	81	58	262
		17	-	-	-	30	51	64	43	32	32	53	60	47	16	100	26	-
		18	8	-	-	27	52	62	31	38	38	55	60	32	0	53	0	-
		19	12	26	39	28	56	72	49	40	36	50	60	50	15	74	53	271
		21	10	31	43	26	55	68	36	30	30	48	58	72	22	100	78	329
	6	22	14	-	-	30	65	91	20	20	31	44	54	17	0	17	0	-
		23	12	-	-	36	72	92	8	21	31	44	56	8	0	17	0	-
		24	17	31	42	28	62	83	21	24	36	50	58	0	0	7	0	158
		25	14	32	44	29	62	78	21	24	38	50	58	27	13	54	31	239
		26	16	32	42	35	66	83	0	22	34	50	55	0	0	0	0	151
		28	15	34	49	30	70	92	23	22	34	46	56	20	7	6	0	177
	10A	47	8	-	-	31	67	82	40	20	36	50	60	10	0	40	0	0
	49	13	25	34	32	63	78	30	25	35	52	59	0	0	0	0	133	
	50	13	28	40	29	63	82	34	26	37	51	57	19	6	60	13	222	
	51	14	31	43	35	71	94	20	23	34	49	55	40	0	65	25	258	
10B	52	15	31	45	26	59	74	30	26	32	45	58	25	5	40	7	195	
	53	15	32	44	23	54	72	50	27	38	50	59	35	0	90	45	286	
	54	10	23	31	26	49	60	41	22	32	45	54	35	10	80	30	225	
10C	55	19	31	50	28	59	80	8	26	35	50	57	6	0	44	0	205	
	56	16	35	48	32	62	88	23	21	31	43	53	21	-	42	0	207	
	57	15	28	40	32	53	86	40	25	37	46	57	5	0	11	0	162	
	58	15	32	48	29	61	86	18	22	33	49	57	5	0	7	0	170	

APPENDIX A. (continued)

Climatic Region	Popu- lation Number	Family, MSTC 8000+	NJR Height in cm.			ACCEL. Height in cm.			Relative Frost Damage	Bad Phenology, 1974			% Blue Trees At Age		% Stool Blue Trees At Age		Selection Index	
			2	5	6	2	5	6		5/7	5/15	5/21	5/29	5	6	5		6
WCOL	15	106	16	36	50	35	67	84	28	25	36	49	59	11	0	16	5	187
		108	14	32	47	30	59	77	25	24	36	50	58	0	0	0	0	153
		109	14	28	41	36	63	78	18	26	37	52	59	20	0	26	5	176
		110	12	33	48	27	65	80	41	28	35	48	58	0	0	28	0	185
		111	14	34	49	31	68	85	14	26	37	50	57	20	0	75	10	251
		114	-	-	-	32	71	93	18	26	36	49	59	11	0	5	0	-
	16A	115	12	33	34	28	51	65	25	24	36	51	60	5	0	5	0	125
		116	13	23	33	31	64	83	36	24	31	49	58	8	0	8	0	144
		117	14	29	39	28	55	77	26	24	31	45	56	5	0	16	0	156
		118	12	23	32	28	47	68	47	22	34	49	59	0	0	12	0	132
		120	15	32	28	30	59	72	23	24	40	50	58	0	0	0	0	117
	27B	160	16	39	58	33	77	98	45	29	40	53	60	50	10	70	25	291
		161	18	41	54	33	67	91	45	29	38	51	60	70	15	100	50	337
	27C	162	20	48	62	31	67	90	26	29	40	55	60	25	0	69	44	311
	163	21	38	51	36	71	93	35	30	40	51	60	39	6	67	17	262	
33	210	15	32	44	26	56	71	39	26	38	50	60	22	0	32	0	174	
	212	-	-	-	28	58	76	41	27	36	50	58	0	0	11	0	-	
	213	18	40	52	23	58	82	21	26	38	53	60	11	0	42	0	208	
35B	227	-	-	-	22	50	72	31	26	37	49	60	39	0	44	6	-	
	228	12	24	34	25	54	75	33	22	32	44	51	27	9	70	10	212	
	229	11	31	26	25	55	75	31	24	35	49	58	42	0	68	5	191	
	230	11	25	37	23	50	64	34	22	32	46	53	5	0	47	0	171	
	231	10	25	36	24	52	67	35	22	31	44	52	10	0	40	0	165	
37A	242	16	28	42	23	46	67	40	23	39	53	60	17	0	35	6	177	
	244	12	21	31	22	45	62	47	29	37	51	60	16	0	58	0	170	
	245	-	-	-	31	63	87	50	24	38	51	59	15	0	44	17	-	
37B	246	14	26	39	32	68	92	21	22	35	51	58	15	0	11	0	166	
	247	18	29	44	28	66	86	28	24	33	46	58	17	6	24	6	188	
	248	-	-	-	29	57	83	23	20	33	44	56	25	0	55	18	-	
40	269	16	40	56	31	64	87	38	28	38	51	60	0	0	15	0	192	
	270	14	29	42	31	66	83	31	22	36	48	58	26	0	63	11	227	
	271	17	33	48	33	65	81	18	23	32	49	58	44	6	72	11	243	
	272	16	33	45	30	67	93	41	25	36	51	58	0	0	42	0	208	
	273	14	37	54	33	63	88	25	25	33	46	56	15	0	50	5	231	
	274	13	28	42	24	55	70	38	30	38	50	56	11	0	11	0	149	
	275	14	36	47	22	51	70	47	25	35	49	59	5	0	5	0	151	
	276	16	36	47	24	57	72	38	23	39	49	60	0	0	6	0	154	
ECOL	8	33	12	-	-	26	65	74	25	20	29	48	52	80	30	73	45	-
		34	12	19	25	29	55	76	36	21	35	49	59	25	0	25	8	151
		35	13	26	38	28	61	89	31	21	31	46	57	58	11	78	33	267
		37	12	30	44	31	68	92	25	24	31	46	58	0	0	47	0	210
		38	16	32	47	29	58	76	34	22	31	43	56	20	5	35	30	222
		40	11	26	34	30	58	72	41	22	29	39	53	60	11	12	0	139
		41	15	30	43	26	58	76	54	26	39	50	58	11	0	6	0	151

APPENDIX A. (continued)

Climatic Region	Popu- lation Number	Family, MSG, 8000+	NUR Height in cm.		ACCEL Height in cm.		Relative Frost Damage	Bud Phenology, 1974		% Blue Trees		% Steel Blue Trees		Selection Index				
			At Age 2	At Age 5	At Age 2	At Age 5		5/1	5/2	5/1	5/2	At Age 5	At Age 6		At Age 5	At Age 6		
ECOL	14A	96	12	31	42	27	55	71	23	27	38	51	60	18	6	17	6	163
		97	14	28	38	27	58	74	36	27	38	48	59	6	6	0	0	141
		98	12	32	45	30	58	79	28	23	33	44	59	25	0	55	5	212
		99	13	28	44	25	48	71	43	23	35	48	58	10	0	26	0	168
		100	12	29	40	26	52	74	31	26	37	50	59	11	0	16	5	160
	14B	101	12	31	44	24	54	68	36	32	38	50	59	17	0	8	0	147
		102	12	30	47	28	59	79	33	25	36	50	58	30	5	40	15	212
		103	12	28	40	24	54	72	26	27	39	57	58	10	0	40	10	188
		104	14	25	35	25	56	71	42	26	33	50	58	12	0	35	0	162
		105	11	21	39	25	58	77	47	27	36	49	59	25	0	63	13	218
24	141	14	30	40	22	52	71	20	23	32	44	57	29	6	50	6	193	
	143	16	28	41	26	48	62	39	28	37	53	60	32	5	47	21	200	
	144	14	30	38	25	56	70	38	26	39	50	58	24	12	50	22	207	
	145	13	30	42	26	61	85	23	25	35	48	60	27	7	67	33	259	
	146	18	29	38	28	64	73	26	26	33	49	58	33	11	50	33	223	
	147	15	31	46	27	62	81	27	21	31	45	54	55	15	50	20	229	
	29	172	14	24	32	28	56	78	34	23	34	48	60	55	10	80	65	286
		173	16	36	50	24	57	80	15	20	30	43	56	30	0	30	5	197
		176	14	30	46	27	62	79	47	24	36	49	58	94	63	100	85	353
		177	14	28	37	28	54	72	24	22	33	46	56	67	40	79	58	279
165		18	34	50	30	63	86	27	28	39	50	59	32	0	63	0	210	
NNMEX	166	16	36	49	31	66	86	18	23	33	47	58	70	25	95	55	325	
	167	17	41	48	25	50	69	33	27	35	49	60	47	11	84	32	268	
	168	16	36	47	26	62	97	28	28	33	59	59	21	0	58	11	244	
	169	18	37	50	28	70	94	38	24	33	51	60	58	5	74	16	267	
	170	18	37	48	30	70	91	33	28	40	51	60	47	11	89	37	301	
	36	237	17	39	52	22	57	76	30	29	37	48	58	44	0	67	17	247
		239	17	28	39	26	52	70	53	27	38	53	58	40	0	53	13	201
		240	14	35	39	26	50	66	58	27	40	53	59	21	0	42	11	184
		258	16	31	44	28	63	84	33	23	31	47	60	60	15	100	75	343
		259	12	30	42	25	64	87	26	25	31	48	56	36	9	55	9	220
48	260	16	37	48	29	61	84	20	27	31	49	60	19	0	43	7	213	
	261	15	39	53	26	67	95	10	23	30	46	58	70	25	68	42	298	
	262	15	40	57	25	67	87	23	26	36	50	60	75	25	100	33	318	
	298	16	29	46	26	63	86	30	26	35	45	59	24	0	53	24	241	
	300	-	-	-	24	63	82	49	28	34	43	57	53	0	80	20	-	
53	302	17	36	54	27	69	97	34	28	36	51	60	30	0	58	5	248	
	326	16	29	38	28	65	88	38	24	38	52	60	95	21	100	71	333	
	328	16	38	54	22	64	70	49	30	40	53	60	40	7	63	11	241	
	329	16	30	40	26	65	86	57	28	37	55	60	58	16	89	42	289	
	331	17	29	44	26	56	74	33	28	38	55	59	75	25	89	47	289	
	332	17	36	49	26	59	78	53	29	40	50	60	60	35	53	18	231	

APPENDIX A. (continued)

Climatic Region	Popu- lation Number	Family, MSRG 8000+	NUR Height in cm.		ACCEL Height in cm.		Relative Frost Damage	Bud Phenology, 1974				% Blue Trees		% Steel Blue Trees		Selection Index		
			At Age 2	At Age 5	At Age 2	At Age 5		5/1	5/15	5/21	5/29	At Age 5	At Age 6	At Age 5	At Age 6			
ARIZ	31A	182	18	36	46	31	64	86	34	30	38	53	60	0	0	6	0	166
		183	16	35	50	28	59	78	54	30	40	54	60	5	0	10	0	189
		184	13	42	57	27	62	88	49	29	40	52	60	0	0	17	0	197
		185	-	-	-	27	64	86	40	27	34	47	60	0	0	0	0	-
		186	16	36	46	25	55	79	49	29	37	54	60	7	0	13	0	166
	31B	187	-	-	-	26	49	70	44	28	34	53	59	0	0	0	0	-
		188	18	39	49	24	58	83	38	27	33	48	58	0	0	11	0	173
		189	16	30	47	29	57	87	23	25	32	41	52	7	0	7	0	170
		190	14	33	43	30	63	88	38	23	34	41	59	9	0	0	0	157
		191	16	34	46	25	72	90	21	26	33	46	59	6	0	11	0	175
31C	192	19	39	49	29	66	92	21	28	36	47	58	0	0	0	0	171	
	193	20	38	49	28	58	76	21	24	36	47	57	25	0	70	5	231	
	194	16	36	48	24	60	78	53	30	39	50	60	0	0	11	0	166	
	196	17	32	42	24	55	80	42	29	37	51	58	5	0	6	0	154	
	197	19	39	53	24	57	79	45	27	38	48	56	0	0	0	0	164	
31D	198	19	44	56	32	67	93	34	29	39	50	60	13	0	10	0	193	
	199	17	41	53	28	64	92	42	28	38	50	60	17	0	40	7	226	
	200	18	37	52	27	50	63	36	29	38	55	60	0	0	19	0	166	
	201	18	39	52	28	62	86	58	29	36	49	59	5	0	20	0	190	
	202	18	37	46	26	69	93	36	27	38	51	60	6	0	26	0	193	
SNMEX	9	44	18	42	56	31	69	90	33	28	39	50	60	55	10	85	20	289
	45	14	39	53	25	59	88	18	27	36	49	58	21	0	74	16	266	
	46	17	36	48	29	61	86	46	29	36	52	60	44	6	89	33	291	
	62	15	39	52	33	57	82	60	29	38	51	60	10	0	24	0	190	
	360	16	46	59	23	52	74	31	27	38	48	60	0	0	0	0	0	169
LSD (0.01)			4.4	8.8	11.7	5.9	15.3	20.1	31.9	4.8	5.1	6.0	5.7	33.9	19.6	40.9	27.2	73.8

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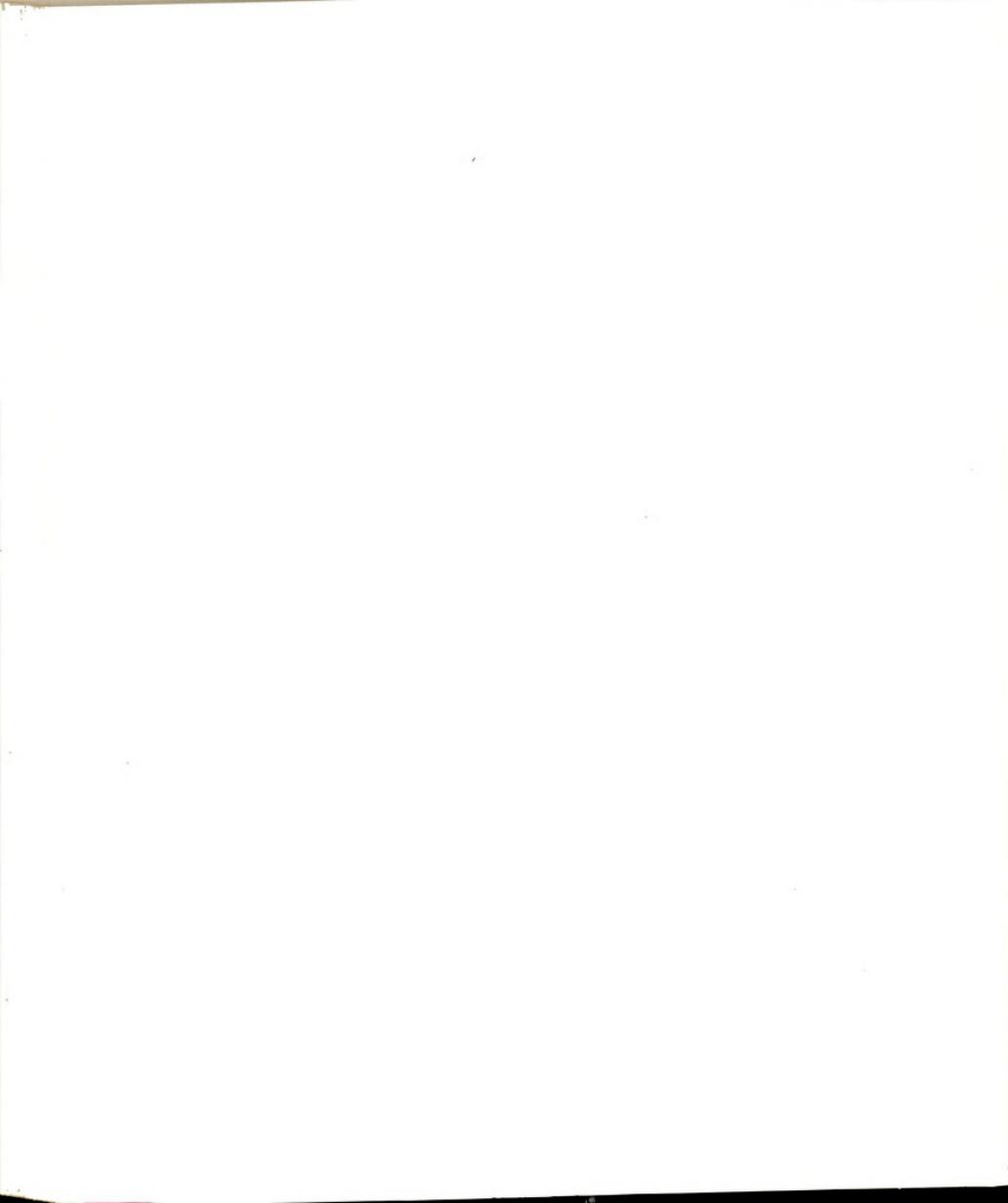
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