STUDY OF GEOGRAPHIC VARIATION

IN EUROPEAN LARCH

by

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SUMMARY

European larch consists of two varieties, *Larix decidua* var. *decidua* Mill. and *Larix decidua* var. *polonica* (Racib.) Ostenf. & Larsen. It belongs to the genus *Larix* Mill. which includes 13 other species or varieties. It is a coniferous tree with deciduous leaves growing naturally in Central Europe, mainly in the Alps and the Carpathian Mountains and adjacent areas. Its range has been considerably increased by planting.

European larch was introduced to the United States at the middle of the nineteenth century and at present individual trees or small stands are found throughout the northern parts of this country east of the Mississippi. It has some economic importance only in New York and Pennsylvania, where it was planted most extensively.

Rapid growth is the most important characteristic of European larch which attracted to use it in plantings. It produces merchantable yields at early ages and its durable wood is valuable for various general use.

First provenance studies of European larch were undertaken at the end of the nineteenth century. These and later investigations in Europe revealed that seed origins from different parts of its range considerably varied, not only in height growth, but also in stem qualities and resistance to disease. This variability was observed also in a few American studies of a limited number of origins.

This study was based on the first large American test plantings of European larch which were established at the Fox State Forest, Hillsboro, New Hampshire, and at the State Forest near Barkersville, New York. The test is known as the "IUFRO Larch '44" experiment because the seed lots were received from the International Union of Forest Research Organizations. It included 31 provenances of European larch collected in various parts in the natural range and a few origins from planted stands. Nursery plantings were established in 1946 and field plantings in 1958. Provenances were arranged in both experiments in unreplicated plots, except a few second-replicates in New Hampshire. Sources were arranged in rows of varying number of trees per plot in New York and in rectangular plots with about 35 trees per plot in New Hampshire. The spacing was 6 x 6 feet in New York and 5 x 5 feet or similar in New Hampshire.

The writer measured and scored these American IUFRO larch plantations in the summer of 1958 when the trees were 12-years old. Data on eight characteristics from these and earlier studies were the basis of this work.

The general pattern of variation in European larch was determined by using the New Hampshire data as more complete and reliable. Analyses were based on the provenance means grouped by 10 geographic and altitudinal regions. Differences between individual provenances and the within-region variations were studied on the basis of combined New Hampshire and New York data, in which case each plantation was considered as a randomized block.

Results are as follows:

1. Altitudinal differences were found in seed weights. Provenances from higher elevations had relatively heavier seeds than those from lower altitudes. Seed weights appeared as a poor factor in determining future height growth, because correlation between 4-year heights and seed weights was negative. Germination in European larch was completed 90 percent in 15 days.

2. Geographic variation in European larch in eight characteristics studied was largely systematic. Provenances from the same geographic or altitudinal regions showed similar characteristics. Altitudinal differences were found among provenances from high and low elevations in Central and Western Austria. A break in genetical characteristics appeared between provenances from the Polish-Sudeten region and those from Slovakia.

Provenances from Poland, Sudetenland and Slovakia had significantly greater 12-year heights than provenances from other regions. Higher elevation provenances from Austria, Italy and Switzerland grew slowest. The pattern of variation in diameter growth was similar to that in height growth except that Slovakian provenances did not differ significantly in diameter growth from other provenances with smaller diameters.

Analyses of variance showed that the general pattern of variation in height performance could be determined on the basis of 4-year height data or on the basis of the means of 4 largest trees measured per plot. However, these data gave less efficient statistical differences between origins.

Analyses of stem form were based on number of crooks in the lower stem and the number of trees with small crooks in the upper stem. The straightest stems were found in the provenances at higher elevations in Austria, Italy and Switzerland. An extremely high number of crooks were found in the provenances from lower elevations in Western Austria. Among the rapidly growing provenances the straightest stems were found in those from Slovakia.

Some provenances in the plantation had many trees with J-shaped bases (basal sweep) and some were entirely out of vertical (lean). Analysis of variance showed these characteristics were more common in the fast growing provenances from Poland and Sudetenland. However this rule did not apply to the rapidly growing provenances from Slovakia, and a separate study of individual trees revealed that lean was not related to tree height. The Austrian provenances from higher altitudes had less lean or basal sweep than from lower altitudes.

In 1958 the IUFRO larch plantation in New Hampshire was subjected to the late snow damage and attack by the woolly larch aphid (<u>Chermes strobilobius</u> Kalt.). The most injury by these agents was caused in the Sudeten, Slovakian and Eastern Austrian provenances and the least in provenances from higher altitudes. Among the rapidly growing provenances, those from Poland were only moderately attacked by the aphids.

3. From these characteristics it appears that Polish provenances, best in cellulose production, are related to provenances from Sudetenland. Slovakian provenances differed from the above origins in several characteristics and were best in quality of wood production.

Origins from the Alps grew slower, in general, and showed altitudinal differences. Low-elevation provenances were somewhat faster growing, had more stem deformities and were more attacked by aphid than the high-elevation provenances.

4. No origins from planted stands grew faster than the best provenances of European larch from the native stands. The provenance (IUFRO-53) from Scotland had fewer trees attacked by the woolly larch aphid than any other provenance of European larch; and Japanese larch (IUFRO-28) was 100 percent free from aphid. Some hybrids (*L. eurolepis* Henry) were observed within the origin IUFRO-55. They were relatively resistant to the aphid and had greater heights than other trees in the plot.

5. Twelve-year heights in American IUFRO larch plantations and heights of similar provenances planted in Great Britain, Germany, and Italy were very strongly correlated. This indicated that data on height performance of different provenances in Europe can be trusted in the United States, and data obtained in this study are probably applicable in other regions of the northeastern United States.

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I. INTRODUCTION

Larch (*Larix* Mill.) is a coniferous genus containing 10 species and a few varieties that are distributed in the cooler regions and mountains of the northern hemisphere.

European larch (*Larix decidua* Miller), from the mountains in central Europe, is one of the most important larch species. It has a relatively small natural range which has been considerably increased by planting. European larch has been present in England since 1629 (51), in Germany since 1700, and in Norway since 1740 (76). It is the third most commonly planted species in Great Britain, occupying an area of 132,000 acres (51). Its plantings in West Germany total about 85,000 acres (75).

Rapid growth was the main reason for its being highly regarded for planting. In Great Britain the 50-year height for site class I is 80 feet and the corresponding volume (over bark) is 7,100 cubic feet per acre (82). European larch is used widely for fence posts, pit-props, boat-, pier-, bridge-, wagon- and river-defense works (51). This wood is highly valued in Europe for its durability. It stayed sound for several centuries in Venice, Italy, when used under water. Some churches built of this material in Poland three to five hundred years ago are still standing (34).

European larch was introduced into the United States about the middle of the 19th century. Individual trees or small stands are found throughout the northeastern United States (2, 35, 50). Hunt studied these larches in New England and New York in 1932 and reported that on well-drained loamy soils they made good growth and proved to be a valuable addition to the forests of the Northeast (35). At the age of 50 years on good soils (site I) the trees were 72 feet high, 10.8 inches d.b.h. and yielded about 5,100 cubic feet outside bark per acre. Cook reported that at Cooxrox Forest in northeastern New York 15-year-old dominant trees had an average height of 40 feet and were beginning to give merchantable products (15).

The greatest interest in this species has centered in New York State where the state forests included about 11 million trees in 1958, and at present nursery inventory is over 1 million trees. In the Pennsylvania state forests about 1.6 million trees were planted between 1899 and 1958. Elsewhere, in the Corn Belt, Lake States, and the Northeast, there is a great deal of current interest in the species because of its rapid growth. The present output in this country is relatively low and its suitability for various market requirements is not finally determined. It may be especially suited for small, privately owned woodlands because its wood is suited for general farm use and merchantable yields are produced at early ages (figure 1).

European larch is a variable species. Because of improper selection of seed sources, as early as the middle of the nineteenth century some plantings in Germany failed (90). By now it is proven that trees of different geographic origins differ from each other in growth rate, stem form, resistance to disease and other characteristics that are important in forestry.

Figure 1.--European larch near the State Forest Nursery in Gerrich, New Hampshire, 42 years after planting. The average height was 75 feet and diameter at breast height, 13 inches.

Cieslar initiated the first provenance study of European larch at Mariabrunn, Austria, in 1879. He included two seed sources from natural stands. One of these was from Sudetenland, Czechoslovakia, and the other from the Austrian Tyrol. A few years later he established another study with 14 provenances from the same regions. As compared with Tyrolean provenances, trees from Sudetenland had more rapid growth, longer live crown, heavier wood, higher wood specific gravity, lower bark percentage, earlier needle appearance in spring and earlier needle fall in autumn (9, 10, 11, 12).

Following the first experiment by Cieslar, provenance studies were established in most European countries: Switzerland, Sweden, Great Britain, Czechoslovakia, Germany, Belgium, Finland, Denmark, and France. None of these experiments was large or well designed. Taken individually, they yielded little valuable new information. However, when summarized as a group by Kalela (38) and Schober (73), they yielded some new information, such as the fact that susceptibility to larch canker (Dasyscypha willkomii (Hartig) Rehm.) was related to origin.

There are a few small seed origin studies of European larch in the United States. These are of limited value because only a few provenances are represented from natural stands. Littlefield and Eliason made a study of three seed origins in New York. Seventeen-year old trees originating from planted stands in Scotland and Silesia had significantly greater heights than those from the Italian Alps (48). Earlier study of 5-year-old seedlings in New York showed that seed origin from Scotland had greater height growth than that from Silesia (47). Stoeckeler reported that in northeastern Wisconsin origins from

Silesia, the German Alps, and Czechoslovakia ranked higher in 4-year height growth than origins from the Austrian and Italian Alps and Germany (81). However, the origin data were insufficient to tell whether or not the faster growing origins are from native stands. Cook observed that an origin from planted stands in Scotland was more attacked by squirrels than a provenance from Silesia (14).

A summary of European larch studies, mainly on its racial variation, was reported by McComb (50). However, the applicability of European findings under American conditions remained untested.

The first extensive study of geographic variation in European larch under American conditions was initiated by Dr. Henry I. Baldwin. He received 42 seed lots of European larch and 3 seed lots of other larches from the International Union of Forest Research Organizations (IUFRO) and shared these with other research agencies. Plantations were established in two locations, the Fox State Forest (Hillsboro, New Hampshire) and a State Forest of New York (Bakersville, New York). Baldwin reported 4-year heights of transplants in New Hampshire and made some studies on the period of height growth in different provenances of European larch (3, 4).

I performed the measuring and scoring of the 12-year-old American IUFRO larch plantings in the summer of 1958. The present study of geographic variation in European larch was based on these and earlier data obtained.

II. OBJECTIVES

The objectives of the present study were as follows:

1. Determine the European larch variation pattern in seed weight and relate this to juvenile tree growth.

2. Determine the geographic variation of European larch with respect to 12-year heights and diameters, stem form, basal sweep, lean, late snow damage, susceptibility to the woolly larch aphid (*Chermes strobilobius* Kalt.) and other characteristics visible at this age.

3. Determine the ultimate natural origin of the planted stands represented in the IUFRO tests.

4. Determine the relationship between the genetic pattern of variation and toxonomic variation in European larch.

5. Determine the consistency of height growth of the same provenances tested at different locations in Europe and the United States.

6. Show the relationship of the results of the IUFRO European larch provenance test to larch improvement programs in general.

7. Determine the reliability of early measurements and possible improvements in conducting experiments.

III. TAXONOMY

1. Distribution

The range of European larch occupies two main distribution areas and a few small, outlying areas (figures 2 and 3).

One of the main portions of the range is in the Alps Mountains of northern Italy (figure 4), southern Switzerland, Austria, and adjacent parts of southern Germany and northeastern Yugoslavia. Within this area European larch grows at elevations between 300 and 2,500 meters. Its southernmost point is in the French Alps at 43°55'N, just a few miles north of Nice (25). Its other southern limit in Italy reaches Lake Garda at 45°40'N (52). The westernmost point of European larch is at Val Jouffrey, France (25). This main portion of the range expands into lowlands of Eastern Austria where it reaches 48°40'N in the North and 16°20'E in the East (86).

The second principal distribution area of European larch is in southern Poland and eastern Czechoslovakia. It grows here at elevations of 150 to 500 meters scattered in flat and rolling regions in Poland, and at 500 to 1,000 meters in the Tatra Mountains and other parts of Slovakia, eastern Czechoslovakia. It reaches its northern limits at 50°05'N, near the town Bronica, Poland, its western limits at 18°13'E and its eastern limits at 22°43'E, near the Polish-Ukrainian border. This principal area of the range of European larch expands throughout Slovakia (eastern Czechoslovakia) and reaches its southernmost point

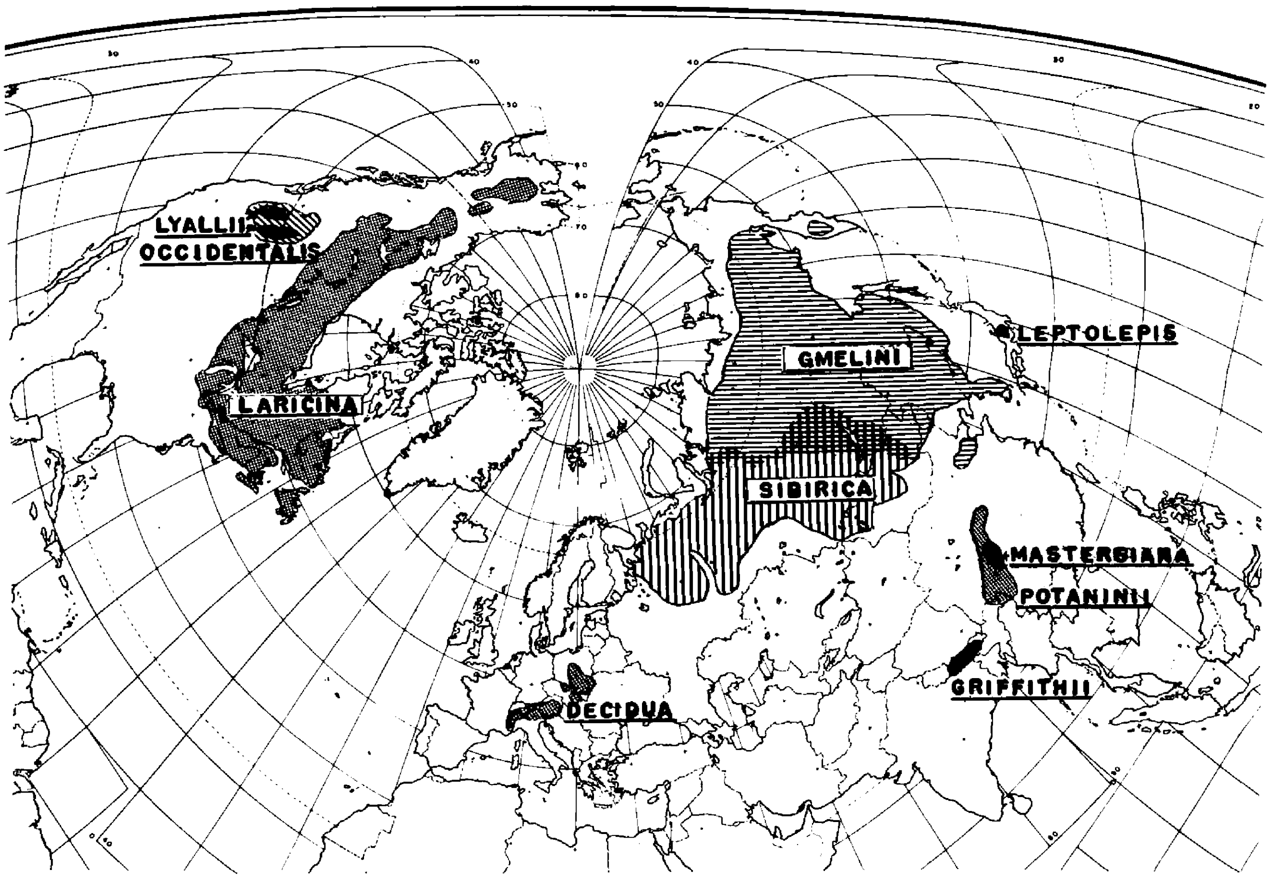

Figure 2.--Distribution of the genus Larix. European larch (Larix decidua Miller), which is isolated from other species, has one of the smallest ranges in the genus.

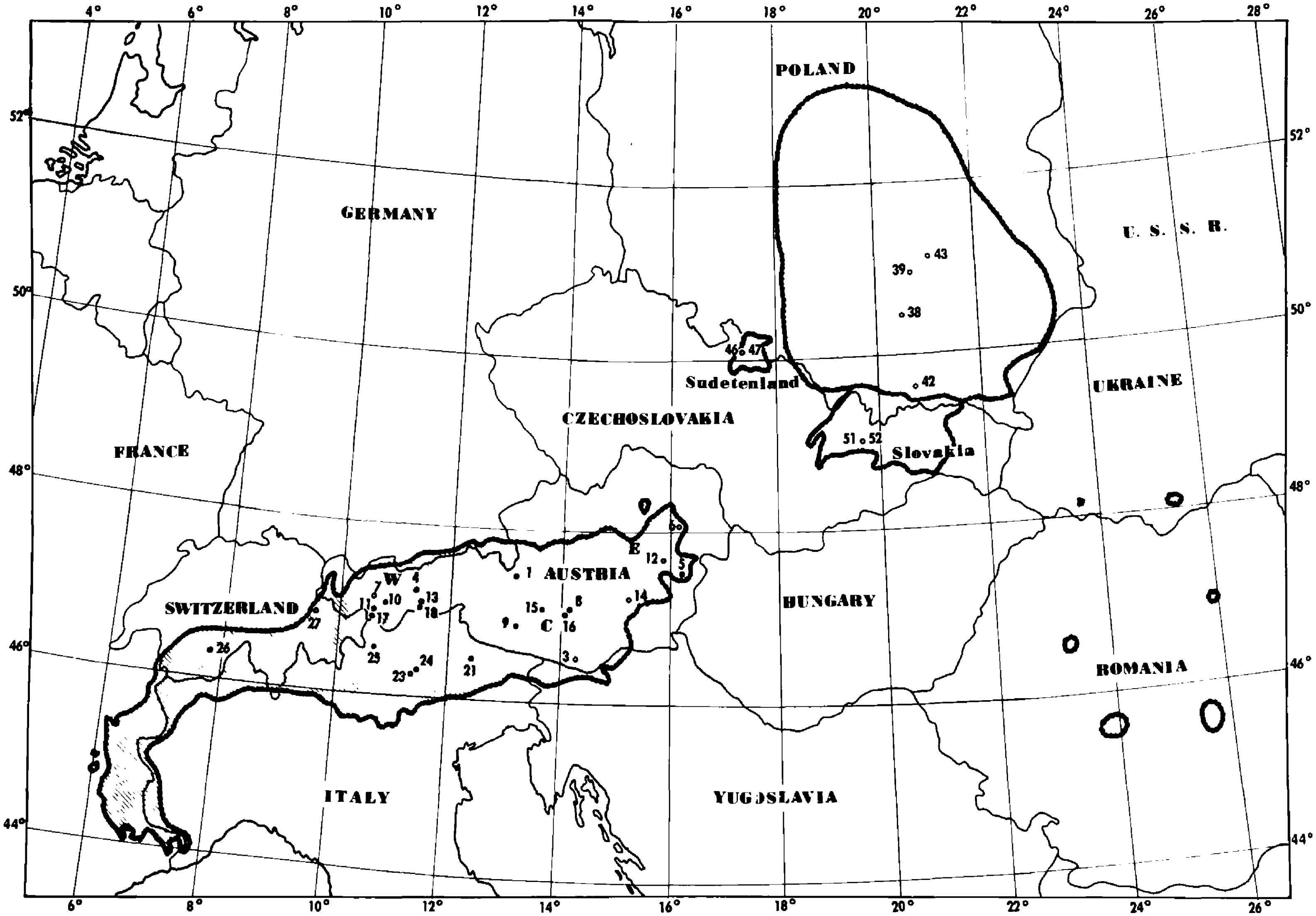

Figure 3.--Natural distribution of European larch in two large and several small areas.

The IUFRO provenances included in this study are indicated by numbers.

Figure 4.--European larch in its natural range at La Val Bondasca in the Italian Alps. Photo from L. Feranoli (22).

at 48°45'N (67, 85). Fourchy, McComb and some other authors have published range maps of European larch which showed a distinct break between European larch in Poland and that in Slovakia (25, 50). However, there is no clear evidence whether or not these ranges are discontinuous (67, 85). I have drawn a line (figure 2) along the southern slopes of the Carpathian Mountains to indicate a possible break between Polish and Slovakian populations as it was supposed by Rubner (67).

Close to the same major area in the Carpathian Mountains is an isolated range of European larch in Sudetenland, northwestern Czechoslovakia, where it grows at elevations of 300 to 1,000 meters (32, 67, 68). There are also six small distribution areas in Romania and the southern part of Ukrainia (U.S.S.R.) (25, 55).

2. Morphology

European larch is a coniferous tree belonging to the genus *Larix* Mill. It is a rapid-growing, tall (to 150 feet) tree with slender, yellow, glabrous branchlets and spirally arranged, horizontal or pendulous branches. The bark is yellowish-brown, smooth on young trees, platy and shallowly ridged on old trees. The crown is conical on young trees (figure 4), irregular in open-growing old trees.

The leaves are deciduous, solitary, soft, linear, flattened, 20 to 40 millimeters long and less than 1 millimeter broad, spirally arranged and remote on the long shoots, densely clustered on the short shoots. The buds are small, about 2 millimeters in diameter, non-resinous, sub-globose with imbricated deciduous scales.

Figure 5.--Open grown European larch near the State Forest Nursery in Gerrish, New Hampshire. The straight bole, horizontal lower branches and the open crown are characteristic.

The flowers are borne on short shoots. They are monoecious, solitary and appear before the leaves. The female flowers are subglobose, consisting of 2-ovuled scales which are longer than the scarlet bracts. The scales are reddish purple in most trees. However, forms with purple, yellow, white, or green flowers have been reported. The male flowers are globose to oblong, consisting of numerous spirally arranged yellow anthers.

The cones are brown, ovoid, erect, short-stalked, 15 to 40 millimeters long, 11 to 24 millimeters broad and mature in one season. The cone scales are thin, loosely appressed at maturity, 30 to 70 per cone. The cone scales have rounded edges and are longer than the bracts.

The seeds are about 3.5 millimeters long and 2.5 millimeters broad with membranous wings about 10 millimeters long. A seed without wings weighs 4.3 to 8.6 milligrams.

3. Geographic Varieties of European Larch

The geographic varieties of European larch have been recognized on the cone characteristics. Taxonomic differences within this species were first recognized in 1890 when Raciborski described the larch in Poland as a separate species. However, Ostenfeld and Larsen classified Polish larch as a variety of European larch (55). More recent studies by Rubner and Svoboda showed also that the larches in Poland, Sudetenland, and Slovakia had common cone characteristics, but differed from those in the Alps (70). According to the morphologic differences, European larch consists of two varieties as follows (55, 61):

1. Larix decidua Mill. var. decidua	2. Larix decidua var. polonica (Racib.) Ostenf. & Larsen
- - - - Cone characteristics - - - -	
Scale edges straight	Scale edges slightly incurved
Scale edges less rounded	Scale edges more rounded, often pilose on the outher side
Scale edges undulating	Scale edges more undulating
Cone length 20 to 40 millimeters	Cone length 15 to 30 millimeters
Cone width 15 to 24 millimeters	Cone width 11 to 20 millimeters
- - - - Distribution - - - -	
The Alps Mountains and adjacent areas	The Carpathian Mountains and adjacent areas

In Table 1 the two varieties of European larch are indicated. Under each variety other names have been listed.

Table 1.--Nomenclature of European larch varieties (61, 62, 55, 76, 77, 78, 37, 70).

1. Larix decidua Miller var. decidua, Gardeners Dict., ed. 8, L. no. 1, 1768.

Other published names:

Pinus Larix Linnaeus
Pinus Larix Larix Weston
Pinus Larix var. alba et var. rubra New
Pinus laeta Salisbury
Pinus Larix α communis (Laws.) Endlicher
Pinus Larix var. β pendula Endlicher

Abies Larix Poiret
Abies Larix (c) pendula Hort. ex Lindley & Gordon

Table 1.--(Cont.)

Other published names (Cont.)

Peuce Larix Richard

Larix caducifolia Gilibert
Larix europea De Candolle in Lamarck & De Candolle
Larix gracilis Dietrich
Larix Europea communis Lawson
Larix europea α *typica* Regel
Larix europea β *pendolina* Regel
Larix Larix (L.) Karsten
Larix pyramidalis Salisbury
Larix vulgaris Fish.
Larix europea var. *scottica* Nilson
Larix decidua α *communis* Henkel & Hochstetter
Larix decidua var. *fastigiata* Dallimore
Larix decidua var. *repens* (Willk.) Hornibrook
Larix decidua f. *Lusus globosa* Klein
Larix decidua f. *Lusus virgata* Tschermak
Larix decidua f. *rubra* Beck
Larix decidua f. *alba* Carriere
Larix decidua f. *sulfurea* Fig.
Larix decidua f. *compacta* (Beiss.) Hornibrook
Larix decidua f. *pendula* (Laws.) R. E. Fries
Larix decidua var. *typica* Soo
Larix decidua var. *vulgaris* f. *macrocarpa* Svoboda
Larix decidua subsp. *alpica* Domin
Larix decidua pendulina Regel
Larix decidua subsp. *alpica* sorta *raetica* Siman
Larix decidua subsp. *alpica* sorta *tirolica* Siman
Larix decidua subsp. *alpica* sorta *italica* Siman
Larix decidua subsp. *alpica* sorta *norica* Siman

2. *Larix decidua* var. *polonica* (Racib.) Ostenfeld & Syrach-Larsen, *Pflanzenareale, 2:63, 1930.*

Other published names:

Larix europea Hoeppen
Larix polonica Raciborski
Larix polonica f. *viridiflora* Szafer
Larix polonica f. *piena* Szafer
Larix decidua var. *sudetica* Domin
Larix decidua subsp. *carpatica* Domin
Larix decidua subsp. *carpatica* sorta *slovacica* Siman
Larix decidua subsp. *carpatica* sorta *polonica* Siman
Larix decidua subsp. *carpatica* sorta *sudetica* Siman
Larix decidua subsp. *carpatica* sorta *romanica* Siman
Larix decidua var. *microcarpa* f. *rosulens* Svoboda

4. The Place of European Larch in the Taxonomy of Other Larches

Taxonomic studies in the genus *Larix* are incomplete. Ostenfeld and Larsen studied the genus by conventional taxonomic methods in 1930 and recognized ten different species (55). Rehder based his treatment of the genus in 1940 and 1949 mainly on Ostenfeld and Larsen's monograph (61, 62). Geyer and others have proposed modified classifications of larches but these appear not to be based on adequate data (27, 77, 78). Consequently, I have followed classification by Ostenfeld and Larsen and Rehder.

The distributions of the species of *Larix* are illustrated in figure 5 and described in table 2; a key to species and varieties is presented in table 3.

The phylogenetic relationship of European larch to other larch species and varieties is schematically illustrated in figure 6, following Sukachev (37). It misleads in showing tamarack as a variety of Dahurian larch and Himalayan larch distantly from Master's and Chinese larches.

Table 2.--Natural distribution of the genus Larix.

Species or Variety Name	Notes on Distribution
European larch	
Larix decidua Mill. var. decidua (Alpine variety)	Elevations of 1,000 to 8,000 feet in the Alps Mountains of Austria, S. E. Switzerland, S. E. France, N. Italy and adjacent parts of S. Germany and N. E. Yugoslavia (25, 52, 55, 61, 62, 86).
Larix decidua (Racib.) var. polonica Ostenf. & Larsen (Carpathian variety)	Elevations of 500 to 5,000 feet in the Carpathian Mountains of Sudetenland and Slovakia in Czechoslovakia and scattered throughout adjacent lowlands of S. Poland and isolated areas in S. Ukraine and Cent. Rumania (25, 55, 61, 62, 68, 67).
Siberian larch	
Larix sibirica Ledeb.	Lowlands in N. E. Russia and W. Siberia, in the Ural and other mountains reaches elevations of 6,000 feet; northern limits expand along and north of the Arctic Circle; in the South is found as far as the Lake Baikal and N. Mongolia (55, 59, 61, 62, 37).
Dahurian larch	
Larix gmelini (Rupr.) Kuzeneva var. gmelini (Dahurian variety)	Extensive lowlands throughout E. Siberia and N. Manchuria, the northern limits are frequently north of the Arctic Circle; at Khatanga the species range extends to 73°N (no other tree species is reported growing that far north) (37, 59, 61, 62, 55).
Larix gmelini var. olgensis (Henry) Ostenf. & S.-Larsen (Olga variety)	Olga Bay along the Sea of Japan and in Korea (37, 55).
Larix gmelini var. principis rupprechtii (Mayr) Pilger (Rupprecht variety)	Isolated range in N. China, mainly in N. E. Shansi and Cent. Chihli provinces (37, 55, 61).

Table 2.--(Cont.)

Species or Variety Name	Notes on Distribution
Larix gmelini var. *japonica* (Reg.) Pilger	Saghalin and the Kurile Islands east of Siberia (37, 61, 62).
Japanese larch *Larix leptolepis* (Sieb. & Zucc.) Pilger	Elevation of 4,000 to 9,000 feet on Mt. Fuji and other mountains of Central Honshu in Japan (54, 74).
Chinese larch *Larix potaninii* Batal.	Elevation of 8,800 to 15,700 feet (the highest for any Pinaceae) in Cent. China provinces of Szechwan, Shensi, Yunnan, and the adjacent N. E. Burma (55, 61).
Master's larch *Larix mastersiana* Rehd. & Wils.	Central China province of Szechwan, adjacent to and overlapping with Chinese larch (55).
Himalayan larch *Larix griffithiana* Hort. ex Carriere	High elevations in the Himalayan Mountains in Nepal, Bhutan and Indian province Sikkim, where the species is found at altitudes of 8,900 to 10,000 feet (55).
Tamarack or American larch *Larix laricina* (Du Roi) K. Koch	Mainly lowlands with the highest elevation of 1,700 feet, from Alaska (reaching the Arctic Circle) throughout Cent. and E. Canada, and Lake States and the Northeast regions in the United States (46, 63, 59).
Western larch *Larix occidentalis* Nutt.	Elevations of 2,000 to 7,000 feet in the Rocky Mountains of N. Idaho, E. Washington and adjacent parts of Oregon, Montana, and British Columbia (5, 83).

Table 2.--(Cont.)

Species or Variety Name	Notes on Distribution
Alpine larch *Larix lyallii* Parl.	Elevations of 4,000 to 10,000 feet in the Rocky Mountains, overlapping range with western larch, usually at higher altitudes than the latter (55, 58).

Table 3.--Key to the species and varieties of larches (55, 61, 62).

1. Bracts longer than cone-scales. Leaves slightly or strongly keeled on both sides; the upper side is, in exceptional cases, without a keel.

    2. Bracts reflexed.

        3. Bracts much longer than the cone-scales. Cone 5-11 cms. long . . . . *L. griffithiana*

        3. Bracts only slightly longer than the cone-scales. Cone 3-5 cms. long . . . . *L. mastersiana*

    2. Bracts straight or slightly recurved.

        4. Cone long and narrow; length to breadth 1.4-1.7; bracts 0-2 mm. longer than the cone-scales. Leaves deeply keeled on the under-side; slightly less keeled on the upper-side, 1.5-3 cms. long . . . . *L. potaninii*

        4. Cone short and broad. Length to breadth 1-1.5, leaves 2.5-4 cms.

Table 3.--(Cont.)

5. Leaves are more strongly keeled on the upper- and under-sides than in any other larch species. The young shoots are densely pilose. Cone 3.5-5 cms. long. Bracts straight . . . . *L. lyallii*

5. Leaves keeled only on the under-side. The young shoots at first somewhat pilose, finally smooth. The cone 2.5-3 cms. long. Bracts straight or slightly recurved . . . . *L. occidentalis*

1. Bracts not exceeding cone-scales. Leaves not keeled on the upper-side and frequently flat.

6. Cone-scales reflexed. Leaves broad, deeply keeled on the under-side. Both sides provided with stomata. Young shoots stout, and of reddish-brown color . . . . *L. leptolepis*

6. Cone-scales straight or somewhat concave. Leaves flat, or slightly keeled on the under-side.

7. Cone-scales distinctly concave.

1. Cones 1.5-2 cms. long. Cone-scales smooth, often shining . . . . *L. laricina*

Cones narrow, 3-4 cms. long. Scales pilose, most frequently strongly so on the outer-side of the basal portion; dull . . . . *L. sibirica*

7. Cone-scales straight.

8. Cones 2.5-4 cms. long, narrow. Scales dull, the free edges evenly rounded or slightly emarginate. Bracts of the same light color as the cone-scales, which are smooth or pilose on the outer side. Cone compact. Scales only slightly open when ripe . . . . *L. decidua* var. *decidua*

8a. Cone is more frequently smaller, shorter, and thicker than 8. Free edges of the cone-scales more rounded, and often pilose on the outer-side . . . . *L. decidua* var. *polonica*

Table 3.--(Cont.)

8. Cones up to 4 cms. long; broad. The free edges of the cone-scales are truncate or emarginate. Bracts are darker in color than the light-colored, shining, cone-scales. Cone-scales are most frequently smooth on the outer-side, but may be slightly pilose. Cones as a whole are of an open, characteristically light construction. Cone-scales open widely when ripe . . . . *L. gmelini* var. *gmelini*

    8a. Cone longer and more cylindrical. The free edges of the cone-scales are rounded or truncate. The usually straight cone-scales may also be slightly concave or slightly recurved. The first year's shoots are more frequently pilose, very often extremely so . . . . *L. gmelini* var. *olgensis*

    8b. Cone is still longer and more cylindrical than in the case of the former variety; length up to about 4 cms. . . . . *L. gmelini* var. *principis rupprechtii*

    8c. Young branchlets bluish red, often gloomy, pubescent, sometimes pale . . *L. gmelini* var. *japonica*

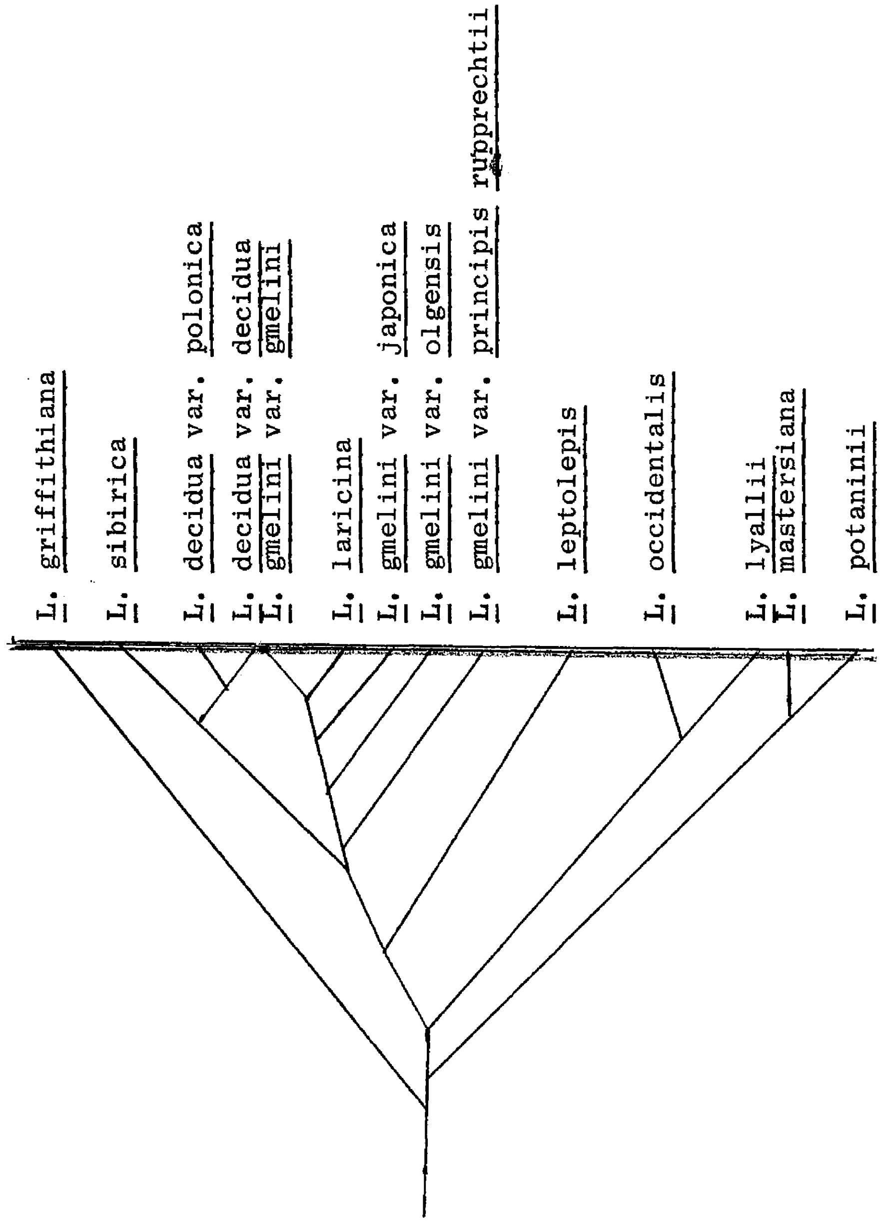

Figure 6.--Graphic representation of the phylogenetic relationship in the genus *Larix*[1/] after Sukachev (37).

1/ Current names have been used.

IV. MATERIAL AND METHODS

1. Plantation Establishment and Care

The International Union of Forest Research Organizations, called IUFRO, was formally organized in 1892 and initiated several cooperative studies. The Subcommittee on Forest Seeds and Forest Tree Races under the leadership of Dr. Werner Schmidt decided to start a larch provenance study at its meeting in 1940. Seed collection for this study continued for three years--1942, 1943, and 1944. The number of mother trees and their ages varied. The majority of collections was made from native stands of European larch; the rest included seed from planted stands of European larch and other larch taxa. The total number of 56 provenances included 51 seed lots of European larch, two of Siberian larch, one of Japanese larch, and one that originated from spontaneous European and Japanese larch hybrids. These seed lots were distributed to 11 different countries in Europe and North America. The experiment in Finland and Denmark failed. In nine other countries experiments were established in 17 different locations (table 4). The number of provenances in these experiments varied from 6 to 56 (88).

United States participation in the IUFRO larch study was initiated by Dr. Henry I. Baldwin, who had been in contact with IUFRO and some members of the Subcommittee on Forest Tree Races since its 1929 Congress in Stockholm. In March 1946, Dr. Baldwin received 46 seed lots of different larch provenances from Prof. Sven Petrini, IUFRO Secretary General. The seed, averaging about 100 grams per provenance, was

Table 4.--Location of IUFRO larch provenance studies in North America and Europe (88).

Expt. No.	Country, District, Location	Latitude	Longitude	Altitude	Seed Sources
				meters	number
1	U.S.A., New Hampshire, Hillsboro	43°09'N	71°55'W	240	46
2	U.S.A., New York, Barkersville	43°07'N	74°02'W	460	37
3	Canada, Alberta, Kanaskis For. Exp. Sta.	50°56'N	115°10'W	1350	10
4	England, Wiltshire, Savernake For.	51°24'N	1°38'W	150	38
5	England, Herefordshire, Haugh For.	52°01'N	2°36'W	150	14
6	England, Herefordshire, Mortimer For.	52°19'N	2°53'W	230	13
7	England, Shropshire, Walcot For.	52°25'N	3°01'W	260	27
8	England, Worchestershire, Wyre For.	52°25'N	2°22'W	80	11
9	Scotland, Pertshire, Drummond Hill	56°34'N	4°06'W	300	20
10	Germany, Niedersachsen, Bremervorde	53°28'N	9°08'E	50	25
11	Germany, Fulda, Neuhof-West	50°40'N	9°33'E		56
12	France, Loiret, Nogent s. Vern	46°50'N	2°48'E	150	9
13	France, Meurthe et M., Arb. d. l. Sivr.	48°45'N	6°09'E	300	6
14	Italy, Pistia, Aquerino For.	44°01'N	11°05'E	960	15
15	Sweden, Halland, Hjuleberg	56°56'N	12°44'E	150	21
16	Switzerland, Zuerich, Hoenggerberg	47°25'N	8°29'E	535	17
17	Czechoslovakia, --, Podbansko For.			950	41

subdivided among four different research agencies. However, plantations were established in two locations only: one by the Forestry and Recreation Commission of the State of New Hampshire and another by the New York State Conservation Department. Details of sites and methods used in establishment of these American IUFRO larch provenance studies are presented in tables 5 and 6.

In New Hampshire a separate study was made with 47 provenances of European larch which were transplanted to the nursery as 2-0 and measured at the age of 4 years as 2-2 (4).

The IUFRO larch plantings in New Hampshire were partially damaged by porcupines (*Erethion dorsatum dorsatum* Linnaeus) particularly in one corner of the area. It was also attacked a few times by woolly larch aphid (*Chermes strobilobius* Kalt.) and other minor pests. At the IUFRO larch plantation in New York a few trees had dead tops because of porcupine damage and some trees had abnormal upper crowns because of snow damage.

2. Range of Provenances Studied

In the summer of 1958, when the major data were collected, the IUFRO larch plantation in New Hampshire consisted of 45 different provenances and the New York plantation included 52 provenances, as shown in the following tabulation:

Table 5.--Description of sites used in establishment of American IUFRO larch plantations.

	Data on the IUFRO Larch Plantation in New Hampshire	in New York
Location	Fox State Forest, Hillsboro, Hillsborough County, New Hampshire	N. Y. State Forest, Barkersville, Saratoga County, New York
Latitude, longitude	43°09'N, 71°55'W	43°07'N, 74°02'W
Altitude	800 feet (240 meters)	1500 feet (460 meters)
Slope and aspect	0-5 percent, east	0-5 percent, southwest
Soil series	Marlow & Whitman (fertile)	Gloucester (submarginal for agriculture)
Soil type	Loam (stony phase)	Fine sandy loam
B horizon	Platy fragipan at the depth of 20 inches	Yellow brown loam
Parent material	Platy olive glacial till	Glacial till from granitic rock
Internal drainage	Well drained on Marlow; poorly drained on Whitman	Very well drained
Past use of site	Old field, in use up to time of planting	Old field, abandoned for several years
Mean total precipitation	45 inches	40 inches
Snow fall	64 inches	69 inches
Mean July temperature	68°F	78°F
Mean January temperature	22°F	20°F

Table 5.--(Cont.)

	Data on the IUFRO Larch Plantation in New Hampshire	in New York
Mean annual temperature	46°F	46°F
Last frost average date	May 12	May 10
First frost average date	October 6	October 1

Species	Seed Source	Number of Provenances in New Hampshire	New York
European larch	Natural stands	31	26
European larch	Planted stands	10	10
European and Japanese larches	Mixed species	1	--
Spontaneous hybrids	Planted stands	1	1
European larch	Origin unknown	--	7
Japanese larch	Planted stands	1	1
Siberian larch	Planted stands	1	1
Tamarack	Natural stands	--	1
Total Number of Provenances		45	52

The most important data were obtained from the 31 European larch provenances from indigenous stands. Description of the origin of these seed lots is presented in table 7. These provenances represented all three major subdivisions in the natural range of European larch: the Alpine, the Polish-Slovakian and the Sudeten (figure 2). The other IUFRO provenances from planted stands of European larch and other larch taxa are described in table 8. Data from these larch provenances and other provenances of unknown origin in the New York plantation were of limited value.

Table 6.--Description of methods used in establishment of the American IUFRO larch plantations.

	Data on the IUFRO Larch Plantation in New Hampshire	in New York
Nursery stock produced at	Fox State Forest, Hillsboro, New Hampshire	Saratoga Nursery, Saratoga Springs, New York
Seed sown at the nursery	May 9 to 23, 1946	June 4, 1946
Stock outplanted in the field	Early April, 1948	April 22 and 23, 1948
Stock age	2-0	2-0
Ground preparation	Sod removed in 1-foot square	No sod removal
Spacing	5 x 5 and 4 x 6	6 x 6
Arrangement of provenances	Rectangular plots	Rows
Plantation cleaning	Sprouts removed several times	One partial cleaning
Pruning	At age of 11 years, to 6-9 feet above ground	None
Present state (1958)	Clean, well marked, roads moved (figure 6)	Brushy, well marked

Figure 7.--The IUFRO larch plantation at the Fox State Forest, Hillsboro, New Hampshire, in 1958, 10 years after planting. It was well marked and well maintained.

Table 7.--Origin data, IUFRO larch provenances from native stands of European larch tested in the United States.

Provenance IUFRO No.	District, Location	North Latitude	East Longitude	Altitude
		° '	° '	meters
	Austria			
1	Salzburg, Blühnbach	49 29	13 10	600
3	Karnten, Hollenburg	46 33	14 18	900
4	Tyrol, Innsbruck	47 14	11 23	900
5	Lower Austria, Krumbach	47 31	16 12	600
6	Lower Austria, Lamerau	48 05	16 10	700
7	Tyrol, Landeck	47 08	10 37	750
8	Steiermark, Murau	47 08	14 10	950
9	Karnten, Obervellach	46 55	13 13	1100
10	Tyrol, Pitz Thal	47 05	10 50	1100
11	Tyrol, Ried-Tossens	47 00	10 37	1050
12	Lower Austria, Wartenstein	47 40	15 55	800
13	Tyrol, Steinach-Muhlbach	47 06	11 28	900
14	Steiermark, Waldstein	47 14	15 15	550
15	Salzburg, St. Michael i.L.	47 05	13 39	1700
16	Steiermark, Murau-Paal	47 04	14 06	950
17	Tyrol, Ried-Pflunds	46 55	10 35	1900
18	Tyrol, Steinach-Gries	47 02	11 28	1900
	Italy			
21	Belluno, Monte Col	46 32	12 26	1350
23	Trento, Lago (V. Fiemme)	46 17	11 23	925
24	Trento, Feugo (V. Fiemme)	46 20	11 27	1400
25	Bolzano, Val Venosta	46 35	10 40	1100
	Switzerland			
26	Wallis, Lötschenthal	46 23	7 47	1500
27	Graubungen, Untervaz	46 57	9 32	550
	Poland			
38	Kielze, Pinczow	50 30	20 30	270
39	Kielce, Zagnansk	50 58	20 42	350
42	Krakau, Nowy Sacz- Toki	49 38	20 42	450
43	Kielze, Starachowice	51 08	21 03	200
	Czechoslovakia			
46	--, Hubertkirch	50 04	17 18	700
47	--, Hubertkirch	50 04	17 18	700
51	Zilinsky, Liptowski C. V.	49 02	19 40	825
52	Zilinsky, Liptowski M.	49 02	19 40	1000

Table 8.--Origin data, IUFRO larch provenances from planted stands tested in the United States.

Provenance IUFRO No.	Species of Larch	Country, District, Location	North Latitude	East Longitude
			° '	° '
28	Japanese	Denmark, Djursland, Meilgaard	56 31	10 37
29	European	Germany, Hannover, Harbke	52 10	11 00
30	European	Germany, Wurtt. Baden, Neckargemund	49 23	8 49
31	European	Germany, Schl. Holst., Neu Munster	54 05	10 00
32	European	Poland, Slask Dabrowsky, Proskau	50 34	17 48
34	European	Poland, Mazury, Schlobitten	54 08	19 47
35	European	Poland, Gdansk, Sobbowitz	54 09	18 37
36	European	Poland, Gdansk, Stolp	54 28	17 06
44	Mixed: Eur. & Jap.	Poland, Warszawa, West Mala Wies	52 10	21 00
45	European	Czechoslovakia, Brenensky, Hrottowitz	49 16	16 07
49	European	Czechoslovakia, Ostravsky, Parchowitz	49 30	17 42
53	European	Scotland, Morayshire, Aldroughty Estate	57 39	3 23
54	Siberian	Sweden, Jonkopings lan, Visingso	58 02	14 20
55	European & Hybrids	Sweden, Jonkopings lan, Visingso	58 02	14 20

3. Plantation Arrangement and Replication

The IUFRO larch plantation in New Hampshire was arranged in 20 x 20-, 25 x 32.5-, 25 x 30-, and 25 x 45-foot square plots. It contained the following plots located at random: one for each of 31 provenances, 2 for each of 13 provenances, and 3 for one provenance. The plantation was divided into three compartments by two roads. However, this subdivision had no statistical meaning. For analysis of the replicated provenances, two completely randomized blocks were recognized. One of these occupied the western third and the other the eastern two-thirds of the plantation. As of the summer of 1958, the plantation included 38 provenances represented by over 20 trees and 7 provenances represented by 10 to 20 trees, border trees not counted.

The IUFRO larch plantation in New York was arranged in 29 rows, each consisting of 50 plants. The rows on either side were planted with tamarack. Each IUFRO larch seed lot was represented by a single plot and the provenances were planted in numerical order. Each plot consisted of a part of a row or parts of two adjacent rows, depending on the amount of planting stock available. In the summer of 1958, this plantation included 11 IUFRO larch provenances represented by over 20 trees, eight by 10 to 20 trees, and 19 by less than 10 trees. This representation did not include trees with broken tops and those growing on the plantation edges.

4. Measuring and Scoring

Seed testing was done at the Saratoga Nursery, New York, by E. J. Eliason. He determined 1,000-seed weights and germination percents at 8, 15, 20, and 45 days after seeding in Petri dishes under room conditions and in a Jacobsen germinator.

The types of measurements and scorings in the field are described in table 9. Heights were measured with simple graded poles at earlier ages; at the plantation age of 12 years a sliding pole was used with a rope and pulley. Diameters at breast height were measured with a diameter tape. Each tree was measured for height and diameter. Other scorings were made on the interior trees, that is, those that were not in the rows exposed to the outside of the plantation or to an open space of 15 or more feet. Early measurements, before 1958, were made by H. I. Baldwin in New Hampshire, and under the supervision of E. J. Eliason in New York. The 1958 measurements and scorings were the author's responsibility.

5. Statistical Analysis

Plot means and provenance means were used in the analyses of variance. Within-plot variation was largely due to natural competition. For this reason separation of genetical from environmental components within plots was not attempted.

When analyzing genetic differences, each provenance mean was based on all live trees in the plot except trees which were facing

Table 9.--Description of measurements and scorings made in the American IUFRO larch plantations.

Character Studied	Plantation Measured or Scored	Date	Age From Seed	Unit of Measuring or Scoring
			years	
Total height	New Hampshire (2-2 transplants)	Oct., 1949	4	0.1 foot
Total height	New Hampshire	Sept., 1952	7	0.5 foot
Total height	New York	Oct., 1954	9	0.5 foot
Total height	New Hampshire	July, 1958	12	0.5 foot
Total height	New York	July, 1958	12	0.5 foot
Diameter at breast height	New York	Oct., 1954	9	0.1 inch
Diameter at breast height	New Hampshire	July, 1958	12	0.1 inch
Diameter at breast height	New York	July, 1958	12	0.1 inch
Stem form	New Hampshire and New York	July, 1958	12	Number of crooks per tree in the lower 3/4 of stem
Stem form	New Hampshire and New York	July, 1958	12	Number of trees that exhibited slight crooks in the upper 1/4 of stem
Basal sweep	New Hampshire	July, 1958	12	Number of trees with basal sweep and exhibiting J-form
Lean	New Hampshire	July, 1958	12	Number of trees diverging more than 5° from vertical
Late snow damage	New Hampshire	July, 1958	12	Number of trees without foliage on the majority of interior branches
Damage by the woolly larch aphid	New Hampshire	July, 1958	12	Number of trees with more than 3 percent of needles attacked by aphids in the lower portion of crown
Damage by porcupines	New Hampshire	July, 1958	12	Number of trees with large sharp crooks

open spaces of at least 12 feet and trees with broken tops. Plots with more than 20 percent porucpine-damaged trees were entirely excluded from calculations of height and diameter means. Justification for these exclusions is discussed later.

Provenance mean heights based on the four largest trees per provenance and on the one largest tree per plot were also calculated. These were used to determine the value of quick measurement methods.

Percentage data used in the analyses of variance were transformed to angles corresponding to percentages, Angle = Arc sin $\sqrt{\text{Percentage}}$.

The IUFRO larch plantations in Hillsboro, New Hampshire, and Barkersville, New York, included 25 identical provenances of European larch from natural stands. These were subject to analysis of variance as follows:

Source	Degrees of Freedom
Total	49
Plantations	1
Provenances	24
Plantations x Provenances (Error)	24

Data of ten replicated provenances in two blocks in New Hampshire and in one block in New York were analyzed as follows:

Source	Degrees of Freedom
Total	29
Blocks	2
Provenances	9
Blocks x Provenances (Error)	18

Data based on the measurements and scorings in the New Hampshire plantation alone were analyzed after grouping the provenances into 10 geographic or altitudinal regions (table 10). This analysis of variance

Table 10.--Provenances of European larch from the native stands classified by geographic regions and elevation.

Origin of Seed Sources Region		Elevation	Provenances of European Larch			
		meters	IUFRO numbers			
Poland	Low	200- 450	38	39	42	43
Sudetenland, Chechoslovakia	Low	700	46	47	--	--
Slovakia, Chechoslovakia	Low	825-1000	51	52	--	--
Eastern Austria	Low	550- 800	14	5	6	12
Central Austria	Low	600- 950	1	3	8	16
Central Austria	High	1100-1700	9	15	--	--
Western Austria	Low	750- 900	7	4	13	--
Western Austria	High	1050-1900	11	10	17	18
Italy	High	925-1400	23	25	21	24
Switzerland	L. & H.	550-1500	27	26	--	--

between provenances from different regions was made by the statistical method as follows:

Source	Degrees of Freedom
Total	30
Between Regions	9
Within Regions (Error)	21

Standard method was used in correlation analyses of provenance means or characteristics of individual trees. Significance of r (correlation coefficient) was determined by Snedecor's method (79).

V. STUDIES RELATED TO SEED

1. Geographic and Altitudinal Variation in Seed Weight

The variation in average seed weight in three species of larch represented in the American IUFRO larch tests is shown below. These values were based on 1000-seed averages which included an unidentified proportion of empties which were difficult to separate from the sample. The seed of European and Japanese larch were of about the same weight but both these species had lighter seed than Siberian larch, as shown in the following tabulation.

Species	Provenances Studied	Seed Weight
	number	milligrams
European larch	33	4.3 to 8.6
Siberian larch	2	11.3 to 14.2
Japanese larch	1	6.2

The geographic pattern of variation in seed weight within European larch is shown in table 11. Analysis of variance based upon provenances classified by 10 different regions showed no significant differences among regions at the 5-percent level.

The possible presence of an altitudinal trend was tested by a correlation analysis in which altitude of provenance was the independent variable and seed weight was the dependent variable. Thirty-one pairs of these values were analyzed and showed a strong correlation (significant at the 5-percent level, with $r = .371$ for 29 d.f.). This

Table 11.--The geographic pattern of variation in European larch with respect to seed weight.

Origin of Seed Source		Seed Weight	
Region	Elevation	By Provenance	Average
	meters	milligrams	milligrams
Eastern Austria	550- 800	6.0, 4.6, 4.7, 4.3	4.9
Central Austria	600- 950	5.0, 5.0, 5.0, 5.2	5.0
Poland	200- 450	6.3, 4.7, 5.9, 4.6	5.4
Slovakia	800-1000	5.4, 5.6	5.5
Sudetenland	700	5.9, 5.0	5.5
Central Austria	1100-1700	6.2, 5.0	5.6
Western Austria	1050-1900	6.2, 5.7, 5.9, 5.6	5.9
Western Austria	600- 950	6.6, 5.7, 5.9	6.1
Switzerland	550-1500	4.4, 8.6	6.5
Italy	900-1400	6.7, 7.1, 6.7, 5.8	6.6

indicated that provenances from higher altitudes had heavier seed. The general trend of this altitudinal variation is illustrated in the following tabulation:

Elevation	Provenances Studied	Average Seed Weight
meters	number	milligrams
Below 750	13	5.2
750 - 1000	8	5.6
Over 1000	10	6.3

Bouvarel studied 37 non-IUFRO seed lots of European larch and found differences in seed weights as follows (8):

Origin and Elevation	Seed Lots Studied	Average Seed Weight
	number	milligrams
Sudetenland-Poland (300-800 meters)	6	3.5
Austria (300-1200 meters)	13	5.5
Western Alps (Brianconais) (1200-1700 meters)	18	9.3

These findings support the conclusion that high-altitude provenances of European larch mainly in the western parts of its range have heavier seeds than those from low altitudes in the eastern part of the range.

At present, this variation must be regarded as phenotypic. As far as known, there have been no critical experiments showing that high elevation sources produce larger seeds if grown at low elevations.

2. Relationship Between Weight and Tree Height

Seed weight is one of the factors which may affect the performance of young seedlings because a higher content of stored food naturally favors early growth. This has been observed in many species. For example, the height of white pine (*Pinus strobus* L.) seedlings at the age of 1 and 2 years depends very strongly on seed weight (57). This was also evident in European larch from Engler's data when provenances came from relatively the same region (21, 38).

In this study a test was made to determine the relation between seed weight and average height of 4-year-old seedlings (table 12). Analysis of 27 pairs of these values showed a significant negative correlation ($r = -.392$, significant at the 5-percent level with 25 d.f.). This negative correlation indicated that provenances with heavier seed (those from higher elevations) exhibited relatively slow growth. Similar results were obtained from an analysis of Cieslar's data (38). Analysis of his data on seed weights and 1-year heights for five provenances showed a negative correlation ($r = -.385$, not significant at the 5-percent level with 3 d.f.).

These results apparently disagree with earlier conclusions that seed weight and juvenile growth are positively correlated. The disagreement is more apparent than real because present data were based on seed sources from a broad geographical and altitudinal range in which case hereditary factors acting with respect to height growth overruled the effect of seed weight on seedling growth.

It is concluded that seed weight in European larch is not a reliable factor in indicating future height growth.

3. Rate of Germination

The IUFRO European larch tested in the United States showed an average germination of 26 percent. The Japanese and Siberian larch IUFRO seed lots had average germination of 27 and 55 percent, respectively.

Table 12.--Seed weights and 4-year heights in 27 corresponding provenances tested in Hillsboro, New Hampshire. The seed weight-tree height correlation was negative (r = -.392, significant at the 5-percent level with 25 d.f.).

Provenance IUFRO No.	Average Seed Weight	Average 4-Year Height
	milligrams	feet
26	8.6	1.7
25	7.1	1.7
21	6.7	1.5
7	6.6	2.7
38	6.3	2.5
11	6.2	2.0
9	6.1	2.0
14	6.0	2.2
46	5.9	2.2
42	5.9	2.9
13	5.9	2.4
17	5.9	2.3
24	5.8	1.8
52	5.7	2.0
10	5.7	1.6
4	5.7	2.6
18	5.6	2.1
51	5.4	2.5
16	5.2	1.9
1	5.0	2.2
3	5.0	2.7
8	5.0	2.5
15	5.0	2.0
6	4.7	2.2
5	4.6	2.1
43	4.6	2.8
12	4.3	2.4

European larch showed a broad variation in germination percentage. The range for individual seed lots was from 1 to 75 percent. However, no attempt was made to relate this variation to the genetics of the species because germination may have depended on many environmental factors such as storage and transportation conditions.

A study to determine the rate of germination was conducted for 45 days in 31 different provenances of European larch and 3 provenances of other species. There were no statistically significant differences among provenances from different regions in European larch. The combined data for European, Siberian, and Japanese larches showed germination rates as follows:

Species of Larch	Germination in Different Periods After Seeding 0-7 Days	8-10 Days	11-15 Days	16-20 Days	21-45 Days	Average Germination Time
	- - - - - -	- - -	percent	- - -	- - - - - -	days
European	58	26	14	1	1	11
Siberian	26	51	23	0	0	9
Japanese	7	10	31	30	22	18

European larch completed more than half of the total germination in 7 days and 99 percent in 20 days. These results agreed with germination data in Germany, where European larch completed 75 percent of its germination in 10 days (60). These results indicate that in this species germination involves few problems to obtain uniform progeny the first year.

In Siberian larch germination did not start quite as soon as in European larch, but once initiated the average germination rate was slightly faster. Japanese larch germination was slower than either of the other two species. This slowness agrees with the results of Langner, who found that Japanese larch may germinate as late as 65 days after sowing (40).

The more rapid germination in European larch appears unrelated to the thickness of seed coat, because the coat is thicker in this species (.2 mm) than in Japanese larch (.1 mm). It may be related to the radicle or the higher rate of respiration in European larch seed than in that of Japanese larch (64).

VI. EFFECT OF SPACING

I studied the effect of spacing on height and diameter growth in order to determine whether to include border trees in the plot means for the comparative analyses and to determine whether differences in spacing of trees within plots affected height growth sufficiently to make an adjustment for spacing necessary.

At the IUFRO larch plantation in New Hampshire, the majority of plots were either inside the plantings or were bordered by one or two rows of trees especially planted to eliminate border effect. However, along the roads 24 plots were exposed on one or two sides to open spaces of 12 feet or more. On the basis of height and diameter measurements which were made for each tree in the plantation, means were calculated separately for interior trees and border trees (table 13). The interior trees averaged 2.5 feet taller and 0.4 inches greater in diameter than the border trees. Analyses of variance based upon plot means showed that these differences were significant at the 1-percent level. Following these findings, the border trees were excluded from the plot means used in genetic analyses.

The IUFRO larch plantation in New Hampshire included 38 plots of European larch from natural stands in which average space per tree was calculated by dividing plot size by number of trees. Only interior portions of the plots were used in calculations. The space per tree in different plots varied from 23 to 63 square feet because of initial spacing and survival. The correlation between space per tree and

Table 13.--Average 12-year heights and diameters at breast height of interior trees compared with those of border trees, based on the New Hampshire IUFRO larch data. The differences between border trees and interior trees are significant at the 1-percent level.

IUFRO No. and Plot Symbol	Mean Heights		Mean Diameters	
	Border Trees	Interior Trees	Border Trees	Interior Trees
	------ feet -------		----- inches -------	
1 b	18.1	20.1	2.2	2.8
3 b	18.1	19.2	2.5	2.6
6 a	21.0	21.0	2.9	2.9
6 b	16.8	17.7	1.7	2.4
7 a	16.8	17.7	2.5	2.5
8 b	14.3	16.5	1.7	2.2
9 a	14.7	17.3	1.9	2.3
12 b	12.1	11.8	1.0	1.4
13 a	11.8	16.9	1.5	2.1
16 a	15.5	17.6	2.6	2.3
21 a	8.0	15.2	.9	2.3
23 b	14.8	18.0	2.0	2.7
26 a	11.0	13.7	1.6	2.0
27 a	13.7	14.6	1.2	2.1
30 a	13.9	19.0	1.8	2.4
31 a	19.8	22.2	2.7	2.7
34 b	16.3	17.9	1.8	2.4
35 a	18.3	21.1	2.7	2.7
36 a	13.3	17.1	1.8	2.0
45 b	23.0	23.6	2.4	2.6
46 a	19.6	21.0	1.6	2.2
47 a	20.9	25.9	2.9	2.9
52 b	14.3	17.9	1.6	2.2
55 b	16.0	18.0	2.2	2.4
Average	15.9	18.4	2.0	2.4

average height per plot was weak ($r = -.158$, not significant at the 5-percent level for 36 d.f.). Accordingly, there was no reason to adjust plot mean heights for differences in spacing.

VII. GENETIC DIFFERENCES IN GROWTH CHARACTERS

1. Twelve-Year Heights and Diameters

The geographic pattern of variation in 12-year heights among origins of European larch was determined on the basis of New Hampshire data. Analysis of variance showed very significant differences among provenances from different regions (table 14). Provenances from Poland, Sudetenland, and Slovakia were significantly (at the 5-percent level) faster growing than those from other regions. The slowest growing origins were from Switzerland, Italy, and the higher elevations in Austria. Among provenances from the Alps, those from lower elevations in Central Austria showed the best height growth and were significantly superior (at the 5-percent level) to provenances in Switzerland.

Differences among provenances from the same region were studied from analysis of variance of the plot mean heights of the 25 provenances which were represented once in New Hampshire and once in New York, and of the 10 provenances which were represented, twice in New Hampshire and once in New York (tables 15 and 16). There were no instances in which provenances from the same region differed significantly.

Similar analyses were made to determine the geographic variation pattern in 12-year diameter breast high (tables 14 and 15). The Slovakian provenances were not significantly larger in diameter than the slowest growing origins although they had been in height. Otherwise,

Table 14.--Geographic variation in European larch with respect to 12-year height and diameter breast high, New Hampshire data.

Origin of Seed Sources: Region	Origin of Seed Sources: Elevation	Average Height	Difference Levels* at Percent: 5	Difference Levels* at Percent: 1	Average Diameter Breast High	Difference Levels* at Percent: 5	Difference Levels* at Percent: 1
	meters	feet			inches		
Poland	200- 450	23.8	S	S	3.07	S	S
Sudetenland	700	23.5	S	S	3.00	S	. S
Slovakia	800-1000	21.6	S	. S	2.50	I	. .
Central Austria	600- 950	18.6	I S	. . S	2.45	I	. .
Western Austria	750- 900	18.4	I .	I . .	2.37	I	I .
Eastern Austria	550- 800	17.4	I .	I I .	2.30	I	I I
Western Austria	1050-1900	17.2	I .	I I .	2.25	I	I I
Central Austria	1100-1700	17.1	I .	I I .	2.25	I	I I
Italy	900-1400	16.0	I .	I I .	2.15	I	I I
Switzerland	550-1500	14.2	I I	I I I	2.05	I	I I

* Provenances from the regions marked "S" had superior growth to those from the regions in the same column marked "I".

the ranking of the provenances and the significance relationships were almost the same for diameter as for height.

2. Stem Straightness

Stem straightness may depend on hereditary factors. Burger observed that offspring from poorly formed mother trees exhibited more

Table 15.--Geographic variation in European larch with respect to 12-year heights and diameters based on the data on the IUFRO larch plantations in Hillsboro, New Hampshire, and Barkersville, New York.

IUFRO No.	Origin of Seed Source: Region	Origin of Seed Source: Elevation	Average Diameter Breast High	Average Height	Levels of Significance in Differences of Heights*: 5-percent	Levels of Significance in Differences of Heights*: 1-percent
		meters	inches	feet		
42	Sudetenland	700	2.95	21.5	S	S
47	Poland	450	3.05	21.5	S	S
38	Poland	350	2.90	20.0	. S	. S
43	Poland	200	2.60	19.4	. . S	. . S
51	Slovakia	825	2.40	18.8	. . . S	. . . S
4	Western Austria	900	2.85	18.0	. . . . S	. . . . S
1	Central Austria	600	2.70	17.9	. . . . S	. . . . S
6	Eastern Austria	700	2.60	17.8	. . . . S	. . . . S
14	Eastern Austria	550	2.65	17.6	. . . . S	. . . . S
7	Western Austria	750	2.80	17.2	. . . . . S	. . . . .
17	Western Austria	1900	2.35	17.0	. . . . . S	. . . . .
23	Italy	925	2.80	16.9	. . . . . S	. . . . .
52	Slovakia	1000	2.20	16.7	. . . . . S	. . . . .
12	Eastern Austria	800	2.15	16.6	. . . . . S	. . . . .
16	Central Austria	950	2.15	16.2	I . . . . S	. . . . .
24	Italy	1400	2.25	15.1	I	. . . . .
8	Central Austria	950	2.35	15.0	I	. . . . .
13	Western Austria	900	2.10	15.0	I	. . . . .
18	Western Austria	1900	2.25	14.5	I I	I . . . .
5	Eastern Austria	600	2.15	14.1	I I I . . .	I . . . .
21	Italy	1350	2.05	13.4	I I I I . .	I . . . .
27	Switzerland	550	1.90	13.0	I I I I . .	I I . . .
15	Central Austria	1700	1.60	12.2	I I I I I .	I I I . .
26	Switzerland	1500	1.65	11.4	I I I I I .	I I I I .
25	Italy	1100	1.35	10.6	I I I I I I	I I I I I

* Provenances marked "S" had significantly greater heights than those in the same column marked "I". The significance relationships were almost the same for the diameter data.

Table 16.--Differences in 12-year height among provenances of larch, based on the data of two randomized blocks planted in New Hampshire and one block in New York.

IUFRO No.	Origin of Seed Sources: Region	Origin of Seed Sources: Elevation	Average Height	Differences in Provenances at the 5-Percent Level**	
		meters	feet		
45*	Czechoslovakia	---	22.0	S	
1	Central Austria	600	18.5	I	S
6	Eastern Austria	700	18.3	I	S
34*	Poland	---	17.7	I	S
23	Italy	925	17.3	I	.
52	Slovakia	1000	17.0	I	.
3	Central Austria	900	17.0	I	.
55*	Sweden	---	16.0	I	.
8	Central Austria	950	15.8	I	.
21	Italy	1350	14.2	I	I

* Provenances from planted stands.

** Provenances marked "S" had significantly greater heights than those in the same column marked "I".

crooks than those from straight stems, but included no statistical proof of his finding (6). Other factors may affect stem straightness, including soil fertility (24, 28).

In the present study two methods were used to score stem straightness. First, I scored the upper stem for crooks of any size. Those crooks were due almost entirely to crooked leader growth. Second, I counted the number of large crooks (more than 1.5 inches offset) per 100 feet of stem in the lower three-quarters of stem of each tree.

The New Hampshire data were used to establish the geographic pattern of variation in stem straightness (table 17). Analysis of variance showed that provenances from Sudetenland, Poland, and low

Table 17.--Geographic variation in European larch with respect to stem form, New Hampshire data.

Origin of Seed Source: Region	Origin of Seed Source: Elevation	Trees With Crooks in Upper Stem	5-Percent Difference Level*	Crooks per 100 Feet of Stem Length	5-Percent Difference Level*
	meters	percent		number	
Sudetenland	700	42.5	H	5.1	L H
Poland	200- 450	41.5	H	4.4	L .
Western Austria	750- 900	38.7	. H	8.8	H .
Eastern Austria	550- 950	25.5	. . H	3.2	L .
Central Austria	600- 950	24.8	. . H	3.3	L .
Slovakia	800-1000	24.0	L . H	2.3	L .
Italy	900-1400	22.3	L L H	2.8	L .
Switzerland	550-1500	19.5	L L .	3.6	L .
Western Austria	1050-1900	16.6	L L .	4.3	L .
Central Austria	1100-1700	8.5	L L L	1.7	L L

* Provenances from region marked "H" exhibited significantly higher values than those from regions in the same column marked "L".

elevation Western Austria had significantly higher percentages of trees with small crooks in the upper stem than most provenances from other regions. Austrian provenances showed altitudinal differences; those from lower elevations (below 1000 meters) had significantly more small crooks in the upper stem than those from higher elevations.

Provenances that had larger number of trees with small crooks in the upper stem also had large number of crooks in the lower stem.

Analysis of variance showed that crooks per 100 feet of stem length were most numerous among provenances from low elevations in Western Austria. Provenances from Sudetenland ranked second and had significantly more crooks than the lowest ranking provenances from high elevations in Central Austria.

In order to determine the variation among provenances within regions, the combined data from New Hampshire and New York were subjected to the analysis of variance. Significant within-region differences were found among provenances from low-elevation Western Austria as shown in the following tabulation:

Origin	Crooks per 100 Feet of Stem
	number
IUFRO- 7 from Landek, Tyrol	15
IUFRO-13 from Steinach, Tyrol	12
IUFRO- 4 from Innsbruck, Tyrol	6

Number of crooks in IUFRO-7 was significantly higher (at the 5-percent level) than in IUFRO-4.

No within-region variation was determined among provenances from other regions.

3. Basal Sweep and Lean

"Basal sweep" is a term used to indicate a bend at the base of a J-shaped tree with an otherwise vertical bole. "Lean" is a deviation of the entire stem from the vertical. Both characteristics resulted from bending of already-formed stems rather than crooked growth of the leader. A great deal of the bending occurred during the first two years after planting and resulted in a basal sweep which was confined to the lower 3 or 4 feet of the bole. Also, a large proportion of the trees appeared to have been bent in 1956 or 1957, just prior to the measurements. Those were the leaners with straight but off-vertical stems. Intermediate types in which there was a bend part way up the bole were uncommon.

Apparently the bending was caused by the weight of snow and ice which laid the recently planted and inadequately rooted trees on the ground. When they subsequently became firmly rooted, they grew vertically. This type of snow damage is not noticeable in firmly rooted larch seedlings grown from seed in the nursery. The explanation for the lean is similar except that the wind acted more strongly and the damage occurred later in the life, involving the partial upheaval of a large root system. Plant characteristics that are associated with the mechanics of basal sweep or lean, such as root size in relation to the tree height or shape and density of crown, are hereditary and may react differently on the basis of origin. Fischer studied eight mother trees and their open pollinated progenies with respect to stem form and found that basal sweep was under genetic control (20).

In extreme cases, such as reported by Burger in Adlisburg, mother trees of very poor stem form with crooks and with basal sweep exhibited in their open-pollinated offspring various distinct crooks on the stem including basal sweep (6).

In order to determine the relation between height and lean, I classed the 109 trees of provenance IUFRO No. 45, that were growing in three plots, as either leaning or vertical. Distribution of 12-year heights in these two classes was as follows:

	Average Twelve-Year Heights, Feet			
	Plot A	Plot B	Plot C	Provenance Mean
Leaning trees	23.2	24.0	25.3	24.2
Vertical trees	22.0	23.8	24.3	23.4

Analysis of variance between the heights of leaning trees and those of vertical trees showed no significant differences at the 5-percent level. This indicated that heights within a provenances had little or no effect on lean. Different results were obtained in the analysis of the correlation between average 12-year heights and corresponding average percentages of leaning trees in 38 different provenances. The correlation coefficient, r = .523, was significant at the 1-percent level, which indicated that provenances with greater heights had higher percentages of leaning trees.

Analysis of variance of the transformed percentages of leaning trees showed distinct differences between provenances from different regions (table 18). Provenances from Poland, Sudetenland and lower elevations in Western Austria exhibited more leaning trees than those from other regions. The fewest leaning trees were found in Italian and high-elevation Austrian provenances. The analysis also showed that there were altitudinal differences among the Austrian provenances. The provenances from higher elevations probably owed their superiority to higher root-stem ratios and firmer anchoring in the ground.

Table 18.--Geographic variation in European larch with respect to percentage of trees with 5° or more lean, and percentage of trees exhibiting basal sweep, New Hampshire data.

Region	Elevation	Trees With 5° or More Lean[1]	5-Percent Difference Level[1]	Trees Exhibiting Basal Sweep[2]
	meters	percent		percent
Poland	150- 300	56.5	H	59.2
Sudetenland, Czech.	700	49.5	H	37.2
Western Austria	750- 900	48.7	H	71.9
Eastern Austria	550- 800	22.3	L H	27.7
Central Austria	600- 950	21.3	L H	41.7
Switzerland	550-1500	20.5	L H	7.4
Tatra Mtns., Czech.	800-1000	11.0	L .	24.7
Italy	900-1400	7.5	L L	36.7
Western Austria	1100-1900	7.3	L L	22.5
Central Austria	1100-1700	4.0	L L	15.9

1/ Provenances from regions marked "H" had significantly more leaning trees than those from regions in the same column marked "L".

2/ L.S.D. 5% 23.0; L.S.D. 1% 37.0.

Analysis of variance of the transformed percentage of trees exhibiting basal sweep also showed significant differences in provenances from different regions (table 18). As in the case of lean, provenances from lower elevations in Western Austria and Poland exhibited the highest percentages of trees with basal sweep. Provenances from higher elevations in Austria exhibited the fewest trees with basal sweep. Italian provenances have been more subjected to bending during juvenile growth than at more advanced ages and consequently exhibited relatively higher percentage of trees with basal sweep than those with lean.

Among the faster growing provenances, those from the Tatra Mountains (Czechoslovakia) and from Eastern Austria exhibited relatively low numbers of trees with lean or basal sweep. However, the fastest growing provenances from Poland were highly affected.

4. Late Snow Damage

In Southern New Hampshire the spring of 1958 was abnormal. The buds of European larch started growing in mid-April and leaves were fully developed by April 26. On that date about one foot of wet snow fell. This late snow caused severe defoliation of the upper portions of the crowns and less severe stripping of the needles on the lower branches. In the two months following defoliation new needles developed on the outer branches but not on the inner branches of damaged trees. This caused the needles to be clustered and trees to have ragged appearance.

In July trees were scored that exhibited the bare branches in the inner portion of the crown. This characteristic was interpreted as related to the late snow damage. Percentages of trees with bare inside branches per provenance provided the data for analysis of variance (table 19). Provenances from Sudetenland and Slovakia showed the highest percentage of defoliated trees. Italian, Swiss and high-elevation provenances were affected the least. Western Austrian provenances showed altitudinal differences; low elevation provenances were very significantly more defoliated than the high-elevation provenances.

Table 19.--Geographic variation in European larch with respect to percentage of trees exhibiting bare branches in the inner portion of crowns as a result of the late snow in the spring of 1958, New Hampshire data.

Provenances From Region	Elevation	Trees Heavily Defoliated	Levels of Significance in Differences* at 5% Level			at 1% Level		
	meters	percent						
Sudetenland, Czech.	700	47.0	H			H		
Slovakia, Czech.	800-1000	44.5	H			.	H	
Eastern Austria	550- 800	34.8	.	H		.	.	H
Western Austria	750- 900	28.3	.	.	H	.	.	.
Poland	150- 300	26.0	.	.	.	.	.	.
Central Austria	600- 900	16.3	L	.	.	L	.	.
Western Austria	1050-1900	14.3	L	L	.	L	L	.
Switzerland	550-1500	13.5	L	L	.	L	L	.
Central Austria	1100-1700	11.0	L	L	.	L	L	.
Italy	900-1400	7.0	L	L	L	L	L	L

* Provenances from regions marked "H" exhibited significantly higher percentages of bare branches inside the inner portions of crowns than those in the same column marked "L".

5. Damage by Woolly Larch Aphid

The woolly larch aphid (*Chermes strobilobius* Kalt.) was first observed attacking the IUFRO larch plantation in Hillsboro, New Hampshire, in 1957, seven years after it was established. This is a sucking insect belonging to the *Chermides* family. It attacks red and black spruces as well as European larch; it appears as white woolly masses on the needles, as dark individuals on the underside of twigs and as clusters of individuals at the base of the leaves (17).

In the spring of 1958 following the snow damage on the foliage at the end of April and subsequent damp weather conditions, the IUFRO larch plantation was again heavily attacked by the woolly larch aphid. In July this attack resulted in yellow or brown stripes on the needles of the short shoots. Injured leaves bent sharply at the point of injury and infested short shoots appeared as dense clusters rather than as open rosettes (figure 8). By August needles that were attacked started to fall, leaving the short shoots of heavily infested trees nearly devoid of foliage.

This IUFRO larch plantation in Hillsboro, New Hampshire, was scored in July with respect to number of trees that showed more than 5 percent of needles injured at the lower parts of the crown. Percentages of such trees per provenance were transformed to Arc sin $\sqrt{\text{Percentage}}$ and subjected to the analysis of variance, which revealed significant differences at the 5-percent level between provenances from different regions (table 20). Provenances from the Sudetenland, Slovakia and Eastern Austria were more attacked by the woolly larch aphid than those from Poland, Central Austria and in high elevations in Western Austria. Italian, Swiss and low-elevation Western Austrian provenances had intermediate damage.

Provenance IUFRO-53, from planted stands, exhibited only two percent of trees heavily infested by the woolly larch aphid, while European larch from natural stands showed 4 to 65 percent.

Figure 8.--Sudeten larch was heavily attacked by the woolly larch aphid (*Chermes strobilobius* Kalt.). The clumps of foliage arose in response to the aphid damage.

Table 20.--Geographic variation in European larch with respect to percentage of trees heavily infested by woolly larch aphid, based on the data of IUFRO larch plantation in Hillsboro, New Hampshire, obtained in July 1958.

Origin Region	Elevation	Heavily Injured Trees	5-Percent Significance Level*	
	meters	percent		
Sudeten Mtns., Czech.	700	55.5	H	
Tatra Mtns., Czech.	800-1000	42.0	.	H
Eastern Austria	550- 800	41.0	.	H
Italy	900-1400	21.5	L	.
Switzerland	550-1400	20.5	L	.
Western Austria	750- 900	18.3	L	.
Poland	170- 270	15.8	L	L
Western Austria	1050-1900	14.5	L	L
Central Austria	1100-1700	12.0	L	L
Central Austria	600- 950	10.7	L	L

* Provenances from the regions marked "H" were significantly more attacked by the woolly larch aphid than those in regions marked "L".

6. Damage by Other Agencies

a. Porcupine Damage

Porcupines (Erethion dorsatum dorsatum Linnaeus) may cause considerable damage in European larch plantations (35, 80). In winter when food is scarce, larch and other conifers are often girdled. Vigorous trees usually recover from partial damage. However, complete girdling or invasion of injuries by disease results in die-back of tops, development of crooks, and delayed height growth.

At the IUFRO larch plantation in New Hampshire, the author tallied the crooked trees whose damage was apparently caused by porcupines. Because of inadequate replication and because attack by porcupines were not random, genetic variation in susceptibility to porcupine injury was not established. In one corner of the plantation, within a radius of about 150 feet of porcupine dens, 40 percent of the trees were damaged. Plots in this area were unsuited for comparative height studies. The remainder of the plantation showed a relatively small number of trees attacked (an average of about 4 percent per plot).

Also, the author scored the porcupine damage in a 21-year-old larch plantation at the Fox State Forest, Hillsboro, New Hampshire. Under similar vulnerability of porcupine attack, 43 percent of European larch trees were girdled while Japanese larch had only 13 percent of the trees damaged.

b. Larch Canker in Europe

Larch canker is caused by the fungus Dasyscypha willkommii (Hartig) Rehm. Its fructification covers the infected areas with red to dirty-white or yellow dots of less than one-eighth inch in size. The fungus causes a depression in the bark of the stem. As the tree grows in thickness, the infected areas on the flanks of the canker remain in bowl-like cavities. At later stages the wood is weakened to the extent that young trees may be killed outright and the older trees are predisposed to wind or snowbreak (29, 35).

The disease is native in the Alps. Thence it spread to planted stands in other parts of Europe where it became the most important destructive agent of European larch (65).

The fungus was probably introduced into the United States on the stock received from Scotland in 1904 or 1907. It was first found in this country in 1927 at the Harvard Forest's plantation at Hamilton, Massachusetts, and was later reported from Ipswich, Massachussetts. The diseased trees were removed from these plantations in 1930. It has not been reported in this country since that time (29, 35).

Larch canker attacks in various degree European as well as Japanese and Siberian larches. Kiellander reported the following data on susceptibility to larch canker (39):

Species	Provenances Studied	Trees: Attacked by Canker	Trees: Dead Tops
	number	% per provenance	% per provenance
European larch	19	29 to 92	3 to 86
Japanese larch	2	3 to 6	1
Siberian larch	1	43	3

I ran a "t" test on his published data and found that provenance IUFRO-51 from Slovakia with 29 percent of attacked trees was significantly less susceptible to larch canker than provenances the most heavily attacked. European investigators believe that provenances from Poland, Slovakia and Sudetenland are more resistant to canker than those from other regions (65).

7. Summary of the European Larch Racial Test Data

Summary of the data on eight characteristics of European larch studied in the New Hampshire IUFRO larch plantation is represented as percents of the plantation means in table 21. Graphic illustration of characteristics of provenances from different regions is shown in figure 9. A key to the origins based on statistically proven differences is presented in table 22.

Within-region variation was studied on the basis of combined New Hampshire and New York data. There were significant differences between provenances from low elevations in Western Austria in stem straightness. The provenance IUFRO-7 had significantly more crooks per 100 feet of stem than the IUFRO-4. No within-region genetic variations were detected in height performance.

Table 21.--Summary of the data of the European larch racial test (IUFRO) at the Fox State Forest, Hillsboro, New Hampshire.

Origin Region, Elevation	Height	DBH	Crooks in Lower Stem	Crooks in Upper Stem	Over 5° Lean	Basal Sweep	Aphid Damage	Bare Inside Branches
	- - - - - -	percent	of the	plantation	mean	- - - - -		
Switzerland 550-1500 meters	76	85	90	73	60	20	86	57
Italy 900-1400 meters	86	89	70	84	29	100	90	30
Western Austria 1050-1900 meters	93	93	108	62	29	61	61	61
Western Austria 750-900 meters	99	98	220	145	198	196	76	120
Central Austria 1100-1700 meters	92	93	43	32	16	43	50	47
Central Austria 600-900 meters	100	101	83	93	83	114	48	69
Eastern Austria 550-900 meters	94	95	80	96	87	76	171	148
Slovakia 800-1000 meters	116	103	58	90	43	78	176	189
Sudetenland 700 meters	126	124	128	159	193	101	232	199
Poland 200-450 meters	128	127	110	156	220	161	66	110
	feet	inches	no.*	- - - -	percent	of trees	- - - -	
Plantation mean	18.6	2.42	4.0	26.7	25.6	36.6	23.9	23.6

* Number of crooks per 100 feet of stem length.

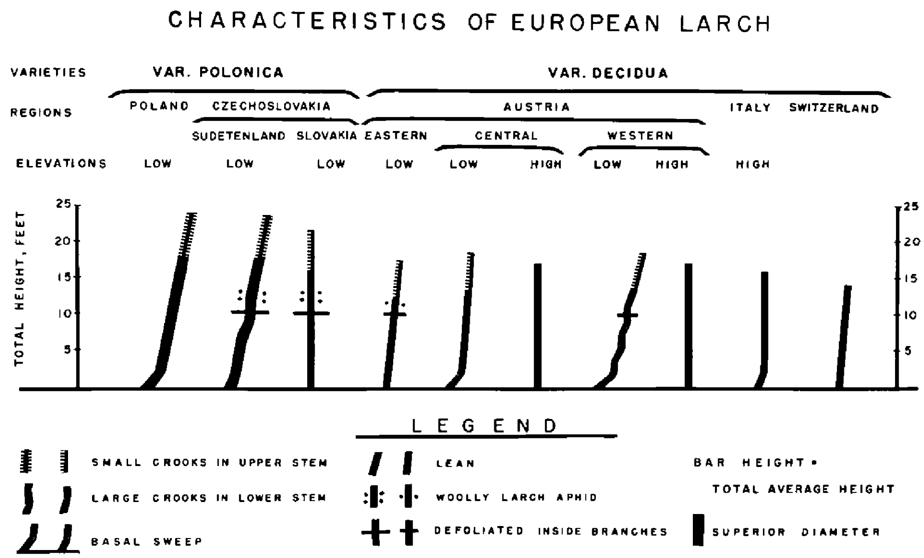

Figure 9.--Graphic summary of the data by characters and regions. Slovakian origins were the best with respect to production of quality timber.

Table 22.--Classification of origins by statistically proven (at the 5-percent level) differences.

1. Rapid height growth (1.8 to 2.0 feet per year)

    2. Large diameters (3 inches in 12 years); many trees leaning (50 to 56 percent) and many trees with small crooks in upper stem (41 to 53 percent)

        3. Few trees attacked by woolly larch aphid (16 percent) . . . . POLISH ORIGINS

        3. Many trees attacked by woolly larch aphid (46 percent) . . . . SUDETEN ORIGINS

    2. Moderate diameters (2.5 inches in 12 years), few leaning trees (11 percent) and few trees with small crooks in upper stem (24 percent) . . . . SLOVAKIAN ORIGINS

1. Slow to moderate height growth (1.2 to 1.6 feet per year)

    3. Many crooks in lower stem (9 per 100 feet of stem), many trees with basal sweep (72 percent), many trees leaning (49 percent) . . . . LOW-ELEVATION WESTERN AUSTRIAN ORIGINS

    3. Few crooks in lower stem (less than 5 per 100 feet of stem), few trees with basal sweep (less than 42 percent), few trees leaning (less than 23 percent)

        4. Few trees lean (21 to 23 percent)

            5. Few trees with basal sweep (28 to 42 percent)

                6. Many trees attacked by woolly larch aphid (41 percent). . . EASTERN AUSTRIAN ORIGINS

                6. Few trees attacked by woolly larch aphid . . LOW-ELEVATION CENTRAL AUSTRIAN ORIGINS

            5. Very few trees with basal sweep (8 percent) . . . . SWISS ORIGINS

        4. Very few trees lean (4 to 8 percent) ITALIAN, HIGH-ELEVATION CENTRAL AND WESTERN AUSTRIAN ORIGINS

VIII. RELATIONSHIP BETWEEN GENETICS, TAXONOMY AND DISTRIBUTION

1. Relationship Between Genetics and Taxonomy

European larch consists of two varieties, *Larix decidua* var. *decidua* and *L. decidua* var. *polonica*. Genetical characteristics of populations belonging to these varieties are illustrated in figure 9. Statistical analysis showed that provenances from Poland, Sudetenland and Slovakia, which belong to the *L. d.* var. *polonica*, had significantly greater heights than those from other regions belonging to *L. d.* var. *decidua*. Other characteristics studied were distributed in both varieties. Provenances from Slovakia of one variety differed from their closest neighbors, the East Austrian provenances of another variety, only in two characteristics, height and lean.

2. The Genetic Variation Patterns Summarized by Regions

The pattern of geographic variation in European larch was largely systematic. Characteristics of provenances originating from the same geographic or altitudinal regions were similar. Evidently most of the geographic variation has taken place because of selection pressure. A discontinuity in genetical characteristics was observed between Polish-Sudeten origins and those from Slovakia. Altitudinal differences were evident in the provenances from Central and Western Austria.

Discontinuities in some characteristics between provenances from different regions were not evident because the data were not precise.

a. Polish Larch

Polish larch grows in scattered stands in central and southern Poland. It was represented in this study by four provenances which grew very rapidly and had large diameters (tables 21 and 22). Many trees exhibited lean, basal sweep and small crooks in the upper stem, but had only a moderate number of crooks in the lower stem. They suffered only slightly from the woolly larch aphid. From the standpoint of cellulose production, these Polish provenances were best of all origins studied.

The rapid growth, resistance to late spring frosts, and resistance to larch canker have been reported as characteristics of Polish larch by several European investigators (23, 33, 36, 73). However, most of these observations were based on unreplicated tests.

b. Sudeten Larch

The Sudeten population of European larch has its isolated range in Sudetenland, Czechoslovakia. It was represented in this study by two provenances. They were similar to the Polish provenances in all characteristics except in their greater susceptibility to the woolly larch aphid.

Provenances from Sudetenland have frequently been represented in European tests. All these agree regarding its rapid growth (9, 10, 18, 19, 24, 45, 73). It was also observed that Sudeten larch, in comparison to larches from the Alps, was less resistant to drought but more

Figure 10.--Polish larch (IUFRO-38) in New Hampshire. Twelve-year height averaged 24 feet and diameter at breast height 3 inches.

resistant to larch canker; it had wider crowns, smaller branch diameters and paler, more pendulous twigs (18, 23, 45, 65).

c. Slovakian Larch

Slovakian larch, which grows in the Tatra and other mountains in the eastern part of Slovakia, was represented in this study by two provenances. They grew rapidly in height but had smaller diameters than Polish or Sudeten larches. Only a few trees had basal sweep, crooks in the lower stem, or lean. However, they were heavily attacked by the woolly larch aphid. Considering both volume and quality production, they seem the best origins to recommend for the Northeast.

Siman suggested that Slovakian population of European larch consists of three ecotypes (77, 78). I have not been able to find the basis for this conclusion. Earlier investigators observed that Slovakian larch is slightly slower growing than either Polish or Sudeten larches, but more rapid than those from the Alps (67, 69, 72, 73). Slovakian larch in Sweden and elsewhere showed a moderate resistance to larch canker (64, 78).

d. Low-Elevation (550-950 meters) Larch From Austria

The low-elevation larches from Austria represented in this study originated from the northern and eastern foothills of the Alps. They grew significantly slower than provenances from either Poland, Sudetenland or Slovakia.

Three provenances were represented from low elevations in Western Austria. On the average they had moderate growth, but exhibited many undesirable characteristics, such as very high number of crooks in the lower stem, many leaning trees with basal sweep and many trees with small crooks in the upper stem.

Provenances from low elevations in Eastern and Central Austria showed a similar growth rate to those from low elevations in Western Austria, but had less crooked lower stems, and less basal sweep or lean. Eastern Austrian provenances were more susceptible to the woolly larch aphid than those from Central Austria.

Rubner considered the low-elevation larch in Austria (and other parts in the Alps) to be a relict of the glacial period and called it low-alpine ecotype (66). Observations were also made in Europe that this larch flushes late, had a long height growth period (80-90 days), but is not exposed to late frosts (6). In general, provenances from Eastern Austria have demonstrated better growth rate than those from the western parts of the Alps (73). A great variability was observed in low-elevation provenances with respect to stem straightness (20).

e. High Elevation Larch From Austria and Italy (925-1900 Meters), And Larch From Switzerland

Provenances from high elevations, mainly in the western and southern Alps, grew slow. They showed, however, desirable stem characteristics, such as few trees with lean, crooks or basal sweep. Only a few trees were attacked by the woolly larch aphid or defoliated by late snow. Exceptions from the above characteristics were as follows: Italian provenances had a moderate number of trees with basal sweep and Swiss provenances had a moderate number of leaning trees.

Rubner reported that origins of medium elevations in the Alps, called "high-elevation" provenances in this study, were highly susceptible to larch canker and had better stem forms and better height growth than provenances from still higher altitudes (above 2000 meters) (66). These origins are found to be more resistant to drought than provenances from low elevations (24), they flush early and are exposed to late frosts (6, 44), especially those from the French Alps (7). The high-elevation origins have a 50- to 60-day period of height growth which is much shorter than that in low-elevation provenances (6, 44). It was also observed that these provenances exhibited heavier branches than the low-elevation origins (44).

IX. LARCH PLOTS OF MISCELLANEOUS ORIGIN

American IUFRO larch plantations in New Hampshire and New York included 11 miscellaneous seed lots originating from planted stands. None of these larches were superior in height growth to the most rapidly growing provenances of European larch (table 24). There is no evidence that European larch planted outside of its natural range may have developed to an independent race. Some investigators interpreted that "Scottish larch", that was introduced to British Isles about 300 years ago, is a separate race (65, 75). However, these plantings were established with different genetical stock on different dates (51), and consequently, one stand of European larch in Scotland may differ from another stand. Edwards reported that "Scottish larch" varies in height growth as well as in cone characteristics (18, 19).

IUFRO-53 (Scotland).--This provenance from a planted stand in Aldrauthy, Scotland, grew slowly (table 24). However, it had some desirable characteristics such as few trees with crooks, lean, or basal sweep and resistance to the woolly larch aphid (2 percent of trees attacked as compared with 4 to 65 percent attacked in the 31 provenances of European larch from natural stands) (figure 11). These characteristics indicate that the parent stand of the IUFRO-53 was probably imported from a high elevation in Austria or Switzerland.

IUFRO-45 and IUFRO-49 (Moravia).--These origins from planted stands in Moravia, Czechoslovakia, grew rapidly (table 24) and

Table 24.--Twelve-year heights and diameters of provenances from planted stands compared with those of rapidly growing provenances of European larch from its natural range, combined New Hampshire and New York data.

	Origin of Seed Sources		Height				
Provenance IUFRO No.	Natural Stands	Planted Stands	Average	Difference Levels at 5 Percent*			Average d.b.h.
			feet				inches
47	Sudetenland		21.5	S			2.95
42	Poland		21.5	S			3.05
45		Moravia	21.2	.	S		2.90
49		Moravia	20.3	.	.	S	2.95
38	Poland		20.0	.	.	S	2.90
43	Poland		19.4	.	.	S	2.60
51	Slovakia		18.8	.	.	S	2.40
35		Poland	18.2	.	.	S	2.50
4	Western Austria		18.0	.	.	S	2.85
1	Central Austria		17.9	.	.	S	2.70
6	Eastern Austria		17.8	.	.	S	2.60
28		<u>L. leptolepis</u>	17.7	.	.	S	2.65
31		Germany	17.6	.	.	S	2.30
36		Poland	16.9	.	.	.	2.20
34		Poland	16.7	I	.	.	2.15
30		Germany	16.5	I	I	.	2.35
55		<u>L. eurolepis</u>	15.8	I	I	.	2.30
29		Germany	15.8	I	I	.	2.25
53		Scotland	12.9	I	I	I	1.95

* Provenances marked "S" are significantly superior in height growth than those in the same column marked "I".

Figure 11.--European larch from planted stands in Scotland (IUFRO-53). It was relatively slow growing, but had straight stems and was highly resistant to the woolly larch aphid.

exhibited characteristics most similar to provenances of Polish-Sudeten origin. This finding agrees with Svoboda's report in which he stated that the majority of the larch planted in Moravia are of Silesian (Poland) origin (84).

IUFRO-28 (Denmark).--This study included one seed source of Japanese larch (*Larix leptolepis* Sieb. & Luce (Pilger)) from a planted stand in Denmark. It was represented in pure plots in both American IUFRO larch plantations and in one plot at the New Hampshire plantation it grew mixed at random with European larch (IUFRO-44).

Japanese larch was 100 percent resistant to the woolly larch aphid (*Chermes strobilobius* Kalt.). When planted in pure plots, it had good height and diameter growth but was not superior to the best European larch (table 24). In 1958 I identified the same origin of Japanese larch (15 trees) being mixed within a plot of European larch, IUFRO-44 (23 trees). Analysis of variance showed that Japanese larch in this random mixture had significantly (at the 5-percent level) greater 12-year heights (averaged 25.1 feet) than European larch (averaged 18.9 feet).

IUFRO-55 (Sweden).--This seed source originates from an old stand of European larch in Vinsingso, Sweden. Swedish records indicate that this stand was probably raised from seed bought in Scotland (76). Schmidt further states that the parental stand in Sweden was subject to pollination by Japanese larch (72). Accordingly, this seed lot may have included some of F_1 hybrids (*Larix* x *eurolepis* Henry) between European and Japanese larches. Kiellander determined that some trees were resistant to *Meria*. I found some resistant to *Chermes*.

X. APPLICABILITY OF THE PRESENT DATA

1. Applicability of Present Data in Other Regions

A study was made to determine the reaction of the same provenances under different environmental conditions. This was done to answer two questions: (1) how applicable are the height data from New Hampshire and New York in other parts of the United States, and (2) how applicable is the European data to our conditions?

In order to reach these objectives, correlation analyses were made between heights of the same provenances planted in Germany, Great Britain, Italy, Sweden or Switzerland, and the United States.

One of the best designed experiments in Europe was performed in Scotland (experiment ~~I~~X in table 4). The 9-year heights reported from Scotland (93) and 12-year heights from the American IUFRO larch plantings showed very strong correlation (r = .833, significant at the 1-percent level with 13 d.f., table 23).

Another well replicated experiment was established in northeastern Germany (experiment X in table 4) (72). Ten-year heights from this experiment and 12-year heights from the American plantings showed very strong correlation on the basis of eight provenances analyzed (r = .925, significant at the 1-percent level with 6 d.f., table 23).

Similar results were obtained with 11-year heights from Italy (experiment ~~XI~~ 14 in table 4) and 12-year heights from America. Correlation analysis showed a very strong correlation (r = .874, significant at the 1-percent level with 12 d.f., table 23).

Table 23.--Correlation between average heights of IUFRO larch provenances tested in northeastern United States (New Hampshire and New York) and the same provenances tested in Europe.

Provenance IUFRO No.	Average Heights at 12 Years U.S.A.	at 9 Years S. Scotland	at 10 Years NE. Germany	at 11 Years N. Italy
	- - - - - - - -	- - - - feet	- - - - - - -	- - - - - - -
47	21.5	--	--	13.1
45	21.2	--	--	13.3
49	20.3	15.4	--	--
51	18.8	--	23.3	12.3
35	18.2	--	23.6	--
4	18.0	14.4	--	--
1	17.9	--	--	12.2
6	17.8	--	--	11.1
31	17.6	14.1	24.9	--
14	17.6	13.5	--	--
7	17.2	12.5	--	--
23	16.9	--	--	11.3
36	16.9	14.1	--	--
34	16.7	13.5	--	12.3
12	16.6	12.5	--	11.8
30	16.5	13.8	22.6	11.9
55	15.8	13.8	22.9	--
29	15.8	13.1	--	--
24	15.1	--	--	11.7
8	15.0	11.5	--	--
18	14.5	12.8	--	--
5	14.1	--	20.3	11.1
21	13.4	--	--	11.5
27	13.0	12.8	--	10.0
53	12.9	--	18.4	--
26	11.4	9.5	14.1	9.0
Correlation with the American height data, *r* =		.833**	.925**	.874**
Degrees of freedom		13	6	12

** Very significant correlation (at the 1-percent level).

Different results were obtained in correlating the American data with those from Sweden and Switzerland. The IUFRO larch plantation in southern Sweden (experiment XV in table 4) was very heavily attacked by larch canker, Dasyscypha Willkommii (Hartig) Rehm. (78). A high percentage of trees had dead tops and height data were of limited value. Correlation between 12-year heights in American and Swedish plantations was not strong (r = .349, not significant at the 5-percent level with 15 d.f., table 4). Another non-significant correlation was obtained between 8-year heights in Switzerland (experiment XVI in table 4) (54) and 12-year heights in the United States (r = .483, not significant at the 5-percent level with 4 d.f.). This poor correlation was probably because the Swiss data were based on an unreplicated data.

The IUFRO larch plantations in Hillsboro, New Hampshire, and Barkersville, New York, included 25 provenances of European larch from native stands which originated from the same seed sources. Provenances which grew faster in New Hampshire also grew faster in New York. This conclusion was based on two types of analyses of height data. Correlation between 12-year heights from New Hampshire and New York plantations was very strong (r = .595, significant at the 1-percent level with 23 d.f.). Analyses of variance showed that between-provenance differences were very significantly greater than the provenance x plantation interactions (F = 4.02, significant at the 1-percent level with 24 d.f. for provenances and 24 d.f. for error).

The results of the above studies showed that consistency of height performance was not dependent on the distance between locations. The height data on racial variation in European larch, obtained in properly conducted experiments in Europe, can be trusted in the United States. Also, data obtained in the northeastern United States will probably be applicable in Michigan and other northern parts of this country.

This information on consistency of height performance in different environments is important not only in genetics research but also in nutrition experiments. Results obtained by testing one variety are probably applicable to other varieties of European larch.

2. Applicability to Future Production of Hybrids

The crossability pattern of larches is not finally determined. According to the present classification, the genus consists of 15 different varieties or species (tables 2 and 3). There are 105 possible intervariatal and interspecific crosses (excluding reciprocals). At the present, however, there are only 10 known interspecific combinations. In five of them one parent species was European larch. Crosses between European larch and other larches have been reported as follows (94):

Larix decidua Crossed With	Scientific Name of Hybrid
Larix leptolepis (Japanese larch)	*Larix* x *eurolepis* Henry
Larix gmelini (Dahurian larch)	--
Larix laricina (Tamarack)	*Larix* x *pendula* (Toland) Salisbury
Larix occidentalis (Western larch)	--
Larix sibirica (Siberian larch)	--
Larix mastersiana (Master's larch)	--

The most publicized hybrids are those between European and Japanese larch. These hybrids occurred naturally at Dunkeld, Scotland, and other locations in Great Britain and are easy to produce artifically (42, 51). Presently "Hybrid Larch" or "Dunkeld Larch" occupies an area of 6,000 acres in Great Britain (51).

Larsen tested *L.* x *eurolepis* hybrids in Denmark and found that they grew faster than Japanese larch (42). In Great Britain nearly all "Hybrid Larch" plots grew better than European larch and were equivalent or better in height growth and volume increment to Quality Class I Japanese larch. They were practically resistant to larch canker and "die-back" (51). These hybrids were tested in many other European countries, and in all cases they grew better than the parent species (30, 41, 94).

There are few American tests of "Dunkeld Larch", a seed source from Dunkeld, Scotland, which included some hybrids of unknown generation. Paton made a study in Wooster, Ohio, and found that "Dunkeld" larches grew slightly better than the parent species (56). Cook reported on good performance of larches from Dunkeld seed in Renselaer County, New York (16). Littlefield found also that 5-year-old seedlings of supposed hybrids grew slightly better than either European or Japanese larches in Montgomery County, New York (49).

The present crosses between European and Japanese larches were made by using parents of unknown origin. Selection of parents from populations with most desirable characteristics may improve the qualities of hybrids considerably. This study showed a great variability of European larch in height growth, stem straightness, resistance to the woolly larch aphid and other characteristics (table 21, figure 9). Naturally, this variation should be taken into consideration when selecting the parents in future production of hybrids.

a. Japanese Larch as a Crossing Partner

Japanese larch (*Larix leptolepis* (Sieb. & Zucc.) Pilger) is a native of the mountains of central Honshu, where it grows in pure or mixed stands at elevations of 4,000 to 9,000 feet (figure 2, tables 2 and 3). Its natural range is small, being encompassed within an area of about 140 miles square and composed of several distinct populations. Some of these populations are only a few acres in size and the largest are only a few miles across. It is superior to European larch in: lower nutrient requirements and is more resistant to attack by *Dacyscypha willcomii*, *Adelges virilis*, *Argysthia laevigitella*, *Theniotrips laricivorus*, *Meria laricis*, *Chermes strobilobius*, and squirrels. However, European larch is less sensitive to drought, early and late frosts, and breakage by ice and snow. Possibly it is more resistant to *Phomopsis pseudotsugae* (1, 6, 14, 39, 74, 91, 92).

In hybridizing European and Japanese larches, it is important to select not only the best parent types in European larch but also in Japanese larch. Very little work has been done on racial variation studies in Japanese larch. Langner reported green weights of 1-year-old seedlings from 25 different provenances (40). However, these depended largely on the differences in spacing. Seven seed lots of

Japanese larch from the native stands were studied at Michigan State University, East Lansing, Michigan.[1/] Two-year data showed differences between provenances in fall-color, branching, susceptibility to early frost and height growth. The provenance from Kumanshiro, Tsumakoi, Gumma (63° 38' 30"N and 138° 29' 30''E, altitude 1750 meters) combined two desirable characteristics: rapid height growth and moderate resistancy to early frosts. The pattern of variation in Japanese larch appeared to differ from that found in wide-ranging species with large continuous populations. Large differences appeared among provenances but these were not related to latitude, longitude, or altitude of origin. In other words, the variation pattern in Japanese larch was not as systematic as in European larch.

1/ Wright, J. W. and Genys, J. B. Unpublished data.

XI. FINDINGS APPLICABLE IN FUTURE PROVENANCE STUDIES

1. Need of Replication

Many past experiments attempting to determine the racial differences between provenances gave only limited results because of poor or no replication. They had a low value even as demonstration plots, because no certainty existed whether differences were due to environment or due to genetics. A great majority of present investigators realize that differences in growth may occur because of soil variation, yet a few fail to consider the remaining complex of environmental factors.

The present study shows that statistical analyses of height and other data reveal large "least significant differences" (table 15). It was impossible to determine which particular provenance was outstanding in one or another characteristic or to find the within-region variation patterns. These and other difficulties arose mainly because provenances were not adequately replicated.

Only a few recommendations are published regarding the number of replications in forest genetic studies. Recently Wright and Freeland reported that statistical efficiency can be increased by replicating the sources as many times as possible and by using as small plots as is practical (95).

2. Reliability of Early Height Measurements

In the New Hampshire IUFRO larch test, heights were measured at ages 4 (on 2-2 transplants), 7 and 12 years. Analyses of variance of provenances from different regions showed that 12-year data gave the highest and 4-year height data gave the smallest F value. The 12-year data showed a higher number of origins that had significantly (at the 5-percent level) inferior height growth to the two best growing origins than those of earlier measurements as follows:

Age of Trees When Measured	Degrees of Freedom Between Regions	Degrees of Freedom Error	Computed F	Origins Significantly Inferior to Two Origins With the Greatest Heights
years	number	number	value	number
4	9	17	4.70**	4
7	9	20	7.87**	5
12	9	19	11.70**	7

** Very significant differences (at the 1-percent level) found among origins

Correlation analyses showed that 4-year heights and 7-year heights were very strongly correlated ($r = .502$, significant at the 1-percent level with 35 d.f.) and 4-year heights were very strongly correlated with 12-year heights ($r = .745$, significant at the 1-percent level).

It is concluded that early measurements can be applied to forecast the approximate variation pattern. However, the measurements in older stands are more desirable and exhibit a better statistical efficiency.

3. Efficiency of Statistical Analyses by Using Different Sample Sizes

Analyses of variance of 12-year heights from New Hampshire and New York plantations were made by using different statistical units representing plots. Most differences between provenances were detected when means of all trees per plot were used instead of the four largest trees per plot. No differences between provenances were detected on the basis of one largest tree per plot used as presentatives. Results are shown in the following tabulation:

Nature of Sample Representing a Plot	Number of Provenances Studied	Computed F Value	Level of Significance of F
One largest tree	25	1.22	Not significant at 5 percent
Mean of four largest trees	19	2.24	Significant at 5 percent
Mean of all trees	25	4.02	Significant at 1 percent

From the practical point of view, the means of four largest trees per plot could be used if a loss of statistical efficiency and a gain of time by measuring smaller number of trees are properly balanced. If the test plots are large, naturally, the sample of trees should be selected at random.

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