

Zusammenfassung

Von *Prunus serotina* sind im Gewächshaus von 30 Samenherkünften aus dem gesamten Verbreitungsgebiet in Canada und den U.S.A. Pflanzen angezogen worden, die nach 9 bis 12 Monaten auf ihre Sproß- und Wurzelsysteme untersucht wurden. Es konnten 2 Gruppen von Herkünften unterschieden werden: (1) 8 Herkünfte aus dem südlichen Gebiet und (2) 22 Herkünfte aus den mittleren und nördlichen Gebieten, die jeweils ähnliche Merkmale aufwiesen. — Alle Provenienzen zeigten nur relativ kurze Pfahlwurzeln. Die Seitenwurzeln der südlichen Herkünfte waren relativ dünn, und von der Pfahlwurzel ging eine dichte Masse feiner Wurzeln aus. Die anderen Herkünfte hatten größere Seitenwurzeln, dagegen weniger feine Wurzeln. — Die Sprosse der südlichen Herkünfte waren im allgemeinen länger, kräftiger und hatten eine größere Anzahl Seitenknospen als die anderen. Innerhalb jeder Gruppe war die Variation erheblich; sie stand aber mit Breitengrad, Höhenlage oder Klima der Herkunft in keiner Beziehung. — Das Gewicht je Längeneinheit des Sprosses, der Pfahlwurzel und der größeren Seitenwurzeln war bei den südlichen Herkünften signifikant höher als bei den anderen. Verursacht wird dieser Unterschied bei der ersten Gruppe

wahrscheinlich nur durch die größere Dichte des verholzten Materials.

Literature Cited

BROWN, J. H.: Variation in roots of greenhouse grown seedlings of different Scotch pine provenances. *Silvae Genetica* 18: 111–117 (1969). — CECH, F. C., and J. H. KITZMILLER, JR.: Geographic variation in seed and seedling characteristics of black cherry (*Prunus serotina* EHRH.). Proc. 15th Northeast For. Tree Improvement Conference: 53–60, 1968. — GENYS, J. B.: Black cherry seedlings differ in height depending on their seed origin in Maryland. Maryland Univ. Nat. Resources Inst. For. Res. Note 63–69, 1961. — GODDARD, R. E., and R. K. STRICKLAND: Geographic variation in wood specific gravity of slash pine. *Tappi* 45: 606–608 (1962). — HOUGH, A. F.: Silvical characteristics of black cherry (*Prunus serotina*). Northeastern Forest Exp. Sta. Pap. 139, 1960. — KITZMILLER, J. H. Jr.: Geographic variation in black cherry. Thesis, Master of Science in Forestry, West Virginia University. — KRAMER, P. J.: The absorption of water through suberized roots of trees. *Plant Phys.* 21: 37–41 (1946). — LITTLE, E. L., Jr.: Check list of native and naturalized trees of the United States (including Alaska). U.S.D.A. Agr. Handbook 41, 472 pp., 1953. — McVAUGH, R.: A revision of the North American black cherries (*Prunus serotina* EHRH., and relatives). *Brittonia* 7: 279–315 (1951). — ZOBEL, B., E. THORBJORNSEN, and F. HENSON: Geographic, site and individual tree variation in wood properties of loblolly pine. *Silvae Genetica* 9: 149–158 (1960).

Altitudinal Variation in Photosynthesis, Growth, and Monoterpene Composition of Western White Pine (*Pinus monticola* Dougl.) Seedlings

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Introduction

Evidence for genetic differentiation within tree species is common but much less is known about the inheritance of morphological and physiological responses of species to environmental gradients, such as those found in mountainous topography. Many previous studies of intraspecific variation have involved widely separated portions of a species' range. The objective of this investigation was to determine the pattern of genetic variation among western white pine seedlings grown from seed collected at different elevations within four areas of northern Idaho — a small portion of the total range of the species. Northern Idaho is characterized by steep and broken topography, with wide climatic and altitudinal ranges and associated habitat variations. Western white pine occurs over a broad elevational belt from 1000 to 6000 feet, in irregular, often attenuated bodies following the more moist creek bottoms, lower benches and flats, and northerly slopes (WELLNER, 1962). Thus there exists opportunity for selective forces to act upon populations separated by relatively short distances. The existence of local ecotypes in western white pine has been reported previously by SQUILLACE and BINGHAM (1958).

The seed used in our work was collected from 24 parent trees located in altitudinal plots of one-half to one acre

each (Figure 1). A portion of the seed was sown in the fall of 1965 in the Michigan State University Nursery at East Lansing. During 1968 and 1969 the following seedling characteristics were studied: (1) cortical oleoresin monoterpene concentrations; (2) photosynthesis and respiration; (3) total height and weekly growth throughout the growing season. The methodology and results of the three studies are reported here.

Monoterpenes

Large differences in terpenoid levels both within and between plant species have stimulated their extensive use in biochemical systematic studies (ALSTON and TURNER, 1963; HANOVER and FURNISS, 1966; and ZAVARIN et al., 1966). HANOVER (1966a) demonstrated strong genetic control of *Pinus monticola* monoterpene concentrations, and suggested their use as markers for population genetic studies involving diverse environmental gradients.

In their study of cortical oleoresin in trees from 12 geographic sources of slash pine (*Pinus elliottii*), SQUILLACE and FISHER (1966) found significant differences in myrcene, β -pinene, and β -phellandrene. Both β -pinene and β -phellandrene showed geographic variability patterns very similar to those expressed for height, needle length, and stomata number.

TOBOLSKI and HANOVER (1971) reported significant differences in 11 cortical monoterpenes collected from trees

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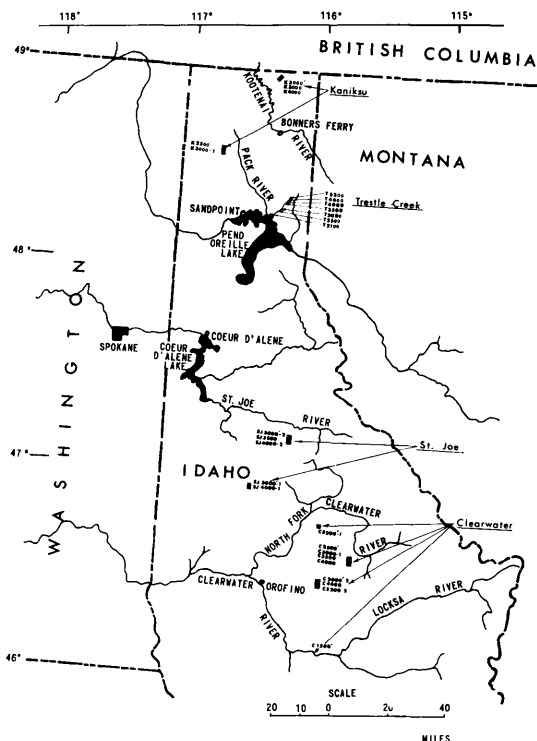


Figure 1. — Location of western white pine seed source plots.

representing 108 European and Asian seed sources of Scotch pine (*Pinus sylvestris*) grown in Michigan. The terpene 3-carene was absent in most southern populations but increased northward to a high of 63 percent of the monoterpene fraction. α -pinene also exhibited wide geographic variability, but in the opposite direction; Spanish sources showed 69 percent α -pinene but some Scandinavian sources were as low as 5 percent.

Materials and Methods

All collections and analyses of oleoresin were done between May and September, 1968, when the seedlings were two years old. The seed sources used are shown in Figure 1. Because slight variation can exist in monoterpene composition among different aged tissues (HANOVER, 1966 b), sampling was limited to the one-year-old main leader. The cortex was sliced with a razor blade and the resulting oleoresin exudate was quickly drawn into a 50 μ l glass capillary tube, which was then placed in a centrifuge tube, sealed and refrigerated until analyses were made, usually within several hours. A total of 239 trees were sampled.

The analysis of monoterpenes was done by gas-liquid chromatography using a hydrogen-flame detector according to the following procedure: Before injection, each sample of oleoresin was diluted with 30 μ l of acetone and a 2 μ l aliquot of this acetone-resin mixture was injected. Separations were obtained with a $\frac{1}{4}$ " \times 8' stainless steel column packed with 10 percent polypropylene glycol on Chromosorb G-AW. Temperature of the injection port was 195° C, hydrogen flame detector, 200° C, and helium flow rate was 130 ml/min. The identification of individual terpenes was determined by comparing retention times of unknowns with those of known compounds, and by peak enhancement of unknowns using standards. The concentrations of the monoterpenes were expressed as a proportion of the oleoresin.

Results and Discussion

Variation. The terpenes which were analyzed are shown below with their respective ranges and mean values:

Monoterpene	Range in tree values	Range in source means
		Percent
α -pinene	2.7 — 34.4	10.9 — 15.0
β -pinene	4.4 — 73.4	31.2 — 38.3
3-carene	0.0 — 23.9	1.5 — 4.1
limonene	0.4 — 10.1	2.1 — 3.4
β -phellandrene	0.3 — 10.8	1.8 — 3.6

Other monoterpenes detected but not included in the analysis because of their very low concentrations are camphene, γ -terpinene, myrcene, and terpinolene.

Simple correlation analyses between individual terpenes and elevation of the seed source showed no significant relationship. An analysis of variance was done using each altitudinal plot as a source of variation. Significant differences between sources were found in the concentrations of α -pinene and limonene but the variation pattern appeared to be random and unrelated to altitudinal or latitudinal differences except for those shown in Table 1. α -pinene and limonene have varied with location in several other species. For example, significant variation in α -pinene among three populations of *Pinus radiata* in California was reported by BANNISTER *et al.* (1962). HANOVER and FURNISS (1966) distinguished three populations of Douglas-fir on the basis of α -pinene and limonene.

Because neither elevation nor latitude and their associated environmental gradients appear to be related to the pattern observed, there is a possibility that terpene synthesizing ability is non-adaptive relative to other growth traits or to the environmental gradients with which we are working. Other recent work (TOBOLSKI and HANOVER, 1971) also supports this hypothesis. Without additional evidence for linkage and natural selection, variation is probably best explained by genetic drift. Random fluctuation and stabilization of gene frequencies could occur in the smaller population subunits of the species' range. Changes in a non-adaptive trait such as terpene concentration could accumulate in each of these subunits. The results of this study, therefore, may be a measure of the impact of genetic drift on intraspecific differentiation over varying geographic distances.

TUKEY's multiple range test showed that significant differences in both α -pinene and limonene exist among, but not within, the four geographic areas of Kaniksu, St. Joe, Trestle Creek, and Clearwater (Table 1). Significant dif-

Table 1. — Seed sources that are significantly different from each other by TUKEY'S test of α -pinene and limonene concentrations.

Seed Sources Compared (Geographic area and elevation of plots)	Difference Between Sources
	percent
α -pinene:	
St. Joe 3000' and Kaniksu 4000'	4.1**
St. Joe 3000' and Clearwater 2500'	3.9*
St. Joe 3000' and Trestle Creek 3500'	3.5*
Limonene:	
St. Joe 3000' and Kaniksu 4000'	1.3*
Clearwater 5200' and Kaniksu 4000'	1.3*

** Significant at the 1% level.

* Significant at the 5% level.

ferences in α -pinene concentration were found between the St. Joe 3000' plot and three other plots in each of the other geographic areas: Kaniksu 4000', Clearwater 2500', and Trestle Creek 3500'. In limonene, the Kaniksu 4000' stand was significantly different from two distant populations, St. Joe 3000' and Clearwater 5200'. The greatest genetic differences were found between Kaniksu 4000' and St. Joe 3000', both from near the northern and southern limits, respectively, of the range sampled. These two sources differed in both limonene and α -pinene levels.

These results suggest that populations must be widely separated to diverge significantly in concentrations of the monoterpenes. It would appear that in western white pine few cross-fertilization barriers exist which isolate contiguous populations from each other to increase the effectiveness of random fixation and loss of genes.

Photosynthesis and Respiration

One primary requirement for the evolutionary success of a population of forest trees is that it be capable of making reasonably efficient use of the energy available in its natural habitat. Photosynthesis provides the original source of chemical energy and the primary substrates to drive all other biological activity. In each particular environment, photosynthetic efficiency therefore is a vital factor in determining the success of a given population. The question may be asked: Does the photosynthetic efficiency differ within species among populations from contrasting habitats as a result of genetic adaptation?

Genetic differences in photosynthesis have been demonstrated in several plant species. MILNER and HISEY (1964) showed that saturation light intensities of *Mimulus cardinalis* from California increase with elevations of the native habitats. BILLINGS *et al.* (1961) found that *Oxyria digyna* plants from an alpine race were clearly more effective in fixing CO₂ and in utilizing high light intensities than a sea-level race. BJÖRKMÄN and HOLMGREN (1963) reported that races of *Solidago virgaurea* from shaded habitats were able to utilize weak light more efficiently than races from exposed habitats. They were also able to relate the temperature optimum for net photosynthesis to the climatic origin of the race. BOURDEAU (1963) demonstrated that *Pinus strobus* seedlings from southern origins were less efficient at low temperatures than more northerly seedlings. KRUEGER and FERRELL (1965) found a higher light compensation point at 20° C for Douglas-fir seedlings from Montana than for seedlings of the same species from Vancouver Island.

The purpose of the following photosynthetic experiments was to compare short term physiological responses of seedlings from the different altitudinal seed sources.

Materials and Methods

Photosynthetic parameters were measured for seedlings placed into four separate controlled-environment chambers constructed of acrylite. Each chamber was approximately 50 liters in volume and was surrounded by a water jacket necessary to stabilize temperature. Four 300-watt reflector spot bulbs were immersed in a water jacket above each chamber. Additional temperature and light control was provided by a large Sherer-Gillette controlled environment room, which housed all four of the acrylic chambers. A Beckman infrared gas analyzer Model 215 and a Servitor recorder were used to detect and record CO₂ concentration changes. Small Rotron fans circulated air inside the chambers, and a Cole-Parmer variable speed pump maintained

a flow rate of 900 ml/min in a closed system. A Drierite (CaSO₄) desiccant column removed water vapor from the air flowing into the gas analyzer.

Dormancy phase measurements. During February and March, 1969, comparisons of photosynthetic response to 22° C and 6600 ft-c were made between high (5200') and low (2100') Trestle Creek seed sources, and between two widely separated seed sources, Clearwater 3500' and Kaniksu 3500'. Prior to each analysis, four seedlings — two from each of the two seed sources to be compared — were picked from the nursery at random, brought into the laboratory, and placed in the four acrylic chambers. Polyethylene bags were wrapped completely around the seedling pots to decrease the effect of evaporation and soil respiration. Net respiration was measured under continuous light for four hours. Dark respiration was measured for two hours immediately following the light period.

Growth phase measurements. From April to July, daily measurements were made to compare seedlings from three sources, Trestle Creek 2100', 3500', and 5200', in a completely randomized design. Two seedlings representing the same source were placed together inside one of the four chambers. By using all four chambers, measurements could therefore be made on eight trees simultaneously. A minimum of 16 trees from each Trestle Creek source were measured under each environmental regime. Light intensities were adjusted to 1400 ft-c, 4600 ft-c, or 6600 ft-c, and temperatures were maintained at either 22° C or 28° C. The rate of depletion of CO₂ from 550 ppm to the compensation point was used as the measure of net photosynthesis.

Results and Discussion

Photosynthesis of Dormant Seedlings. No differences in photosynthetic ability were found between the high- and the low-elevation Trestle Creek sources in their response to constant conditions of 6600 ft-c and 22° C. Comparison of eight seedlings from the most northerly source, Kaniksu 3500', with eight seedlings from the southernmost seed source, Clearwater 3500', also failed to show significant differences in net respiration. Seedlings brought inside and immediately measured displayed no net photosynthesis. Several trees were exposed to varying lengths of preconditioning at 22° C which showed that at least 72 hours were required for most seedlings to achieve positive net photosynthesis at 22° C and 6600 ft-c. BOURDEAU (1959) brought four-year old Scotch pine seedlings indoors in March and found that three out of nine reached positive rates of net photosynthesis in less than 24 hours, and the balance after less than 48 hours. This response is comparable to that shown by western white pine during March. It should be

Table 2. — Analysis of variance of net photosynthesis by three Trestle Creek sources at 1400 ft-c; 500, 450, 400, and 350 ppm CO₂; 22° and 28° C; based on 24 pairs of trees.

Source of Variation	Percent of Total Variance
Source (2100', 3500', and 5200')	5**
Temperature (22° C and 28° C)	22**
CO ₂ (500, 450, 400, and 350 ppm)	18**
Source × temperature	2
Source × CO ₂	0
Temperature × CO ₂	0
Source × temperature × CO ₂	0
Error	53

** Significant at the 1% level.

Table 3. — Analysis of variance of net photosynthesis of juvenile foliage by Trestle Creek sources at 2100', 3500', and 5200', at 500, 450, 400, 350 ppm CO₂, 22° C, and 1400 ft-c.

Source of Variation	Percent of Total Variance
Source (2100', 3500', and 5200')	9**
CO ₂ (500, 450, 400, and 350 ppm)	26**
Source × CO ₂	0
Error	65

** Significant at the 1% level.

emphasized that the response of quiescent seedlings during winter to the unusually high (for winter) temperature of 22° C gives no sure indication of the net photosynthetic capacity at colder, more natural temperatures.

Photosynthesis During Active Growth. A factorial analysis of Trestle Creek 2100', 3500', and 5200' sources at three light intensities showed that the overall effect of seed source on photosynthetic efficiency was non-significant. Genetic differences were found, however, at the lowest light intensity, 1400 ft-c, at both 22° C and 28° C. (Tables 2 and 3). Under these conditions, seedlings from Trestle Creek 2100' showed less photosynthetic efficiency when compared to the progeny of Trestle Creek 3500' and 5200' (Figure 2). DECKER (1947) has pointed out that, although carbon dioxide concentrations may be the same at high altitudes and low altitudes, the partial pressure decreases with decreasing atmospheric pressure, and this decreases the actual amount of CO₂ diffusing into the leaf. BILLINGS *et al.* (1961) demonstrated that alpine plants of *Oxyria digyna* were more effective in fixing carbon dioxide than sea-level plants of the same species. In a similar way, perhaps the Trestle Creek 3500' and 5200' sources have evolved a more efficient photosynthetic system in order to compensate for low CO₂ partial pressures. This adaptation

seems unlikely, however, because of the lack of significant source differences at 4600 and 6600 ft-c. It is possible, however, that there are differences in the photosynthetic mechanism which are expressed only when plants are actually grown at high altitudes.

In all sources, a shift temperature from 22° C to 28° C resulted in a marked decrease in net photosynthesis (Figure 2). It should be apparent, therefore, that the optimum temperature at 1400 ft-c for rapidly growing western white pine seedlings must be lower than 28° C, and perhaps is even less than 22° C. Additional studies are needed to determine the effects of varying temperature regimes on photosynthesis of altitudinal populations.

Effect of CO₂. Figure 2 illustrates that photosynthetic uptake varied directly with carbon dioxide concentration from the compensation point (where net CO₂ uptake is zero) to 500 ppm CO₂; an orthogonal analysis indicated that a linear line best describes this response. Figure 2 also demonstrates the importance of high light intensities in modifying the net CO₂ absorption; the slope of the photosynthetic-response lines to increased CO₂ levels is greater for high than for low light intensities. This effect has been described in several tree (KRAMER and KOZLOWSKI, 1960) and crop (LEOPOLD, 1964) species. It is clear that small changes in atmospheric concentrations of CO₂ could cause large changes in rates of photosynthesis, especially at the high light intensities occurring in the field.

Effect of Light. Light curves drawn from the data presented in Figure 2 indicated that, even at 6600 ft-c, the seedlings were far from light-saturated. This was particularly evident at high CO₂ concentrations; the saturation light intensity appeared to be much lower at low CO₂ levels. The curves were similar to those derived from BOURDEAU'S (1963) experiments with three-year-old *Pinus*

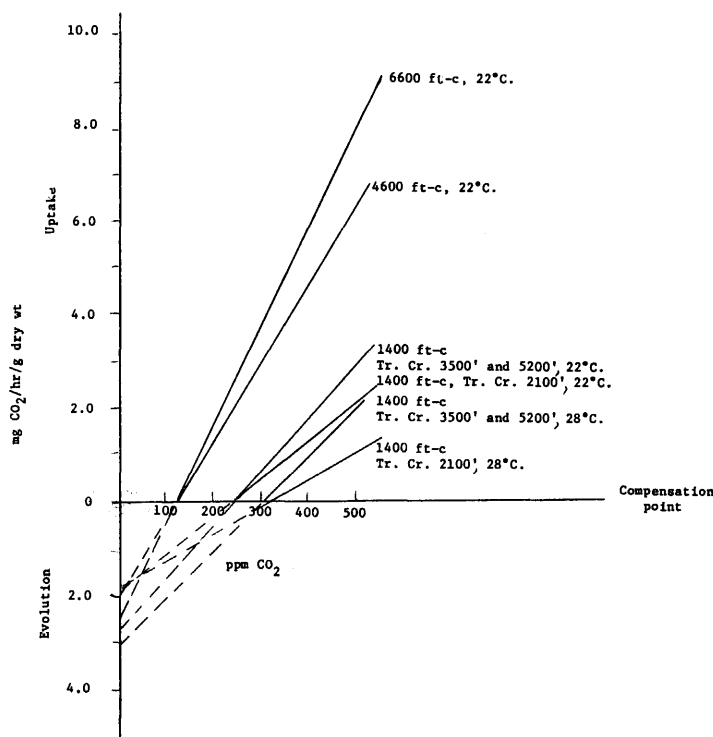


Figure 2. — The rate of net photosynthesis and respiration of western white pine seedlings as a function of CO₂ concentrations at different light intensities and temperatures.

Table 4. — Estimated photorespiration ($\text{mg CO}_2 \cdot \text{hr}^{-1} \cdot \text{g}^{-1}$ dry wt) of 48 western white pine seedlings from three sources in relation to light intensity and temperature.

(ft-c)	Trestle Creek 2100'		Trestle Creek 3500' and 5200'	
	22° C	28° C	22° C	28° C
Dark	2.5	2.8	2.5	2.8
1400	1.9	1.9	2.7	2.9
4600	1.9		1.9	
6600	2.4		2.4	

strobis, except that *Pinus monticola* appeared less efficient under illumination of less than 2000 ft-c.

Photorespiration. In order to estimate photorespiration, the photosynthetic response curves were extrapolated to zero CO_2 concentration. Although it is simple and easy to apply to photosynthetic data, this method does have major limitations. One serious error may result from assuming that the straight line relationship which exists above the compensation point continues to be linear below this point. BRIX (1968) compared the extrapolation method with a technique involving CO_2 evolution into a CO_2 -free air-stream, and presented evidence that the slope of the line does in fact change below the compensation point. The accuracy of the method is also dependent on how large the stomatal and internal diffusive resistance are together with the "resistance" to refixation of evolved CO_2 (BRAVDO, 1968).

The estimates of photorespiration (Table 4) did not help explain the inefficiency of low-elevation sources at low light intensities. According to ZELITCH (1966), inefficiency in net photosynthesis is usually caused by high rates of photorespiration. However, photorespiration as measured by the extrapolation method was lower in the less efficient source, 2100' at both 22° C and 28° C (Table 4). More extensive experiments on photorespiration are required to define temperature and seed source effects at all light intensities.

CO_2 Compensation Point. A commonly used measure of photosynthetic efficiency is the CO_2 compensation point, or the atmospheric concentration of CO_2 at which respiratory release of CO_2 from illuminated leaves is in balance with photosynthetic CO_2 fixation. Seed source proved non-significant in determining the compensation point at three light intensities and two temperatures. At 22° C, a change in light intensity from 1400 ft-c to 4600 ft-c markedly lowered the compensation point, but a further increase from 4600 to 6600 ft-c caused no significant change (Table 5).

Raising the temperature from 22° C to 28° C increased the compensation point, at both high and low light intensities. Because a decrease in total photosynthesis with the increase from 22° C to 28° C appears unlikely (KRAMER, 1958), temperature must be raising respiration more than photosynthesis. This explanation has been given for similar

Table 5. — Mean CO_2 compensation points of western white pine seedlings from Trestle Creek, Idaho seed source. Twelve seedlings were measured in April and 48 seedlings in late May and June.

Light intensity	22° C		28° C	
	April	Late May and June	April	and June Late May
ft-c	ppm CO_2			
1400	332	251	553	305
4600	— ¹⁾	138	—	—
6600	265	141	313	—

¹⁾ A dash indicates no measurements were obtained.

temperature responses by DECKER (1959) for *Mimulus* and by BRIX (1968) for Douglas-fir.

The temperature effect was more pronounced at low than at high intensities. BRIX (1968) observed a similar temperature effect on Douglas-fir seedlings. He reasoned that low light was more restrictive for photosynthesis than for respiration.

The increase in photosynthetic efficiency at low CO_2 concentrations as the growing season progressed through May and June was indicated by a corresponding decrease in compensation points (Table 5). The implication of high CO_2 compensation points in April is important; when growth is just beginning, the photosynthetic abilities of seedlings at normal CO_2 concentrations can be negligible.

Height Growth

BARNES (1967) demonstrated significant phenotypic variation in height growth among western white pine populations growing naturally at different elevations in one watershed in northern Idaho. Periodic height growth was significantly less for trees at higher elevations (4600 and 5200 feet) than for trees growing at lower elevations (2500 to 4000 feet). SQUILLACE and BINGHAM (1958) gave evidence that height growth of western white pine progeny was associated with the elevation at the seed source. Progenies from two high elevation sites grew faster at a high elevation planting site than did progenies from two low-elevation sites. However REHFELDT and STEINHOFF (1970) reported that when high and low elevation progenies were grown for 14 years at low and medium elevation planting sites, significant growth differences were not observed.

Materials and Methods

Growth curve patterns were determined by making weekly measurements from March to October, 1969, on 240 three-year-old trees. Measurements were made using as a base insect pins which were inserted at or below the 1967 node in each tree. Four trees in each of four blocks were measured to give growth data for each of the sources.

The comparison of sources was based on analyses of variance of the number of days from January 1, 1969, to five, 25, 50, 75, and 95 percent of the total seasonal growth. The number of days to 5 and 95 percent of growth was used to define the beginning and ending dates of growth. The number of days required to complete 25, 50 and 75 percent of growth was used as a relative measure of the rapidity of growth.

In late August, 1969, measurements were made of the total height of the first 10 trees representing each source and block. The means of the 10 trees measured in each replicate were used in an analysis of variance of seed source effects.

Results and Discussion

Total Height. An analysis of variance of total height after four growing seasons indicated that variation could be attributed to blocks within the nursery beds but not to origin of seed sources. It is possible, however, that the nursery environment masked genetic differences in height growth, as HERMANN and LAVENDER (1968) found for Douglas-fir. Also, inherent differences in height growth may be more apparent if trees are grown at different elevations and under environmental conditions which are identical to those of the seed sources. Such a differential response to outplanting site has been demonstrated by SQUILLACE and BINGHAM (1958) as mentioned above.

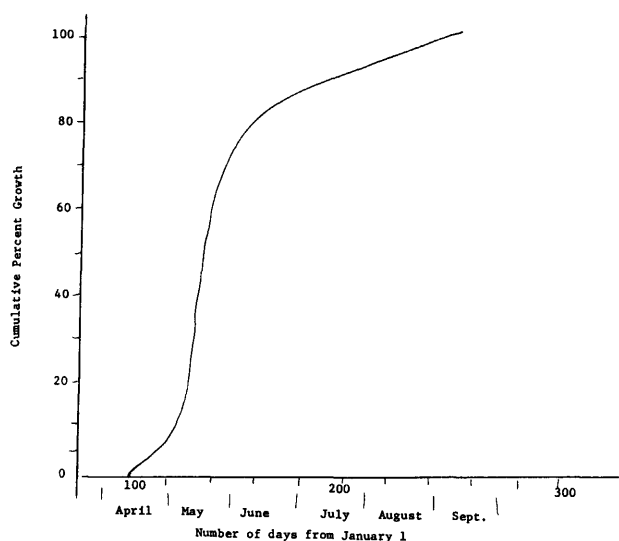


Figure 3. — Average cumulative leader growth of 240 western white pine seedlings grown at East Lansing, Michigan, 1969.

Table 6. — Ranking of western white pine seed sources by the number of days from January 1, 1969, to 25 percent and 50 percent of seasonal growth.¹⁾

25 Percent		50 Percent	
Source ²⁾ (Hundreds of Feet)	Mean Number of Days	Source ²⁾ (Hundreds of Feet)	Mean number of Days
C 15	125.7	C 30	133.7
T 46, SJ 30, SJ 40.	128.2	C 15	136.0
T 52	129.7	SJ 30	137.0
T 30	130.0	SJ 40, T 52, T 46	137.2
T 35, C 30	130.2	K 25, T 30	137.7
C 52	130.5	T 35	138.0
K 25, C 25, T 21	130.7	C 52, C 25.	138.2
K 40	133.0	T 25, T 21	139.2
T 25	134.0	K 40	142.0
T 40	134.2	T 40	142.2

¹⁾ Means included within the same line are not significantly different.

²⁾ Symbols used to denote seed sources: T = Trestle Creek; K = Kaniksu; C = Clearwater; SJ = St. Joe.

Seasonal Growth Rates. The average growth curve pattern of the 240 seedlings studied is shown in Figure 3. Analyses of variance indicated common beginning (April 29) and ending (August 4) dates of growth for all sources. Seed source also did not affect the number of days needed to complete 75 percent of growth, but did influence the number of days to 25 and 50 percent of seasonal growth.

Differences among progenies were analyzed using DUNCAN'S new multiple range test. The differences were not consistently related to the latitude or elevation of the seed source (Table 6). The Trestle Creek seed sources 2100', 3500', and 5200', which were used in the photosynthetic study, were not significantly different in growth patterns. The Kaniksu 4000' and Clearwater 1500' sources, which probably possess the greatest dissimilarity in environments also appear to have distinctly separate growth patterns, at least during the grand period of growth (Table 6). The warm climate of the Clearwater 1500' source apparently has promoted the evolution of a population which can take advantage of good growing conditions in early May by growing more rapidly in the first half of the grand period of growth.

Lammas shoots resulting from bursting and elongation of current-year, terminal buds were observed in 64 percent

of the 240 trees. Seed source was not a significant factor in determining the frequency of lammas shoots, however.

The pattern of growth shown in Figure 3 differs somewhat from the pattern displayed by western white pine seedlings grown in Oregon (WILLIAMS, 1968) and in British Columbia (WALTERS and SOOS, 1963). In both of these cases, the grand period of growth occurred later and total growth terminated earlier than that of the seedlings observed in this study. This is to be expected because of the climatic differences between the test areas.

Summary and Conclusions

The main conclusion that can be drawn from this study is that the western white pine seed sources studied represent quite variable populations but the variability appears to have only a slight association with environmental gradients. Genetic differentiation was detected among seed sources in the concentrations of two of the five monoterpenes analyzed. The chemical differences occurred only between widely separated areas, and were unrelated to the elevation or latitude of the parent trees. Seed origin also did not appear to be an important determinant of photosynthetic efficiency or CO₂ compensation point. At only one of the three light intensities examined was the seed source important in influencing photosynthetic efficiency. No differences among sources were observed in the compensation point, at three light intensities and two temperatures. Height growth parameters were characterized by a similar homogeneity. There were no clear differences among sources in total height, and only slight differences in the form of their growth curves.

Despite marked differences in elevation and geographic separation of certain sources, no evidence of racial differentiation was observed after four years of growth in the nursery at East Lansing, Michigan. Because the native site conditions of many of the populations were not markedly different, it is likely that any genetic differences associated with the slight environmental differences can only be detected after many years of growth in a common environment. Furthermore, the site factors at some of the locations may be compensating thereby eliciting similar genetic responses which probably could not be distinguished under any circumstances.

It was expected that populations from markedly different habitats, for example the 1500-foot Clearwater River source versus the 5200-foot Trestle Creek source, would exhibit height growth differences in the juvenile stage. However, the breeding system of western white pine, cross-pollination, promotes a high level of heterozygosity and through recombination much genetic variation is expressed within populations. Because of this substantial within-population variation, much larger sample sizes than we have tested may be required to detect genetic differentiation between the populations, even from those whose site conditions are apparently quite distinct. In addition the genetically determined differences in the capacity of populations to react adaptively to their respective habitat conditions may be obscured when they are grown in a single location — particularly an artificial environment completely outside the native range. It is possible that only by reciprocal tests in their respective native habitats, or ones similar to them, can the adaptive differences be evoked and measured.

Zusammenfassung

Aus Saatgutproben von 24 Einzelbäumen von *Pinus monticola*-Versuchsflächen aus verschiedenen Höhenlagen wurden in der Baumschule in East Lansing (Michigan) Sämlinge angezogen. — 3- bis 4jährige Sämlinge wurden auf den Gehalt an Monoterpenen, auf ihr photosynthetisches und ihr respiratorisches Verhalten und auf ihr Höhenwachstum untersucht. Die angewandten Methoden werden

beschrieben. — Als Hauptergebnis wird herausgestellt, daß die einzelnen Herkünfte selbst schon sehr variable Populationen darstellen, daß aber diese Variabilität die Herkünfte nicht unterscheiden läßt. Man hält die *Pinus monticola* für eine hochgradig heterozygote Species, so daß man solche Untersuchungen mit viel größeren Herkunftsproben durchführen müßte, um mögliche Unterschiede feststellen zu können. Außerdem sollte die Anzucht des Untersuchungsmaterials nicht nur an einem Ort, sondern an mehreren verschiedenen Plätzen geschehen.

Literature Cited

ALSTON, R. E., and B. L. TURNER: Biochemical systematics. 404 pp. Prentice-Hall, Inc., Englewood Cliffs, N. J. (1963). — BANNISTER, M. H., A. L. WILLIAMS, I. R. C. McDONALD, and M. B. FORDE: Variation of turpentine composition in five population samples of *Pinus radiata*. New Zealand Jour. Sci. 5: 486—495 (1962). — BARNES, B. V.: Phenotypic variation associated with elevation in western white pine. Forest Sci. 13: 357—364 (1967). — BILLINGS, W. D., E. E. C. CLEBSCH, and H. A. MOONEY: Effect of low concentrations of carbon dioxide on photosynthesis rates of two races of *Oxyria*. Science 133: 1834 (1961). — BJÖRKMAN, O., and P. HOLMGREN: Adaptability of the photosynthetic apparatus to light intensity in ecotypes from exposed and shaded habitats. Physiol. Plant. 16: 889—914 (1963). — BOURDEAU, P. F.: Photosynthesis and respiration of *Pinus strobus* L. seedlings in relation to provenance and treatment. Ecology 44: 710—716 (1963). — BOURDEAU, P. F.: Seasonal variation of the photosynthetic efficiency of evergreen conifers. Ecology 40: 63—67 (1959). — BRAVDO, B. A.: Decrease in net photosynthesis caused by respiration. Plant Physiol. 43: 479—483 (1968). — BRIX, H.: Influence of light intensity at different temperatures on rate of respiration of Douglas-fir seedlings. Plant Physiol. 43: 389—393 (1968). — DECKER, J. P.: Effect of air supply apparent photosynthesis. Plant Physiol. 22: 561—571 (1947). — DECKER, J. P.: Some effects of temperature and carbon dioxide concentration on photosynthesis in *Mimulus*. Plant Physiol. 34: 103—106 (1959). — HANOVER, J. W.: Geographic variation in ponderosa pine leader growth. Forest Sci. 9: 87—95 (1963). — HANOVER, J. W.: Genetics of terpenes. I. Gene control of monoterpene levels in *Pinus monticola* DOUGL. Heredity 21: 73—84 (1966 a). — HANOVER, J. W.: Environmental variation in the monoterpenes of

Pinus monticola DOUGL. Phytochem. 5: 713—717 (1966 b). — HANOVER, J. W.: Genetics of terpenes. II. Genetic variances and interrelationships of monoterpene concentrations in *Pinus monticola* DOUGL. Heredity (in press). — HANOVER, J. W., and M. M. FURNISS: Monoterpene concentration in Douglas-fir in relation to geographic location and resistance to attack by the Douglas-fir beetle. U. S. Forest Service Res. Paper NC-6: 23—28 (1966). — JUVONEN, S.: Über die Terpenbiosynthese beeinflussenden Faktoren in *Pinus sylvestris*. Acta Botanica Fennica 71, 92 pp. (1966). — KRAMER, P. J.: Photosynthesis of trees as affected by their environment. pp. 157—186. In: THIMANN, K. V. (ed.). The Physiology of Forest Trees. The Ronald Press Company, New York, 678 pp. (1958). — KRAMER, P. J., and T. T. KOZLOWSKI: Physiology of Trees. McGraw-Hill Book Company, Inc., New York, 642 pp. (1960). — KRUEGER, K. W., and W. K. FERRELL: Comparative photosynthetic and respiratory responses to temperature and light by *Pseudotsuga menziesii* var. *menziesii* and var. *glauca* seedlings. Ecology 46: 794—801 (1965). — LEOPOLD, A. C.: Plant Growth and Development. McGraw Hill Book Company, New York, 466 pp. (1964). — MILNER, H. W., and W. M. HIESBY: Photosynthesis in climatic races of *Mimulus*. I. Effect of light intensity and temperature on rate. Plant Physiol. 39: 208—213 (1964). — REHFELDT, G. E., and R. I. STEINHOFF: Height growth in western white pine progenies. USDA Research Note INT-123 (1970). — SMITH, R. H.: Variations in the monoterpene composition of ponderosa pine oleoresin. U. S. Forest Service Res. Paper PSW-15, 17 pp. (1964). — SQUILLACE, A. E., and R. T. BINGHAM: Localized ecotypic variation in western white pine. Forest Sci. 4: 20—24 (1958). — SQUILLACE, A. E., and G. S. FISHER: Evidences of the inheritance of turpentine composition in slash pine. U. S. Forest Service Res. Paper NC-6: 53—59 (1966). — TOBOLSKI, J. J., and J. W. HANOVER: Genetic variation in the monoterpenes of Scotch pine (*Pinus sylvestris* L.). Forest Science 17: 293—299 (1971). — WALTERS, J., and J. SOOS: Shoot growth patterns of some British Columbia conifers. Forest Sci. 9: 73—85 (1963). — WELLNER, C. A.: Silvics of western white pine. U. S. Forest Service Intermountain Forest and Range Exp. Sta. Misc. Pub. 26, 24 pp. (1962). — WILLIAMS, C. B., JR.: Seasonal height growth of upper-slope conifers. U. S. Forest Service Res. Paper PNW-62, 7 pp. (1968). — ZAVARIN, E., N. T. MIROV, and K. SNAJBK: Turpentine chemistry and taxonomy of three pines of southeastern Asia. Phytochem. 5: 91—96 (1966). — ZELITCH, I.: Increased rate of net photosynthetic carbon dioxide uptake caused by the inhibition of glycolate oxidase. Plant Physiol. 41: 1623—1631 (1966).

Geographic Variation in Japanese Larch in North Central United States Plantations

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Japanese larch (*Larix leptolepis* [SIEB. and ZUCC.] GORD.) has a limited natural range in the central part of the principal Japanese island, Honshu (Figure 1). The species

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grows naturally in scattered stands at elevations of 900 to 2,500 meters. All the natural stands are included in an area about 200 km square.

This larch has been planted extensively in Japan and also in Europe. It has recently attracted the attention of American foresters, particularly in New York. When planted on suitable sites it usually outgrows the commonly planted pines and spruces.

Hybrids between Japanese and European (*Larix decidua* MILL.) larches have been known since 1900. They grow vigorously in many parts of northern Europe and can be produced easily. In the past decade tree breeders in Hokkaido, northern Japan, have concentrated on hybrids between Japanese and Dahurian larch (*L. gmelini* [RUPR.] LITVIN.) which can be produced in large quantities and show promise for northern localities.

Data on genetic variation within Japanese larch have been scanty, based on a few unreplicated progeny tests. The present provenance study was undertaken to determine the range of genetic variability within the species, determine the nature of the variation pattern, and to provide practical