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IUFRO's Role in Coniferous Tree Improvement

History, Results, and Future Trends of Research and International Cooperation with European Larch (Larix decidua Mill.)

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(Received 20th February 1992)

Summary

European larch has many favourable traits and was therefore, at an early stage, of great interest to forest tree breeders and forest geneticists. The first systematic provenance trials go back to the time when IUFRO came into being. The big trial series of 1944 and 1957/1958 are impressive evidence of the value of international cooperation. The most important results of those investigations are reported. On their base research has been going on particularly in the last 3 or 4 decades in the field of intra- and interspecific hybridization. Comprehensive information from progeny tests is on hand, above all for "growth", "stem shape" and "susceptibility to canker". These already allow the use of "tested reproductive material" as stipulated in the EC and OECD legal regulations. Besides seed production in seed orchards vegetative methods will also be able to utilize the gain of hybridization when these methods will be applicable. The report contains information on the present state of knowledge on this subject, covering conventional propagation by cuttings and also in vitro techniques.

It is suggested that future larch research should be intensified particularly in the field of hybridization. Selective measures should not lead to an irretrievable loss of a wide genetic variation. The utilization of the diverse possibilities for international cooperation that IUFRO offers is seen as a guarantee for the success of this line of research.

Key words: Larix decidua, provenance research, intra- and interspecific hybridization, vegetative propagation.

1. Natural distribution and distinguishing characteristics of European larch

European larch, which is one of ten species of the genus *Larix*, ranks among the most important managed forest trees of the northern hemisphere. Its natural range, with four completely separate sub-areas in the Alps, the Sudetic mountains, the Carpathian mountains and in Poland represents the remains of a former larger and probably continuous source in the early post-glacial period (roughly 6000 B. C.). Larch was excluded from those regions initially by oak and later by beech, fir and spruce.

The natural distribution of larch demonstrates its preference for continental climatic influences and for transitional forms in the direction of a temperate low mountain climate. Its altitude distribution ranges from 150 m above sea level in the north of the Polish sub-area to around the timberline in the Alps (2400 m). Mountain and low mountain situations are obviously colonized more successfully than colline areas.

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The ecological demands made by larch are marked by a broad spectrum. Because of its high transpiration needs favourable conditions for growth are, however, primarily provided by soils with a good water retention capacity and at the same time sufficient aeration. As a result of its relatively high light requirement, larch is particularly subject to competition stress from other tree species. The optimal utilization of site advantages can be considerably reduced by competition influences of this kind; this can be true in different ways according to region.

Natural larch populations are, therefore, found primarily on free spaces (e. g. after a forest fire, avalanches or cattle grazing). Mixtures with other tree species such as *Picea abies, Abies alba,* or *Pinus cembra* prove stable only when the lead achieved by larch's fast growth at the juvenile stage can be maintained.

Larch produces durable and robust timber with distinct heartwood. It can be used in diverse ways such as for building, both inside and outdoors, and as valuable timber for furniture and industry. Good yields in both volume and value were decisive for the early spread of European larch by man in large parts of Europe beyond its natural range. For example it can be proved that afforestation was carried out in Franconia with seed from Alpine larch from southeastern Carinthia at the end of the 17th and beginning of the 18th centuries (Elsner, 1966). Sudetic larch was evidently planted in all areas bordering its original sources in Czechoslovakia and in different parts of Germany at about the middle of the 18th century (Rubner, 1943; Puchert, 1967; Šindelář, 1967a). Probably the largest artificially cultivated area of this species in central Europe from earlier times, which has become well-known unter the name of "Schlitzer" larch, originated at the end of the 18th century and mainly at the beginning of the 19th century, most likely from seed mainly from the valleys of the Tyrol Alps (Gothe, 1961).

Outside its natural range the European larch is cultivated chiefly mixed with other tree species, most often with *Fagus silvatica.* Beech is characterised by comparatively slow juvenile growth, high shade tolerance and good ground shading so that the two tree species with the same rotation complement each other in their ecological behaviour. The drier sites such as plateaus and upper slopes are assigned to a greater degree to larch.

2. Provenance research findings on an international basis

2.1. Motives and first investigations

The cultivation of larch outside its natural distribution area was only partially successful in the beginning. If one compares the amount of seed and plant material used for cultivation as regards quantity and quality with that of the stands reaching maturity, the result must be described as wretched in many central European regions. Many reports have been given concerning the reasons for these disappointments and failures, the last in synoptic form by Bürgi (1990/1991).

Initially there seemed to be no explanation for the fact that young larch stands, after a good growing start, often began to perform poorly and finally died, especially as no impairment at all could be observed in other plantations of the same tree species under comparable site conditions. This was referred to as the "larch mystery" (Münch, 1933, 1936; comp. also Schädelin, 1941).

Nevertheless, it seemed logical to suspect that an extreme racial differentiation in larch might be as the fundamental cause of the variable success in cultivation. At the turn of the century Cieslar (1899, 1904, 1914) and Engler (1905) already reported findings which pointed to this fact. For the first time, they were able to refer to comparative cultures on the same site. The differences observed there in growth and health according to which plant material was used were later impressively confirmed by numerous research studies in different countries.

Rubner(i. a. 1931, 1939, 1951), Tschermak (i. a. 1932, 1933, 1935), Münch (1933, 1936) and Fourchy (1952) were the first to succeed in collecting comprehensive data on site requirements, growing behaviour and canker susceptibility in the four larch sub-areas. Simultaneously, or a little later, first results were reported from comparative tests with provenances from these distribution areas. The publications by the following authors are particularly well-known: Burger (1935, 1943), Rubner (1938, 1941), Zimmerle (1941), Dengler (1942), also Geyr von Schweppenburg and Oelkers (comp. Schober and Fröhlich, 1967).

The investigations proved that failures in larch cultivation were attributable primarily to the utilization of unsuitable provenances. Above all, it was perceived that poor growth, early flushing and susceptibility to late frosts are to be expected when high mountain provenances from the Alps are planted in lowlying situations. Similarly, the severe attack, in some cases, by larch canker and needle diseases was seen to be connected with provenance problems and also with local site influences.

After this, numerous reports appeared on findings obtained from trials. They may be rated as the first significant contributions toward establishing the geographical and genetic variation pattern of European larch, at least in rough outline, and drawing conclusions for genetic adaptation strategies.

It is easy to see from literature that the research work, which was based at first on a few provenance comparisons, was gradually supplemented and intensified by additional projects (i. a. Schmidt, 1955; Rohmeder and Schönbach, 1959). Furthermore, it is worthy of note that interest in these investigations grew considerably, not only in the already important larch cultivation areas of central Europe, but also in countries outside the natural range of this tree species, such as Scandinavia (Gøhrn, 1956; Heikinheimo, 1956).

Schober (1958) was the first to carry out a comparison of all findings known at the time from 29 test series from the age of 8 years to 46 years from different European countries. This showed that, as a rule, provenances from the Sudeten, from the Tatra mountains, from Poland and also from lower regions in the eastern Alps grew better than the average. Provenances from the central and western Alps, on the other hand, were mediocre in growth performance. Polish larch was seldom susceptible to canker. Susceptible trees were only slightly affected. Larch from the Alps, on the other hand, was more often susceptible and, in some cases was severely affected.

For many reasons, however, it proved difficult, to interpret the results of older provenance trials to obtain generally valid conclusions that could be widely used in practical silviculture. One must recall that in the first half of this century there was no good scientific basis for planning and conducting statistically designed field experiments.

One cannot overestimate the groundwork laid by the pioneers of international provenance research who, despite the difficulties reported important early results that refuted prevailing doubts about the cultivation value of European larch, especially outside its natural range.

2.2. Successes of international cooperation

As a result of these early investigations and the problems described, international cooperation expanded and provenance trials were established on a broad basis. The International Union of Forestry Research Organizations (IUFRO) provided the structure for this well-organized cooperation.

The First International Larch Provenance Trial was established in 1944 at the initiative of the IUFRO commission for questions of tree races. Its object is to test (1) 48 provenances from all four sub-areas as well as non-indigenous sources of *Larix decidua*, and (2) two additional provenances each of *Larix leptolepis* and *Larix sibirica*. Research institutes from 12 European and North American countries participated in the project with a total of 23 partial trials.

Werner Schmidt, who was at that time the director of the Institue for Forest Seed Science in Eberswalde, had taken on the difficult task of preparing and coordinating the trial and sending the seed to all participants. Everything had to be carried out at a time of immense international tension during the last phase of the Second World War. This was made possible by the active support of the IUFRO general secretary at that time, Sven Petrini, and also of Olof Langlet who succeeded in arranging for some of the seed to be sent via Sweden. Schober (1981) paid fitting tribute to the events and services related to the project's establishment with the following words: "We owe an informative provenance trial today to the belief of the scientists mentioned and all those taking part in future international cooperation in the spirit of IUFRO".

Most of the participating research institutes published detailed reports on the results of this first big larch trial series covering many countries. *Table 1* gives information on further literature on this subject. The most important results generally agree with those from other trials and are, therefore, described together with them in the following section 2.3.

The continuing interest in larch cultivation after the Second World War and the need for better information on provenance-specific suitability for cultivation led to the establishment of the Second International Larch Provenance Trial on the initiative of Schober 1958/1959. This time the objectives were to include more populations of the Sudetic and Poland larch and more extensive elevational sampling of the Alpine and Tatra larch. For purposes of comparison, other well-known, non-indigenous sources of *Larix decidua* and one provenance of *L. leptolepis* and the Scotch F_2-hybrids ("Dunkeld-hybrids") of *L. decidua* and *L. leptolepis* were included in the

Table 1. — Survey of literature on the 2 International Larch Provenance Trials of 1944 and 1958/1959.

Country	1st International Trial 1944	2nd International Trial 1958/1959
Belgium		Jacques, 1991
Canada	Graham et al., 1983	
Czechoslovakia	Šťastný, 1965, 1970, 1971; Kočiová, 1978	Šindelár, 1971, 1974a and b, 1983, 1984; Kočiová, 1975; Fer, 1979
Finland	Heikinheimo, 1956	
France	Lacaze and Birot, 1974	Lacaze and Lemoine, 1965; Lacaze and Birot, 1984; Ferrand and Bastien, 1985
Germany	Schober, 1958, 1981	Bachler, 1969; Merkel, 1971; Dietze, 1976; Schober, 1977, 1985; Weisgerber, 1990; Braun and Hering, 1991
Great Britain	Lines, 1967	
Italy	Morandini, 1958; Morandini and Tocci, 1975	Morandini and Tocci, 1975
Netherlands		Kriek, 1974
Poland	Chodzicki, 1967; Giertych, 1979	
Sweden	Kiellander, 1956	Simak, 1962, 1967
Switzerland	Fischer, 1950, 1952; Schütz, 1979; Bürgi, 1990/1991	
USA	Genys, 1960; Eliason and Carlson, 1969	Barnes, 1977
Yugoslavia		Pintarić, 1969, 1973, 1979

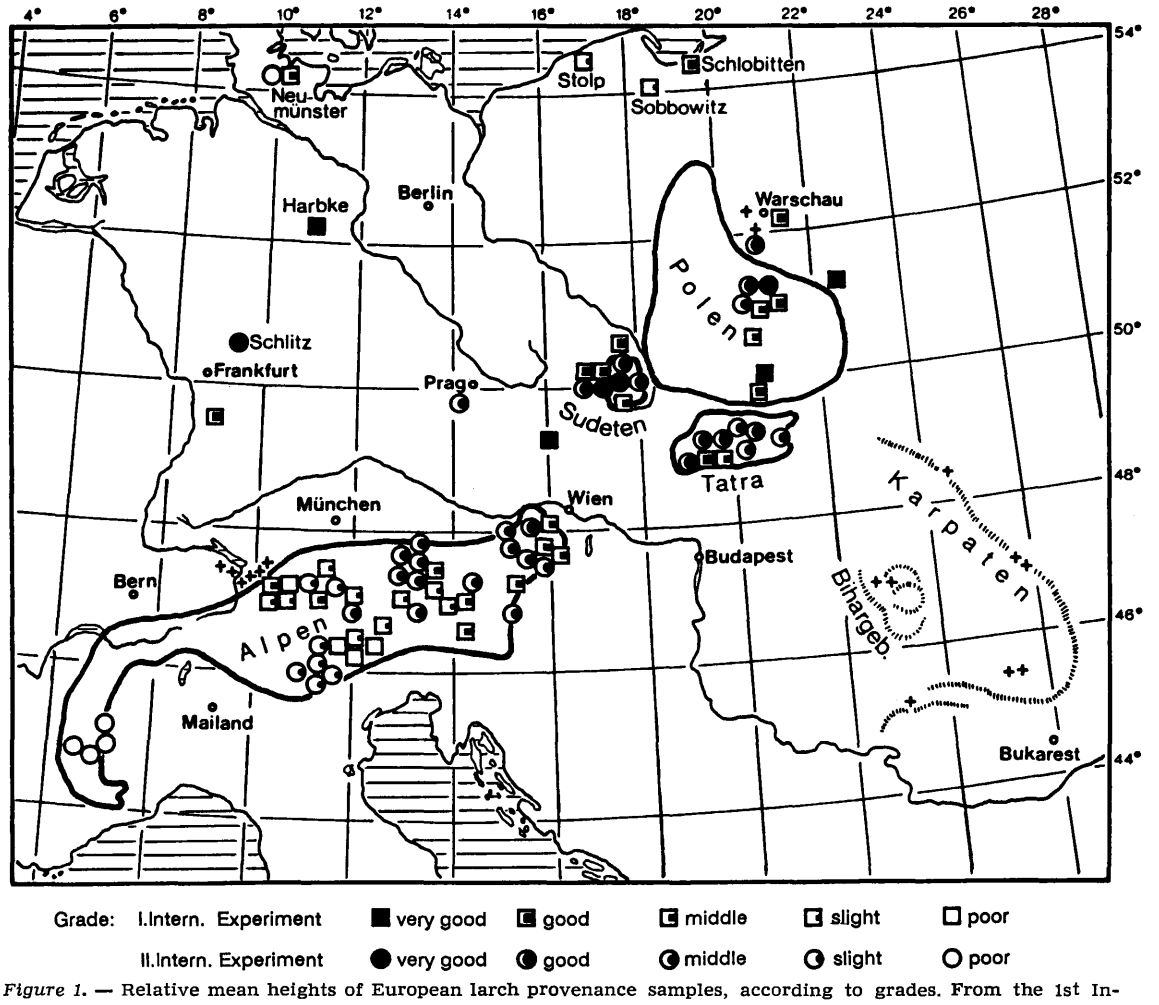

Figure 1. — Relative mean heights of European larch provenance samples, according to grades. From the 1st International Trial, sub-trial Neuhof, at age 29, and also the mean of 26 sub-trials of the 2nd International Trial at age 20 (from SCHOBER, 1981, 1985).

project. Comparative tests were planned on an extensive region and site basis.

Since conditions for cooperation were much more favourable than they were for the First International Trial, it was possible to bring together interested scientists from 14 European countries and the USA. These contacts led in 1976 to the establishment of IUFRO working group S2. 02—07 (Today's name "Larch provenances and breeding").

In the Second International Series a total of 75 partial trials with 63 provenances were established by 22 research institutes in the participating countries. Uniform methods were prepared and agreed upon for the establishment and treatment of the tests and for data collection and evaluation.

Nearly all participating countries have reportet results of this trial series (*Tab. 1*), which has a planned observation period of about 60 years. SCHOBER (1977, 1985) discussed most of the partial trials up to approximately age 20 in survey form. Clearly, it has been possible to obtain substantial knowledge of the variation pattern of European Larch as a result of careful and foresighted planning by the initiators and the desciplined method of procedure. In particular important statements can be made about the adaptability and growth of representative provenances from all sub-areas of this tree species under very different ecological conditions.

These two large international trial series stimulated numerous other investigations with the same or similar provenance material in many countries during the last three decades (i. a. LEIBUNDGUT and KUNZ, 1952; MCCOMB, 1955; LEIBUNDGUT, 1959, 1985; FRUND, 1960; SCHREIBER, 1960/1961, 1964; EDWARDS, 1962; KOCIEÇKI, 1962, 1968, 1969; TROEGER, 1962; HAASEMANN, 1967, 1986; SEIDENSCHNUR, 1974; HAASEMANN and TZSCHACKSCH, 1986; BOYLE et al., 1989; GÜNZL, 1990; BÜRGI, 1990/1991). In some cases, these studies dealt with specific responses of certain provenances or groups of provenances, such as light sensitivity (LEIBUNDGUT, 1962; KRAL, 1963), drought resistance (LEIBUNDGUT, 1965) or canker disease (MANNERS, 1953; HOPP, 1957).

2.3. Current state knowledge and conclusions for practical forestry

Results of the many experiments with *Larix decidua*, particularly in Europe and North America, all show that three criteria are decisive for the choice of site-suited provenances: growth, stem shape and larch canker caused by *Trichoscyphella willkommii* (comp. also RÖHRIG, 1980). These characteristics can only be touched on in this paper. The statements mostly refer to the two IUFRO trials, because the international network provides better comparability.

It is remarkable that trees of the provenances in the individual partial trials of these series and in numerous other tests behave similarly regardless of very different

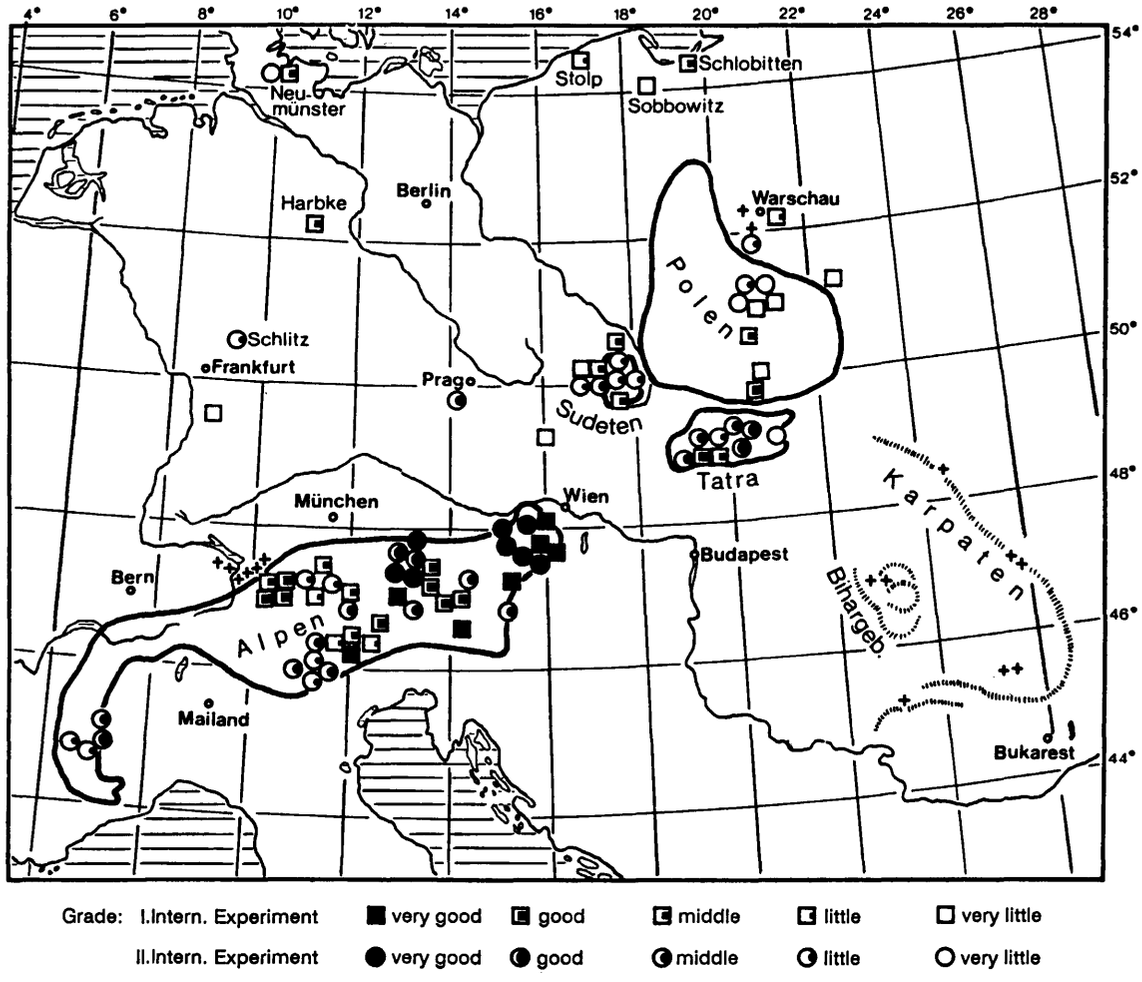

Figure 2. — Stem shape of provenance samples of European larch. From the 1st International Trial, sub-trial Neuhof, at age 23 and also as the mean of 24 sub-trials of the 2nd International Trial at the age of up to 20 years. Proportion of straight and slightly bent stems (1st Trial) and straight stems (2nd Trial) in the total number of stems, according to grades (from SCHOBER, 1981, 1985).

ecological conditions. Even in countries far removed from the natural larch sources, such as the USA (GENYS, 1960) or New Zealand (MILLER, 1967), treatment rankings were similar to those of European countries as far as adaptability, growth and stem form were concerned.

2.3.1. Growth

In both of the IUFRO series of experiments, a clear relationship can be shown between growth rate and provenance regions in the form of a northeast-to-southwest decline (*Fig. 1*) This is especially true for height growth but also to a lesser extent for growth in diameter and volume.

The Polish and Sudeten larches are mostly characterised by very good to good growth performance; in the Tatra larches it is good to medium. Larches from the eastern Alps also have a good (Wienerwald) to average growth rate; those from the northern Alps are average. There is a considerable difference in performance between these and the adjacent, mainly high mountain provenances in the central and southern Alps. Larches from an altitude of 1200 m to 1900 m above sea level in the French and Italian southwestern Alps have been especially poor growing.

2.3.2. Stem straightness

Straightness of stem and growth-intensity are evidently not correlated positively in the way that had been hoped for from an economic standpoint.

Figure 2 shows for both large international trials combined that stem shape, which is the decisive factor for high quality yield, is mainly poor in trees of the best-growing provenances of Poland and the Sudetan region of Czechoslovakia. Tatra larches are marked by variable form ranging from straight to crooked stem. On the average, the best stem form was found in east and north Alpine provenances. Larches from the central Alps and those from the southern and south-western Alps were mainly classified as "medium" or "poor".

2.3.3. Larch canker

In both international trials the spread and intensity of attack by the pathogen *Trichoscyphella willkommii* varies according to the specific provenance. The disease development and course can also be substantially influenced by site conditions.

Among the Polish, Sudetan and Tatra larches only slight symptoms of the disease could be observed on a few trees. The Alpine larch, on the other hand, demonstrat-

ed a considerable attack diversity. High elevation provenances from the central and southwestern Alps were frequently susceptible to the disease. This finding, which is confirmed by other trials (*Fig. 3*) is an additional indication of a negative correlation between susceptibility to canker and vigor; provenances with a high growth potential are evidently less damaged whereas those with poor growth suffer the greatest damage.

2.3.4. Assessment of cultivation value

A total assessment of all results so far known on provenance research on *Larix decidua* makes us realize that there are no ideal provenances from the standpoint of forest management.

Alpine larch with good form characteristics is often threatened by canker or, like the Wienerwald population, shows a lower growth potential compared with the Sudetan provenances. Polish larch is practically free of canker and has a good rate of growth, but also has a relatively high proportion of crooked and tapering trees. Sudetan provenances are remarkably uniform, with good site adaptability, growth rate and resistance to canker, but stem form is only fair. There are similar results for well-known, non-indigenous larch populations as, for example, "Schlitz" or "Harbke" (comp. *Figs. 1 to 3*). Finally, trees of the Tatra provenances rank average to good; stem form is variable.

On the basis of present knowledge, SCHOBER (1988) recommends the following provenances for cultivation in central Europe outside the natural distribution area:

— provenances from the Sudeten and from the lower Tatra in case optimal stem straightness is not required;
— provenances from the eastern Alps at elevations of up to 1200 m in case optimal growth performance is not necessary.

Failures can be avoided by not using canker-susceptible Alpine provenances in humid-cool regions, especially near coasts, on the luff side of north European low mountains, in narrow valleys, and on sites exposed to recurrent spring frosts.

Since about 1970, specific reommendations for larch cultivation have been compiled on the basis of present knowledge in different countries. These recommendations have proved value and are of considerable importance for practical forest management. They give priority to provenances from the Sudeten and eastern Alps. Trees from these provenances evidently have a superior genetic potential that ensures ecological stability, and a high site-tolerance that favors high yields even outside the natural distribution area. The cultivation of well-known non-indigenous larch ("Schlitz") is also often reommended. They seem to be equipped with a remarkable genetic buffering capacity, like local races, in spite of secondary adaptation processes. Therefore they offer a high performance level on different sites.

3. Advanced breeding work

3.1. Progeny tests with selected trees

Information on genetic variation in *Larix decidua* soon led to further research on differences in growth characteristics specific to individual trees within populations.

As early as 1888, KRÖMMELBEIN examined the stem shape of progenies of individual larch trees. Similar research work was later carried out to asses the genetic traits of plus trees (i. a. KLEINSCHMIT, 1955).

The hope of improving growth rate, timber quality and resistance to disease by individual selection led to the establishment of seed orchards in many countries in the last four decades. There are many references to the function and efficiency of European larch seed orchards (i. a. THÜMMLER, 1963; ŠINDELÁR, 1967b; WEISGERBER, 1976, 1983; OTTO, 1977; comp. also FEILBERG and SOEGAARD, 1975).

Larch plus tree seed orchards have been contributing for a long time and to an increasing extent to the supply of

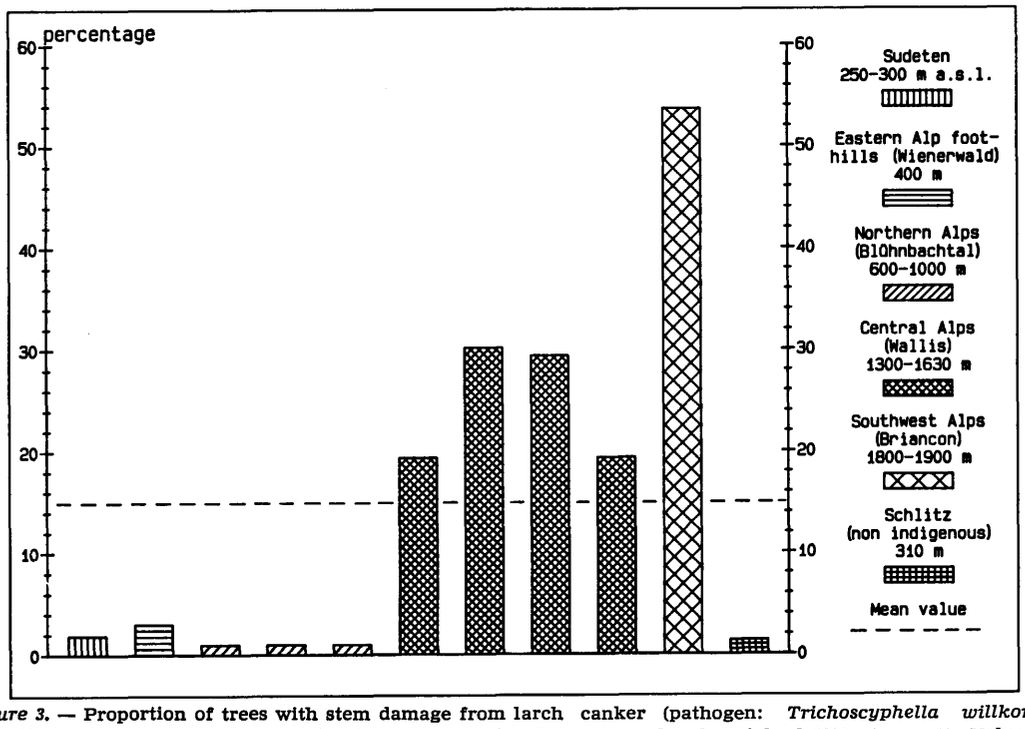

Figure 3. — Proportion of trees with stem damage from larch canker (pathogen: *Trichoscyphella willkommii*) from 11 provenances, ordered according to regions, in the Gahrenberg Larch Trial of 1933 at age 50. Values are compared with the mean value of all provenances (from WEISGERBER, 1990).

high-quality larch seed for the production of "selected reproductive material", in compliance with the regulations established by the OECD and the EC concerning trade with forest reproductive material. In addition to seed production, seed orchards and special breeding plantations are often used for research on the genetic value of selected trees and to create the preconditions for the production of higher-class "tested reproductive material".

Different test methods are used to verify and quantify the genetic superiority of selected plus trees in important quantitative and qualitative features (FRÖHLICH et al., 1967). An efficient approach has been to use both sexual and asexual propagation. Vegetative propagation of larch is used to test the response of plus trees on different sites. The early flowering of this species, particularly on grafted seed orchards, has proved advantageous and has provided information, by means of controlled pollination on the clone genetic constitution and the combinating ability. The progenies resulting from these crossings are then studied under a variety of site conditions.

A number of reports have been published on the results of progeny tests after intraspecific crossing with *Larix decidua* (i. a. HAASEMANN, 1972; DIETZE, 1976; HALL, 1985; ŠINDELÁR, 1986; HERING, 1990). All report outstanding growth of many progenies, particularly those of Sudeten larch. DIETZE (1976) estimated the expected genetic gain for volume growth, from provenance selection to the combination of tested plus trees, to be at least 15% to 20%. Moreover, proof has repeatedly been found of the clear superiority of crossing progenies to comparable commercial seed (comp. also KLEINSCHMIT, 1988; RAU, 1988). As a result, the best clones have already been assembled in advanced generation seed orchards in some countries. Clones with negative characteristics are excluded of further breeding programmes (WEISGERBER, 1982). Individual tree progenies from free pollination or controlled crossing can also be used as a basis for selection for the second breeding generation.

When establishing seed orchards, it is necessary to bear in mind the fact that self-pollination is possible with European larch. DIECKERT (1964) and KOSINSKI (1981) showed that fertility is reduced by self-pollination and that the viability of a self-pollinated progeny is relatively low. In our investigations in Hann. Münden, progenies from controlled crossing had up to 56% less mortality than self-pollinated progenies. The proportion of trees with straight stems at age 10 within the same group of test trees was, on the average, 52% for outcrossed progenies and only 21% for the self-pollinated progenies.

3.2. Provenance and species crossings

Initially, hybridization concentrated mainly on combinations within a provenance region or at least within the same sub-area of *Larix decidua*. It has only been within the last decade that any significant amount of crossing has been carried out among provenances from distant regions or from different sub-areas. In addition to recombination involving useful characteristics, heterosis effects are also expected from these crossings.

On the basis of provenance research, interest is concentrated primarily on crossing vigorous Sudeten larch with well-shaped and finely-branched east Alpine larch, especially from the Wienerwald. Combinations involving some provenances from the Tatra with low susceptibility to canker and good form also appear very promising. Early results indicate good prospects of success of these crossing programmes (HERING, 1990). It seems opportune to assemble the best clones in provenance hybrid seed orchards for the production of "tested reproductive material" after the requisite progeny tests have been completed.

More information and, in some cases, long experience are available on species hybrids of European larch. Early information on the spontaneous origin of hybrids between *Larix decidua* and *L. leptolepis* in Dunkeld Park in Scotland provided the stimulus for research on larch hybrids (ELWES and HENRY, 1907; HENRY and FLOOD, 1919). Natural species crosses are also known between other larches, e. g. *Larix decidua* x *L. gmelinii* (ROHMEDER and DIMPFLMEIER, 1952/1953), *L. sibirica* x *L. gmelinii* (KRUKLIS and MILUTIN, 1977; quoted from IROSHNIKOV, 1987) and *L. kajanderi* x *L. kamtschatica* (BOBROV, 1972, 1978; quoted from IROSHNIKOV, 1987). DIMPFLMEIER (1959) described various spontaneously-originating larch hybrids in botanical gardens and parks in Denmark, the USSR and Switzerland.

The "Dunkeld-larches", which are referred to as *Larix eurolep's* HENRY and are clearly more vigorous then their parents, caused geneticists and breeders of many countries to examine reasons and possibilities for using hybrid effects of this kind. As early as 1914, the first artificial crossings between *Larix decidua* and *L. leptolepis* were successfully carried out (EKLUNDH and PEDERSEN, 1933; quoted from LANGNER 1951/1952). Later, the extensive cross-breeding

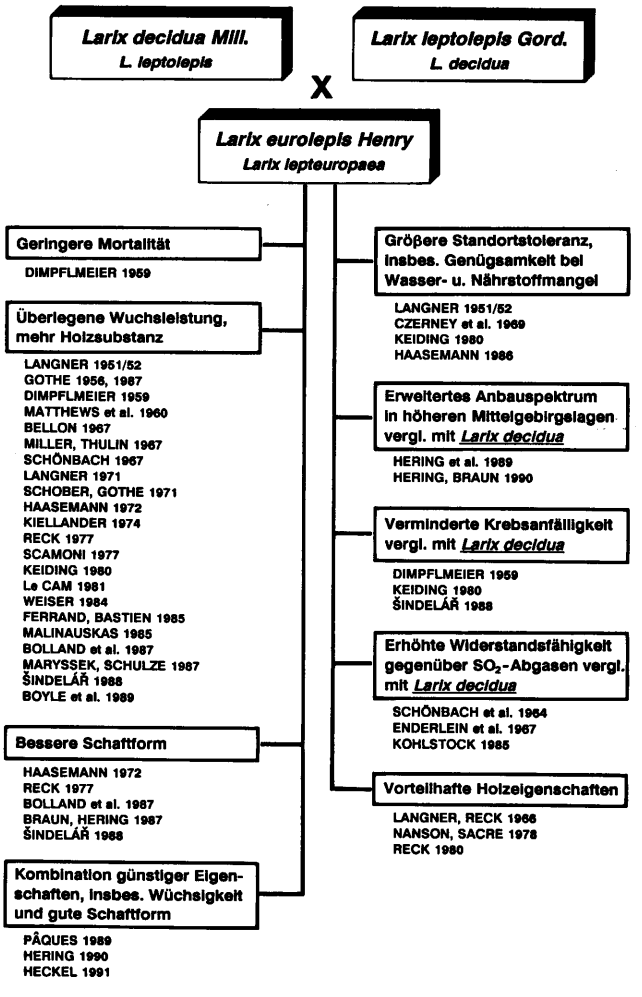

Figure 4. — Results of research on the merits of interspecific larch hybrids as opposed to *Larix decidua* and/or *L. leptolepis* as crossing partners.

programmes of SYRACH-LARSEN (1937, 1956) in Denmark, ALBENSKIJ (1939) in the USSR and DENGLER (1942) in the research garden of the Institute for Silviculture in Eberswalde were an incentive for subsequent intensive larch hybrid research.

The great international interest in this field of work and the success already achieved is summarized in *figure 4* in a greatly simplified, rough outline form. More comprehensive bibliographical information is found in HERING (1990) and HECKEL (1991).

Many authors stress the hybrid's often clear superiority in growth to that of the crossing partners, at least in the juvenile stage. Similar heterosis effects have also been discovered in some cases in wood production.

The species hybrids were also rated superior to their respective pure species parents in other characteristics, including stem shape, canker susceptibility, timber quality, and in the combination of these with growth. The assessments varied according to the material used for testing. Particular attention has been paid to findings showing the greater site-tolerance and hardiness of hybrid larch compared with *Larix decidua*, especially where there is a water shortage, or under the influence of SO_2-emission. These advantages are already being utilized to a large extent in the higher mountain regions of Saxony, mainly in parts of the Ore Mountains which have suffered damage from air pollution.

A critical evaluation of the *Larix eurolepis* investigations shows clearly the importance, particularly in hybrid research, of longterm observation of as varied plant material as possible and on a broad international basis. A wide exchange of experience revealed the fact that the growth rhythm of hybrid larch differs distinctly from that of European larch, and was thus able to prevent premature large-scale cultivation. The lead in growth which the progenies of crossings exhibit in the juvenile phase diminishes considerably by age 33, according to GOTHE (1987). Similar observatons have frequently been reported (i. a. SCAMONI, 1977; KEIDING, 1980; ŠINDELÁR, 1988). RECK (1980) proved with other test material that the hybrid's annual increment falls behind that of the pure species between the ages of 10 and 20. He also concluded that superior timber quality can be expected at a later age from the pure species in comparison with the species hybrids.

Widely-divergent research results make it impossible to generalize from single results in hybrid research. HERING (1990) showed from analyses of the quantitative genetics of interspecific larch progenies that the desired hybrid effects can only be expected from certain combinations. The establishment of hybrid seed orchards to supply "tested reproductive material" depends on the general suitability of the clones of both larch species used in the crossing programme, and also on their particular effectiveness when crossed.

The production of hybrid seed in seed orchards requires coincidence of the flowering periods of the participating clones and low degree of selfing. The method tested by LANGNER for avoiding selfing by introducing a self-incompatible clone of *Larix decidua* into *L. leptolepis*-stands seems questionable because of the greatly reduced genetic variation entailed.

Considerable research is still needed into the much discussed establishment of F_2 seed orchards (KLEINSCHMIT, 1988). Investigations carried out so far on F_2 and F_3 hybrids show that they can be more vigorous at least during the juvenile phase, than pure species and can also be characterized by straight stem shape and fine branching (HOLST, 1974; LE CAM, 1981).

3.3. Vegetative propagation

Until now, applied breeding programs have mainly used sexual propagation, although there has always been interest in the cloning of valuable plant material.

Research between 1940 and 1960 was primarily concerned with physiological problems and technical requirements for propagation by cuttings (MUHLE LARSEN, 1946; HEITMÜLLER, 1952; FRÖHLICH, 1955; KLEINSCHMIT and FRÖHLICH, 1956; KLEINSCMIT, 1958). Later research was mainly directed to conventional methods for rooting of cuttings (i. a. CHANDLER, 1960, 1967; ISIKAWA, 1962; JANSON, 1976; JOHN, 1978, 1979; PAULE and ŠKOLEK, 1983; SCHACHLER et al., 1987, 1991; comp. also MORGENSTERN, 1987).

Results from this work show that 50% to 100% rooting can be obtained from both fully-lignified and partially-lignified cuttings, provided these are taken from young stoolbed plants up to the age of about 4 years. There is a rapid decrease in rooting ability in older original material. The use of lignified cuttings appear best for advanced root growth and shoot growth and to the fastest-possible change from a plagiotropic to an orthotropic form.

Tissue culture techniques have also been tested in recent years for their suitability for the propagation of European larch. Numerous investigations deal in particular with in vitro organogenesis.

BONGA and VON ADERKAS (1988), LALIBERTÉ and LALONDE (1988) and MATSCHKE, EWALD and ZOGLAUER (1991, unpublished report) all found that the regeneration potential of buds depends to a large extent on (1) the original position of long-shoots or short-shoots, (2) time of explanting and (3) age of source material. KARNOSKY and VERVILLE (1988) and HÜBL and ZOGLAUER (1991) describe systems of micropropagation with explants of seedlings.

The technique may be of interest from an economic viewpoint particularly for mass-propagation. It presupposes success in improving rooting and the prevention of vitrification of the shoots. In Hann. Münden we have had favourable results using a cooling shelf system for in-vitro cultures of various tree species that are sensitive to vitrification (comp. also MCLAUGHLIN and KARNOSKY, 1989).

Adult larches are the focus of attention in research on better propagation technique (i. a. BONGA and POND, 1991). In Germany, an interdisciplinary working group is currently working on the propagation of old trees of various species by in vitro techniques. Initial results have been obtained for larch (comp. also ZOTT et al., 1991).

Possibilities of utilizing somatic embryogenesis, a more recent approach, are also being investigated (NAGMANI and BONGA, 1985; DURZAN, 1989). KLIMASZEWSKA (1988, 1989) was the first to report on the cloning of early zygotic embryos and the development of plantlets of *Larix eurolepis*. Combined with suspension culture techniques, or by using bioreactors, embryos can theoretically be produced in unlimited numbers. However, regeneration success is substantially dependent on their quality and on the continuity of production. Initial results were published by VON ADERKAS and BONGA (1988) and VON ADERKAS et al. (1989) on the formation of haploid larch embryos after cultivation of the gametophyte. Regeneration from the female gametophyte appears more promising than regeneration from the male gametophyte.

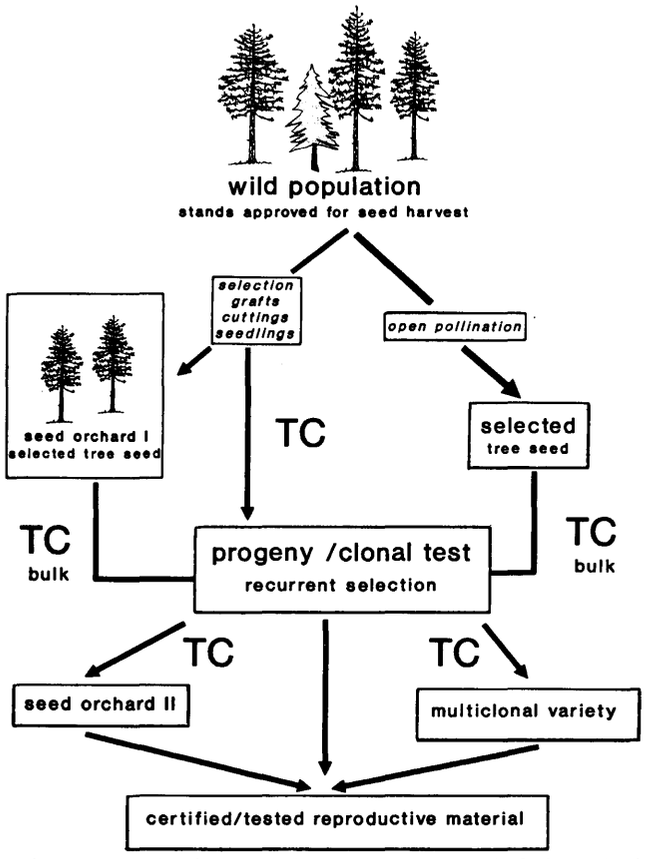

Figure 5. — Potential utilization of tissue culture techniques (TC) in breeding programmes with European larch.

The application of biochemical genetics appears to have the potential for considerable improvement in the efficiency of vegetative propagation. BERGMANN and RUETZ (1987) have shown, for example, that isoenzyme markers can be used to determine the proportion of hybrids in seed lots. Additional isoenzyme research on population structure of *Larix laricina* has recently been published (YING and MORGENSTERN, 1990, 1991).

Vegetative propagation techniques, either by rooting of cuttings or by tissue culture, is not presently sufficiently developed for *Larix decidua* to permit large scale use in forestry practice in an economically acceptable way, although the techniques are becoming increasingly important in breeding programmes. *Figure 5* gives information on the range of application of tissue culture. Progeny and clonal tests can be made comprehensive, varied and conclusive by this means.

4. Conclusion and prospects

Systematic research on European larch is as old as IUFRO and has received great impulse from this organisation. Genetics and breeding of this tree are impressive in their range, in their diversity and in the state of knowledge now reached.

In this paper we have shown the main research fields in their historical development up to the present. It was neither intended nor possible to give a comprehensive account of all work on this subject. Thus it must be understood that little or no mention has been made of some related fields such as cytology, mutation breeding or wood technology, although important research results have also been published in these fields (comp. i. a. the publications by ILLIES or LEWARK).

Intensive provenance breeding over many decades has succeeded in collecting vital information on the variation pattern of European larch. Extensive knowledge now exists on variation in growth characteristics and canker susceptibility, not only between the sub-areas of this tree species, but also within large provenance regions. This knowledge is today the most important basis for site-suited larch cultivation, particularly outside its natural distribution area.

In addition, hybridization and progeny tests in numerous countries have shown that considerable breeding progress can be achieved with *Larix decidua* by paying attention to individual variation and by utilising heterosis effects. In this field particularly, intensification of future research work seems indicated. This applies both to previously-neglected provenance hybrids and additional species hybrids with *Larix leptolepis*. Crosses with other Asiatic larch species may also be worth studying. Differences in growth rhythm are to be expected between hybrids and pure species and should not be disregarded in an assessment.

Considerable research is needed in the field of vegetative propagation with European larch, since at present no method is economically acceptable.

Research work on in vitro culture is also of interest because it promises progress for propagation of adult source material.

This technology may increase the efficiency of recurrent selection, accelerate the development of advanced breeding seed orchards, and facilitate more rapid development of multiclonal varieties.

Selection should, however, be carried out in a responsible way and, especially in combination with cloning, bearing in mind their expected range of effect. With larch as with other tree species, possible genetic gain can in no way justify the irretrievable loss of wide genetic variation.

Some new fields of research on larch have, so far, received little attention including protoplast fusion and the utilization of recombinant DNA technology for genetic analysis, gene mapping, and distinguishing the frequency of recombination.

Success in the fields of larch research depends in no small measure on close international cooperation including task distribution among institutes. In the past, IUFRO has proved its value in the complex research on this tree species. Faced with many new study fields, both in genetics and breeding, we consider IUFRO to be a more indispensable institution than ever for productive research on larch.

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IUFRO's Role in Douglas-Fir (Pseudotsuga Menziesii (Mirb.) Franco) Tree Improvement

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(Received 2nd April 1992)

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Abstract

Douglas-fir, today one of the most important timber species in the world, was first discovered in 1792 by Archibald Menzies and introduced to Europe in 1826 by David Douglas. About 1850, extensive plantations were