

xis. Hybridschwäche und Inzuchtprobleme, Klärung der Befruchtungsverhältnisse mit Hilfe der Mendelspaltung eines Aurea-Faktors bei Fichte, Resultate über Provenienzversuche und Nachkommenschaftsprüfungen und vor allem seine in die Dutzende gehenden Artikel über die Möglichkeiten und Grenzen der forstlichen Züchtung, die er im Zusammenhang mit dem „Forstlichen Saat- und Pflanzgutgesetz“ als unnachgiebiger Mahner an die Praxis, an den Gesetzgeber und Fachkollegen richtete.

Neben einem funktionsfähigen Institut in der Bundesforschungsanstalt für Forst- und Holzwirtschaft, das sein Lebenswerk darstellt, verdanken wir dem Jubilar mit, die

forstliche Züchtung und Genetik in der BRD auf den ihr gebührenden Platz gestellt zu haben. Neben unserem Glückwunsch zum Geburtstag gebührt ihm daher unser aller Dank. Mögen ihm — auch für das jetzt begonnene und von ihm geleitete Cashew-Züchtungsprogramm in Malaysia — noch viele gesunde und erfolgreiche Jahre vergönnt sein.

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Genetic Variation in Rocky Mountain Douglas-Fir

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Douglas-fir (*Pseudotsuga menziesii*) is one of the most widespread conifers of western America. Its natural range extends from Canada to Mexico and from the Pacific Ocean to the eastern slopes of the Rockies. It has been successful as an exotic, too and plantations are to be found on nearly all continents. In Michigan, where there are many vigorous specimens 50 feet or more tall, foresters are interested in Douglas-fir as a high-value Christmas tree, as an ornamental and possibly as a timber tree. In Nebraska the main interest is for Christmas trees and environmental-ornamental purposes.

RAPHAEL ZON of the U.S. Forest Service started the first provenance test in this species in 1912 when he initiated the now classical provenance tests in western Oregon and Washington. These have been reported by MUNGER and MORRIS (1936, 1942), MORRIS et al. (1957) and were remeasured recently by ROY SILEN. There are many recent genetic experiments on Douglas-fir in Oregon, Washington and British Columbia. Also, the West Coast populations have been tested in several foreign countries (SWEET, 1965, SCHÖBER and MEYER, 1954, 1955, ROHMEDE, 1956).

Arboreta in eastern United States contain almost no trees from the Douglas-fir region of the Pacific Northwest. The oaks, maples, pines, spruces, hemlocks and rhododendrons from coastal regions have been tried numerous times but have proven no match for the cold eastern winters. On the other hand, trees from the Rocky Mountains have succeeded. Thus, our interest was in the interior rather than the coastal forms of Douglas-fir.

Genetic studies of interior populations have been few. BALDWIN and MURPHY (1956) grew four Rocky Mountain seedlots for 9 years in New Hampshire. Trees from New Mexico grew the best. BYRNES et al. (1958) grew a considerable number of origins in a series of mostly unreplicated tests in Pennsylvania, in a design which precluded exact comparisons. Trees from Colorado were winter hardy but

grew more slowly than trees from northern Idaho and western Montana. GERHOLD (1966) received a duplicate set of provenances used in the present experiment and reported on their early growth in Pennsylvania. HEIT (1958) has tested a large number of western origins for 1 or 2 years in his nursery in New York. In general, he found that Arizona and New Mexico seed produced the fastest growing trees. STEVENS and LEMMIEN (1964) tested two Montana sources in southern Michigan. Their relative growth rates were nearly the same as those of similar origins grown in the present experiment at the same forest.

Materials and Methods

The present study was started in 1961 with the following objectives: determine the geographic variation patterns in interior populations of Douglas-fir, determine the best provenances for commercial planting, and provide information and breeding material for more intensive future improvement work.

In 1961 seeds were obtained from 128 native stands in western U.S. and Canada through the courtesy of the U.S. Forest Service and numerous other agencies (figure 1). The seeds were sown in East Lansing, Michigan in spring 1962, using a randomized complete block design with four replications and row-plots 1.2 m. long and 30 cm. apart. The trees were transplanted as 1-0 stock in another Michigan nursery where a 2-replicated randomized complete block design was used. In 1965 the taller origins (12 to 30 cm tall) were field-planted in three permanent test plantations in southern Michigan. The remainder were lined out for an additional two years and were field planted (as 1-2-2 stock) in 1967, in new plantations or in alternate rows within the 1965 plantations. In Nebraska, the 1-0 seedlings from the Michigan nursery were lined out in 1963 and field planted at one location in 1965.

The planting sites were free of competing woody vegetation. At each site, 2-foot strips were sprayed with amino-triazole the autumn prior to planting then sprayed with simazine immediately after planting. The weed-control was renewed annually by means of amino-triazole or simazine sprays at the Nebraska plantation; it was renewed three years at the Russ and Kellogg forests in Michigan.

The location of the planting sites is shown in figure 2. The Nebraska plantation is on level upland with a silt loam soil derived from loess. The growing season there is

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²⁾ The paper is dedicated to W. LANGNER on the occasion of his 65th birthday.

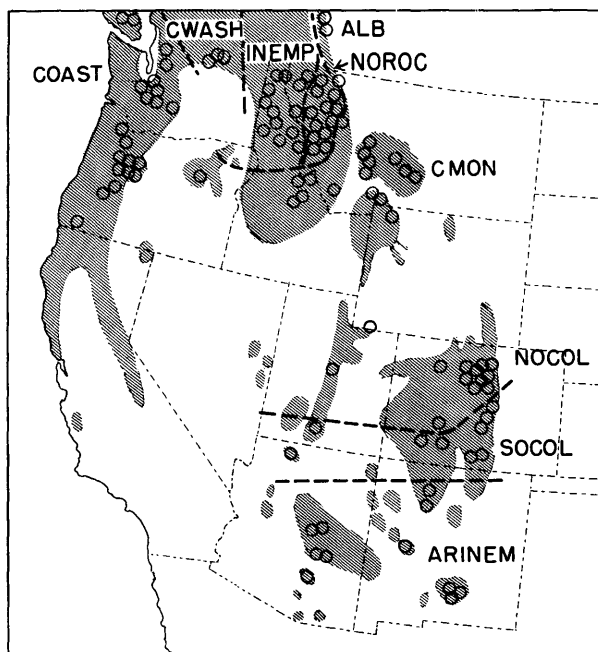


Figure 1. — Location of seed collections (black circles) and natural range (shaded) of Douglas-fir.

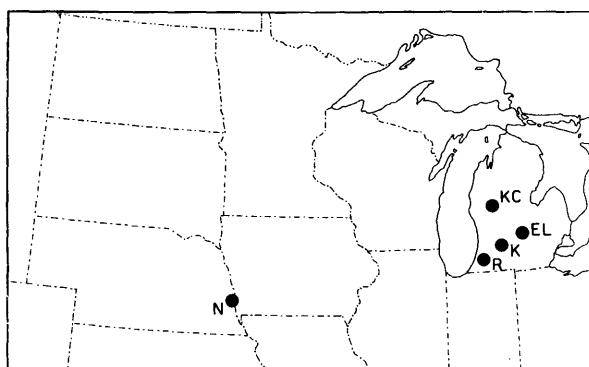


Figure 2. — Location of the East Lansing nursery (EL) and of the Camp Kett (CK), Kellogg (K), Russ (R) and Nebraska (N) plantations at which the Douglas-fir trees were grown.

nearly the same length as in southern Michigan but the precipitation-evaporation ratio is lower and the summers hotter. The Russ plantation in southwestern Michigan is on a lowlying level area with a sandy loam soil. It is subject to late-spring frosts and is not protected from the prevailing west winds. The Kellogg plantation, 60 miles northeast of Russ, is on a level hilltop with a sandy loam soil and excellent air drainage as a protection against late-spring frosts, but like the Russ plantation it is exposed to prevailing west winds. The Camp Kett plantation is 150 miles north of Kellogg and has a generally cooler climate. It has a sandy loam soil and the trees were planted near a hilltop with protection against frost and wind.

A randomized complete block design with 1- or 4-tree plots and a 6 × 6-foot spacing was used in the permanent test plantations. Because of uneven germination and nursery mortality, the number of trees per seedlot varied from few to several hundred. Well-represented origins were planted in 10 replications on each site. Origins which were under-represented were planted on two or more replications per site and on as many sites as possible; the assign-

ment of origins was such as to made the first few replications on each site the most complete.

Measurements in Michigan were made over a period of years up to age 8 from seed. All measurements were reduced to plot averages. Frost damage was estimated as the proportion (to the nearest 10 percent) of buds killed. Foliage color was estimated in terms of live-tree grades on scales of 0 to 5 or 0 to 10, the data being reduced to a uniform basis for publication. In Nebraska only height and mortality were measured.

An analysis of variance was performed on each set of measurements from a single nursery or plantation, using plot means as items. Such analyses were confined to the well represented origins. Then the standard error of a provenance mean was calculated by multiplying the standard error of a provenance mean by 3.2 (5 percent level) or 4.2 (1 percent level). To determine seedlot × plantation interaction, a pooled standard-error-of-a-difference estimate was calculated and multiplied by 3.2 or 4.2. The interaction was considered significant if origins A and B were equal in one plantation but differed by more than this amount in another plantation. Rank correlations were also used for the same purpose.

Trees from different regions grew at such different rates as to have very unequal variances. Also, the number of plots per seedlot varied. Hence overall analyses of variance were misleading sometimes. Therefore many individual "t" tests were calculated to compare particular origins or groups of origins.

Geographic and Elevational Trends

Mortality. — In Michigan, transplanting at age 1 was followed by low mortality in fast growing interior seedlots, by 25 to 50 percent mortality in very slow growing northern seedlots and by 80 to 100 percent mortality in West Coast origins which had suffered very serious top damage the previous winter. The few West Coast survivors were discarded before field planting.

Mortality rates at age 8 (5 years after planting) in the 1965 Michigan plantations were 8, 21 and 25 percent respectively in the Kellogg, Russ and Camp Kett plantations. Most deaths occurred during the first year in the field. At age 8 an additional 1 percent of the trees appeared so weak that they might die soon. Among-seedlot differences in the plantations were not different statistically.

In Nebraska, nursery mortality was more than 99 percent in the West Coast origins, 95 to 98 percent in the origins from the northern interior and about 70 percent in origins from the southern Rocky Mountains (table 4). Mortality was low in the plantation.

Within-seedlot variability. — Twenty-five trees of each of several origins were planted as permanent demonstration plots in the East Lansing nursery and given optimum care. Mortality was nil and growth was uniform in these plots. The uniformity was such as to indicate that the offspring of different trees in the same stand could differ from each mother by no more than 3 percent in height at age 8.

This 3 percent is a negligible proportion of the differences among provenances from different regions. It is also small when compared with the differences among stands from the same region. However, the average height at age 8 of one seedlot in one plantation was accompanied by a standard error of 10 percent or more, so it is impossible to compare the relative amounts of genetic variation within stands and between stands in the same general area.

Table 1. — Similarities (indicated by low numbers) and differences (indicated by high numbers) among Douglas-fir progenies grown from seed collected in different parts of the interior, based upon summation-of-difference analyses of five traits.

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Table 2. — Relative height superiority (+) or inferiority (—) of low- to high-elevation seedlots from the same region when grown in Michigan or Pennsylvania. None of the differences were significant statistically. (a)

Region of origin	Median elevation in region	Percent superiority (+) or inferiority (—) in height of low- to high-elevation seedlots from the same region				
		Nursery age 3		Michigan plantation age 8		
		Mich.	Penn.	Kellogg	Russ	Kett
	meters	percent of high-elevation mean				
C MON (b)	1,800	— 5	+ 7	— 9	—	—
NOROC	1,300	+13	— 1	+ 4	—	—
INEMP	1,100	— 7	+14	+ 5	— 1	+20
NOCOL	2,500	+ 7	—23	— 7	—	—
SOCOL	2,600	— 6	— 7	—24	—	—22
ARINEM	2,400	— 4	+ 3	— 5	—	—10

(a) The F values varied from 0.2 to 3.0. F values of 5 to 7 were needed for significance at the 5 percent level.

(b) C MON = central Montana; NOROC = northern Rockies; INEMP = Inland Empire (northern Idaho and adjacent northwestern Montana); NOCOL = northern Colorado and northern Utah; SOCOL = southern Colorado, parts of adjacent Utah and Arizona; ARINEM = New Mexico and most of Arizona.

varied between 3 and 8 cm at the same age. They approximately doubled in height the next year and were more variable as the result of transplanting. At age 3 in Michigan the seedlot averages varied from 8 to 53 cm, nearly the same as reported in Pennsylvania (GERHOLD, 1966). The West Coast origins grew even faster the first year, attaining heights of 8 to 15 cm. Because of persistent winter injury, their relative growth rate decreased by the third year.

Recovery from field planting required 1 to 2 years in Michigan, 3 years in Nebraska. Only then was there a resumption of the rapid growth typical of the seedbeds. Most trees doubled in height between ages 6 and 8 from seed.

Among the Michigan plantations, that at the Kellogg Forest, which received good weed control and was on high ground, grew fastest. The Camp Kett plantation, also on high ground but with less effective weed control, grew 10 percent slower. Growth was about 40 percent less on the frost-prone Russ site than at Kellogg.

In Michigan, the fastest growing interior seedlots were from two widely separated parts of the range (table 3). The ARINEM group from Arizona and New Mexico was tallest at all ages. The SOCOL group was second tallest at age 3 but its relative growth rate decreased in later years so that second place was taken by the INEMP group from northern Idaho and adjacent northwestern Montana. The ALBERTA and Central MONTANA (also including scattered seedlots from Wyoming and northeastern Oregon) groups were the shortest at all ages.

At age 3 all interior groups were of approximately the same height in Michigan as in the Pennsylvania nursery reported by GERHOLD (1966). Also, all groups grew at relatively similar rates (not distinguishable statistically) in the three Michigan plantations.

The northern groups maintained the same relative growth rates from nursery to plantation in Michigan. SOCOL trees, however, lost their early growth superiority over INEMP trees, probably because of greater frost and winter cold damage. ARINEM trees also lost some of their early growth superiority. They were 50 percent taller than INEMP trees in the nursery but only 20 to 30 percent taller at age 8 in

the Michigan plantations. Measurements made in two successive years indicate that these downward trends of southern trees may continue.

Rank correlation analyses were made to determine the degree to which individual seedlots within groups maintained their superiority in different nurseries or in different plantations in Michigan. None were significant at the 5 percent level. In other words, individual seedlots grew at different rates in different places. We do not know whether this interaction has a large enough genetic component to be considered in planting recommendations.

Survival and growth rate in the Nebraska plantation are shown in table 4. The ARINEM origins grew more than twice as fast as any others although the SOCOL and NOCOL origins grew at nearly the same rate as in Michigan. The INEMP and C WASH origins grew faster than other northern origins but did not survive or grow well enough to be considered for general use.

Injury from frost and cold. — Douglas-fir is subject to damage by the frequent late-spring frosts in Michigan. Some trees suffered injury in four of their eight years. Death of many buds made the trees unsightly but the growth loss was not proportional to the amount of damage. Because terminal buds elongate last, they suffered the

Table 3 — Relative height of Douglas-fir from different geographic regions at ages 3 (Michigan and Pennsylvania) and 8 (Michigan).

Region of origin	Relative height, as a percent of that of the INland EMPIre seedlings, when grown at				
	Nursery in		Permanent plantation at		
	Mich.	Penn.	Kellogg Forest Mich.	Russ Forest Mich.	Camp Kett Mich.
	Age 3	Age 3	Age 8	Age 8	Age 8
ALB	58	58	45	—	—
C MON	51	50	46	—	62
NOROC	67	66	92	85	85
INEMP	100	100	100	100	100
C WASH	108	86	80	79	86
NOCOL	79	74	65	74	91
SOCOL	131	121	91	74	89
ARINEM	165	154	132	117	130
COAST	135	177	—	—	—
C ORE	121	147	—	—	—
Absolute mean height of INEMP trees, cm	21	23	85	63	74

Table 4. — Survival and growth of Douglas-fir of different geographic origins in Nebraska.

Region of origin	Surviving		Height at age 8	
	Origins	Trees	Trees	from seed
	no.	no.	%	cm
ALB	2	2	2	30
C MON	1	1	1	18
NOROC	4	4	1	34
INEMP	5	15	4	52
C WASH	2	5	3	67
NOCOL	3	33	22	58
SOCOL	4	25	17	73
ARINEM	6	99	26	183
COAST	0	0	0 (a)	—

(a) 0 of 590 planted

least damage. Near-normal leader growth could occur even on severely injured trees.

Recently expanded buds suffered most when below-freezing temperatures occurred. They were more sensitive than dormant buds or twigs with fully expanded leaves. Also, light frosts which hugged the ground caused most damage to the smallest trees. Because small northern trees leafed out several days earlier than southern ones, they might be damaged much more severely by a light frost on May 10. But the next season they might escape damage from a May 20 frost which hurt southern trees.

Because of these conflicting trends, the damage pattern varied from year to year and from plantation to plantation. Of 11 ARINEM seedlots grown at Kellogg Forest, No. 1647 suffered the least damage in 1968 and next to the most damage in 1969. The changes in damage pattern are evident in table 5. ARINEM seedlots suffered little from a late-May frost which occurred at the start of the second growing season, soon after the seedlings had been transplanted. Their normal late start of growth had been delayed even more by the transplanting. But in later years the ARINEM and other southern groups suffered more injury than northern trees.

A frost in late September of the first growing season did not hurt the foliage of interior origins but caused severe browning of the late-season growth of the COAST and C ORE trees. Peculiarly, these trees withstood the late-May frost of the next season (table 5).

Injury from winter cold took the form of bud death, needle burn and occasional twig dieback. It was estimated to the nearest 10 percent as the proportion of leaves killed (table 5).

The COAST and C ORE seedlots suffered the most winter injury whether planted in Nebraska, Michigan or Pennsylvania.

Of the three Michigan plantations, that at the Russ Forest received the most winter injury — damage was too slight to warrant measurement at the other two sites. There was an interesting difference in damage pattern between the nursery and the Russ Forest plantation. The NOCOL and SOCOL origins from the southern Rocky Mountains

suffered little damage when young but suffered more damage than northern origins when older.

Date of bud set. — Date of bud set was studied intensively the first year only, when numbers of trees having terminal buds were counted at intervals from early August to early October. There was more than a 2-month difference between the earliest northern origins and the latest southern or coastal ones (table 5). Date of bud set was the most diagnostic characteristic for the ARINEM, SOCOL and NOCOL groups of origins; those groups showed little overlapping in this trait.

There was generally good correspondence between the bud set and winter hardiness data. Evidently trees which formed buds earliest were prepared best for the coming winter. There was, however, an interesting and unexplained exception. SOCOL trees, which were a month later than northern trees, suffered significantly less winter damage while in the nursery. Later, as expected, they proved less hardy than the northern origins.

Foliage color. — Leaf color was measured in terms of live-tree grades in the Michigan nursery and at the Kellogg Forest plantation. Although color varied from blue to very green within some 4-tree plots, there was enough consistency that some seedlots could be characterized as entirely green and others as entirely blue. The following list shows the average condition in the interior groups of seedlots:

ALB — dark green in nursery, moderately blue at age 8, uniform within seedlots

C MON, NOROC, INEMP, C WASH — uniformly dark green,

NOCOL — individual seedlots were uniform but varied from light green to intermediate blue-green, with the average color similar to that in trees from the northern Rockies,

SOCOL — nearly all seedlots varied from blue-green to very blue-green but a few were indistinguishable from northern origins,

ARINEM — uniformly among the bluest.

Table 5. — Damage from growing-season frosts and winter cold, and date of first-year bud set of Douglas-fir of different geographic origins grown in Michigan and Pennsylvania. (a)

Region of origin	Damage from frost occurring in late May		Damage from winter cold			Date of bud set, Mich, Age 1
	Mich. Age 2	Kellogg, Russ, Camp Kett, Mich. Ages 7 and 8	Nursery in		Russ Forest.	
			Mich. Age 3	Penn. Age 3	Mich. Ages 5 to 8	
	% of trees	% of buds	% of leaves			
ALB	18	—	13	9	—	Aug. 10
C MON	24	23	23	8	—	Aug. 10
NOROC	33	21	24	10	14	Aug. 12
INEMP	44	23	34	8	19	Aug. 18
C WASH	44	23	26	8	19	Aug. 21
NOCOL	32	34	6	2	20	Aug. 22
SOCOL	37	43	9	2	24	Sept. 11
ARINEM	10	35	32	6	29	Oct. 5
COAST	0	—	85	32	—	After Oct. 5
C ORE	2	—	80	20	—	Sept. 18

(a) The differences among groups were statistically significant at the 1 percent level in all characteristics. The interaction between nursery and plantation performance was also significant at the 1 percent level.

Twig color. — Young twigs were characteristically green. That was true of all northern seedlings. However, seedlings of the NOCOL, SOCOL and ARINEM groups from the southern Rocky Mountains were variable. Some seedlots were uniformly green but in others up to 90 percent of the trees had reddish-purple twigs at age 1. Although the trait was studied intensively only in the nursery, casual observations indicate that the color remained unchanged until age 8.

The twigs of most COAST and C ORE seedlings were orange-red during the first year in the nursery. This color was present also in one of the four seedlots from central Washington.

Evolutionary Considerations

Although many trees grew well, mortality was higher and growth more variable in this experiment than in similar experiments with pines and spruces. Commercial growers in eastern United States have had similar experience. This indicates that individual Douglas-fir trees are especially sensitive to adverse site conditions and that adaptation of a population to a very different new environment must be by genetic change. If this is true, it explains why populations from different regions exhibit very large differences in growth rate and date of bud set.

The average number of hours of sunshine per year varies from 3,200 to 3,800 in Arizona and New Mexico, from 2,400 to 2,600 in Montana and northern Idaho. The average annual relative humidity varies from 25 to 40 percent in Arizona and New Mexico, from 45 to 55 percent in Montana and northern Idaho. The blue foliage of trees from the southern Rocky Mountains probably represents an adaptation to the dry sunny conditions found there. The blue color is due to a waxy covering which can serve as a protection against desiccation and against inactivation of growth hormones by the intense solar radiation. Similar protective mechanisms consisting of pubescence, surface irregularities of the leaves or waxes, have developed in other trees (*Pinus ponderosa*, *Abies concolor*, *A. lasiocarpa* var. *arizonica*, *Picea pungens*, *Pinus strobiformis*) inhabiting the southern Rockies as well as in desert shrubs.

Adaptation to the drouthy conditions of the Arizona and New Mexico forests was evident also in the relatively low mortality and excellent growth of ARINEM trees in the prairie region of Nebraska. Whereas survival was equally good for many groups in the more mesophytic Michigan plantations, only trees from the southern Rockies survived adequately in the prairie plantation.

The Douglas-fir seed collections were from an elevational range of 1,700 to 2,700 meters in Arizona and New Mexico, and of 2,300 to 3,100 meters in the states of Utah and Colorado immediately to the north. The lower elevation and more southerly location combine to produce a much warmer climate for Douglas-fir in the ARINEM than in the SOCOL region. Natural selection resulted in adaptation to the very different conditions, resulting in an ARINEM type which grows almost one month longer and 50 percent taller in Michigan (150 percent taller in Nebraska) than SOCOL trees.

In the north, Douglas-fir grows at the lowest elevations (down to 600 meters) in the Inland Empire of eastern Washington, northern Idaho and adjacent northwestern Montana. Douglas-fir grows in a warmer and moister climate there than it does farther south or east. Adaptation to the more favorable climate resulted in INEMP trees with faster growth than NOROC and C MON trees.

The coastal and interior populations are well separated geographically except in British Columbia and northern Washington. They are also very distinct genetically although there is a possibility that intensive sampling in British Columbia would reveal intergrades. The populations inhabiting the northern and southern interior regions are also well separated geographically (figure 1) and almost distinct genetically (table 1).

The ARINEM and SOCOL groups were very distinct genetically in the Nebraska plantation although there was some overlap according to the Michigan data. The other group distinctions within both the northern interior and southern interior populations were more or less arbitrary.

Practical Recommendations

The differences among seedlots were large, but so were differences caused by the environment. A grower who wants to take full advantage of the seed origin data must practice good cultural methods.

Growth rate, hardiness and foliage color are the most important considerations in choice of seed for ornamental use or Christmas tree plantations. No one type of seed will be best for all conditions, and a grower should base his decision partly on performance in studies such as this and partly on local climatic conditions.

ARINEM trees had the most consistent blue color and were the tallest, but suffered rather heavy frost and winter damage in the Michigan plantations. They are undoubtedly the most suitable for eastern Nebraska and probably are the most suitable for the warmest parts of southern Michigan and for milder climates such as found in Pennsylvania or Kentucky. SOCOL trees from southern Colorado had the same desirable blue color but grew less rapidly and suffered more frost damage than the ARINEM trees. They are planted commonly at the present time but seem to possess no special advantage for eastern United States.

The northern origins are probably the most hardy even though the experimental data are contradictory on this point. Their color is good, although not as desirable to most people as the blue foliage of the southern origins. They are probably the safest for use in northern areas. Of these, the INEMP origins are the fastest growing and are the only ones which can be recommended for large-scale planting. Christmas-tree culture is not apt to be profitable in areas suited only to the slower growing NOROC and C MON origins.

There is enough variability within regions that planters could probably achieve an additional 10 to 20 percent gain in growth rate by using seed from specific stands. Unfortunately, however, such superior stands can not yet be identified except as they have been tested in this or a similar experiment, and those stands do not suffice for large-scale seed production. The present data indicate that a grower in eastern United States will obtain no advantage by specifying that his seed be collected from a particular elevational zone, aspect or soil type within a region. We do not know whether selection of the best parental trees in a locality will result in better seedlings.

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