douglasie. Forst und Holz 46, 267—272 (1991). —— SCHÄDELIN, W.: Ergbnisse der Lärchenforschungen von Prof. Dr. ERNST MÜNCH und waldbauliche Folgerungen. Schweiz. Z. Forstwes. 92, 41—49, 67—79 (1941). —— SCHMIDT, W.: Lärchenherkünfte und *eurolepis*-Bastarde im nordwestdeutschen Küstengebiet. Allg. Forst- u. J.-Ztg. 126, 24—28 (1955). —— SCHOBER, R.: Ergebnisse von Lärchen-Art- und Provenienzversuchen. Silvae Genetica 7, 137—154 (1958). SCHOBER, R.: Vom II. Internationalen Lärchenprovenienzversuch. Ein Beitrag zur Lärchenherkunftsfrage. Schr. Reihe Forstl. Fak. Univ. Göttingen, Bd. 49 (1977). —— SCHOBER, R.: Vom I. Internationalen Lärchenprovenienzversuch 1944. Bericht über drei deutsche Teilversuche. Allg. Forst- u. J.-Ztg. 152, 181—195, 201—211, 221—233 (1981). —— SCHOBER, R.: Neue Ergebnisse des II. Internationalen Lärchenprovenienzversuches von 1958/1959 nach Aufnahmen von Teilversuchen in 11 europäischen Ländern und den USA. Schriften Forstl. Fak. Univ. Göttingen und Nieders. Forstl. Versuchsanst. Bd. 83 (1985) —— SCHOBER, R.: Einfluß der Provenienz auf die Ertragsleistung. In: Kramer, H.: Waldwachstumslehre. Parey, Hamburg und Berlin (1988). —— SCHOBER, R. und FRÖHLICH, H. J.: Der Gahrenberger Lärchen-Provenienzversuch. Schr. Reihe Forstl. Fak. Univ. Göttingen, Bd. 37/38 (1967). —— SCHOBER, R. und GOTHE, H.: Ein Kreuzungsversuch mit *Larix europaea* D. C., Herkunft Schlitz, und *Larix leptolepis* GORD.. Allg. Forst- u. J.-Ztg. 142, 211—217 (1971) —— SCHÖNBACH, H.: Ertragssteigerung durch interspezifische Hybridisierung bei Aspen und Lärchen. Wiss. Zeitschr. Techn. Univ. Dresden 16, 563—567 (1967). —— SCHÖNBACH, H., DÄSSLER, H.-G., ENDERLEIN, H., BELLMANN, E. und KÄSTNER, W.: Über den unterschiedlichen Einfluß von Schwefeldioxid auf die Nadeln verschiedener 2jähriger Lärchenkreuzungen. Züchter 34, 312—316 (1964). —— SCHREIBER, M.: Zur physiologischen Reaktionsweise von Provenienzen der Europäischen Lärche (*Larix decidua* MILL.), der Japanlärche (*Larix leptolepis* GORD.) und der Sibirischen Lärche (*Larix sibirica* LEDEB.) auf gleiche Umweltbedingungen. Cbl. ges. Forstwes. 77/79, 18—26, 1—17 (1960/1961). —— SCHREIBER, M.: Über neuere Forschungsergebnisse auf dem Gebiet der Lärchenrassenbiologie. Schweiz. Z. Forstwes. 115, 44—74 (1964). —— SCHÜTZ, J.-P.: Einige Erfahrungen aus dem 1. Internationalen Lärchenprovenienzversuch 1944 im Höngerberg bei Zürich, Schweiz. IUFRO-Arbeitsgruppe 2.02—07. Wien (1979). —— SEIDENSCHNUR, W.: Ergebnisse von Lärchenart- und Lärchenherkunftsversuchen der Niedersächsischen Forstlichen Versuchsanstalt. Diss., Göttingen (1974). —— SIMAK, M.: Karyotype analysis of *Larix decidua* MILL. from different provenances. Medd. Stat. Skogsforskningsinst. 51, 1—22 (1962). —— SIMAK, M.: Seed weight of larch from different provenances (*Larix decidua* MILL.). Stud. For. Suec. 57, 1—31 (1967). —— ŠINDELÁR, J.: Notes to taxonomy and chronology of species *Larix decidua* MILL. Internat. Symposium on Biology of Woody Plants. Nitra, May 10—17, 1967, 25—33 (1967a). —— ŠINDELÁR J.: Některé poznatky o plodnosti semenných modřínových plantáží a jakosti jejich osiva. (Some new views on the fructification of larch seed orchards and on the quality of their seed). Lesnický Časopis 13, 329—342 (1967b). —— ŠINDELÁR, J.: Auswertung von einigen Lärchenprovenienzflächen der zweiten internationalen Serie in der ČSSR. Zbraslav Strnady (1971). —— ŠINDELÁR, J.: Další příspěvěk k Poznání proměnlivosti modřínu evropského (*Larix decidua* MILL.). (Weiterer Beitrag zur Erkenntnis der Veränderlichkeit der Europäischen Lärche (*Larix decidua* MILL.)). Lesnictví 20, 625—644 (1974a). —— ŠINDELÁR, J.: Stručný přehled výsledků šetření na výzkumných plochách modřínu evropského. II. mezinárodni série. (A short outline of results of investigation on experimental plots of European larch of the 2nd International Series). Práce Vúlhm 45, 113—138 (1974b). —— ŠINDELÁR, J.: Evaluation of some Czechoslovak experimental provenance areas of larch IUFRO 1958/1959 series at age of 20 years. Commun. Inst. For. Čechoslov. 13, 59—72 (1983). —— ŠINDELÁR, J.: Zachování reprodukce a dokonalejší vyuzití genofondu modřínu opadavého — (*Larix europaea* MILL.) v ČSR se zřetelem k modřínu jesenickému. (An outline of measures for conservation, reproduction and better use of the genofound of European Larch in the CSR, with respect to the Jeseniky Larch). Lesnictví 30, 569—587 (1984). —— ŠINDELÁR, J.: Nektere vysledky ověřovani vyběřovych stromu modrínu opdavého (*Larix dec.* MILL.) potomstvy z kontrolované-ho křiženi. (Einige Ergebnisse der Überprüfung von Auslesebäumen der Europ. Lärche durch Nachkommenschaften aus kontrollierter Kreuzung). Lesnictví 32, 1047—1068 (1986). —— ŠINDELÁR, J.: Results of hybridization within the genus *Larix* with emphasis on interspezific hybrids. Rozpravy Ceskoslov. Akad. 98, 7 (1988). —— ŠTASTNY, T.: Assessment of the 20 years old first international provenance experiment with *Larix* sp. from the year 1944 in the forest district Podbanské Commun. Inst. Forest. Cechoslov.., 115—126 (1965). —— ŠTASTNÝ, T.: Die Bewertung von Lärchenherkünften auf einigen Flächen der IUFRO aus dem Jahre 1944. Vedecké, Práce No. XII, 65 (1970). —— ŠTASTNÝ, T.: Modifikovanie Prejavu Genetickej Podstaty Rastu *Larix decidua* MILL. Vplyvom Podmienok Prostredia. (Die Modifikation der Äußerung der genetischen Wachstumsgrundlage von *Larix decidua* MILL. unter dem Einfluß der unterschiedlichen Umweltbedingungen). Zvolen, Lesnicke Studie No. 10 (1971). —— SYRACH-LARSEN, C: The employment of species, types and individuals in forestry. Yearb. R. Vet. Agric. Coll., Copenhagen (1937). —— SYRACH-LARSEN, C.: Genetics in Silviculture. Oliver and Boyd, London (1956). —— THÜMMLER, K.: Blüh- und Ertragsverhältnisse der Pfropfbäume einer Lärchenkreuzungsplantage. Soz. Forstwirtsch., Berlin, Sonderheft "Forstliche Samenplantagen III" (1963). —— TROEGER, R.: Die Lärchenprovenienzversuche in Württemberg. Allg. Forst- u. J.-Ztg. 133, 127—144 (1962). —— TSCHERMAK, L: Die natürliche Holzartenverbreitung (mit besonderer Berücksichtigung der Lärche) und die ökologischen Bedingungen im Waldviertel und im Dunkelsteinerwald in Niederösterreich. Cbl. ges. Forstwes. 58, 73—106 (1932). —— TSCHERMAK, L.: Die Standortansprüche der Lärche. Deutsch. Forstwirt 15, 581—589 (1933). —— TSCHERMAK, L.: Die natürliche Verbreitung der Lärche in den Ostalpen. Mitt. Forstl. Bundesversuchsanstalt Wien-Schönbrunn, H. 43 (1935). —— WEISER, F.: Vorschlag von Hybrid-Hochzuchtsorten der Lärche. F/E-Bericht A4. Institut Forstwissenschaft, Eberswalde (1984). —— WEISGERBER, H.: Die Bedeutung von Samenplantagen für die Versorgung mit forstlichem Saat- und Pflanzgut in Hessen. Fortschritte des forslichen Saatgutwesens III. Mitt. Hess. Landesforstverw. Bd. 14, 71—84 (1976). —— WEISGERBER, H.: Züchtungsfortschritte durch Nachkommenschaftsprüfungen. Forstarchiv 53, 9—13 (1982). —— WEISGERBER, H.: Forstpflanzenzüchtung. Aufgaben, Ergebnisse und Ziele von Züchtungsarbeiten mit Waldbäumen in Hessen. Mitt. Hess. Landesforstverw., Bd. 19 (1983). —— WEISGERBER, H.: Beiträge zur genetischen Variation der Waldbäume und Gefahren der Genverarmung durch Pflanzenzüchtung. Forstl. Forschungsber. München, Nr. 107, 204 S. (1990). — YING, L. and MORGENSTERN, E. K.: Inheritance and linkage relationships of some isozymes of *Larix laricina* in in New Brunswick, Canada. Silvae Genetica 39, 245—251 (1990). —— YING, L. and MORGENSTERN, E. K.: The population structure of *Larix laricina* in New Brunswick, Canada. Silvae Genetica 40, 180—184 (1991). —— ZIMMERLE, H.: Beiträge zur Biologie der europäischen Lärche in Württemberg. Mitt. Württ. Forstl. Versuchsanst. 11, 206 (1941). —— ZOTT, U., ZOGLAUER, K. und DEMBNY, H.: Adventivsprosse aus Nadelexplantaten juveniler und adulter Lärchen. In: Abstracts IAPTC, Tag. Deutsch. Sekt., 18.—19. Sept. 1991. Hamburg. Poster No. 82 (1991).

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

By J. KLEINSCHMIT[1]) and J. CH. BASTIEN[2])

(Received 2nd April 1992)

[1]) Lower Saxony Forest Research Institute, Dept. of Forest Tree Breeding, D W-3513 Staufenberg-Escherode, Federal Republic of Germany

[2]) INRA, Station d'Amélioration des Arbres Forestiers, Ardon, F-45 160 Olivet, France

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

started in different European countries, which were initially very successful. With increasing seed import from the interior part of the natural range, problems occurred in plantations. This stimulated interest into the provenance question. First provenance experiments, which covered only limited parts of the natural range and a limited number of plantation sites, were established in Europe and the Pacific North-West of America in 1910/1912. To get more complete information about Douglas-fir variability, adaptability, physiology, and provenance suitability, IUFRO started in 1967 under the leadership of HELMUTH BARNER from Denmark a systematic and representative collection of 182 indigenous provenances, covering the whole natural range. These were distributed to 59 institutions in 36 countries. The IUFRO working party "Douglas-fir provenances" stimulated a lot of research activities, exchange of ideas and information, and created cooperation and friendship among scientists all over the world. Today the IUFRO provenance experiments together with the research of other institutions, especially in North-America on provenance variability, form an unique basis for decisions on seed transfer, gene conservation, and tree improvement for Douglas-fir. They have had far reaching consequences, especially for European forestry, for which Douglas-fir will be one of the most important timber species in the future.

Key words: Pseudotsuga menziesii, Provenance experiments, breeding, natural range, variation, adaptability, IUFRO, survival, growth, resistance.

1. Introduction

Douglas-fir is one of the most important timber species in the world. It is number one in the Pacific North-West of America, where it reaches up to 126 m in height and 5 m in diameter (ISAAC and DIMROCK, 1965) and a standing volume of old growth stands up to 5,460 m^3/ha (WORTHINGTON, 1958). Douglas-fir is the most important exotic in Western and Central Europe due to its adaptability, growth and wood quality. The annual plantation area is about 10,000 ha in France (OSWALD and PARDÉ, 1984) and 5,000 ha in Germany.

In a long term view Douglas-fir will be one of the most important tree species in France, the Netherlands, Belgium, Germany, and Great Britain, exceeding 10% of the total woodland area. It is also very important in some other European countries, including Italy, Portugal, Spain, Austria, Ireland, Denmark, Romania and Czechoslovakia, and in the southern hemisphere in New Zealand, Australia and Chile.

The genus *Pseudotsuga* was native to European Tertiary flora and disappeared along with many other species and genera during the glaciations (HERMANN and CHING, 1973; HERMANN, 1980). Douglas-fir was discovered by the Scottish physician and naturalist ARCHIBALD MENZIES in 1792 on the west coast of Vancouver Island where he accompanied Captain VANCOUVER on board the Discovery. The first seed originating from the vicinity of Ft. Vancouver at the Columbia River was sent to Great Britain by DAVID DOUGLAS in 1826 (HERMANN, 1982; POURTET, 1951). Since then, seed has been continuously imported to England and especially Scotland. Plantations in different European countries started about the middle of the last century, mostly on the initiative of JOHN RICHMOND BOOTH a nursery-man near Hamburg (FLÖHR, 1958).

The first plantations were quite successful. The 1881 decision of the German Forest Research Institutes, influenced by Bismarck, to include testing of exotic tree species into their programs was the beginning of forest research interest in this species. The first plantations of Douglas-fir established by the Prussian, Badische, Württembergische und Braunschweigische Forest Research Institute, mostly between 1881 and 1890, resulted in excellently growing, healthy stands of the coastal variety (SCHOBER, 1972).

The problems with Douglas-fir resulting from later imports to Europe from the more continental part of the natural range led to the reasoning of SCHWAPPACH (1907), the head of the Prussian Forest Research Institute from 1899 to 1925, that the extended natural range must have resulted in very different ecotypes with different suitability for Europe. He therefore argued that research into the provenance question of Douglas-fir was one of the most important bases for future plantations. He started a provenance collection that was used in the two first provenance experiments in Chorin (1910) east of Berlin established by SCHWAPPACH. The material was also used in Kaiserslautern in south-west Germany (1912) in a trial established by MÜNCH (SCHOBER, 1973) at the same time as the Douglas-fir heredity study was established in the Pacific North-West (see paragraph 2). These tests were followed by the experiments of WIEDEMANN (1932/1933) in 9 locations, by GEYR VON SCHWEPPENBURG in Gahrenberg with similar provenances and by SCHOBER 1954 to 1961 in 15 locations. Similar tests have been planted in various other European countries. The bibliography of more than 400 publications covering provenance studies mainly in Europe and North America from 1907 to 1974 was compiled by HERMANN and CHING (1975).

Up to 1967, tests were mostly established on one or a few sites with a limited number of commercial seed lots covering only parts of the natural range, without control of the locations of the respective origins. They indicated, nevertheless, that there was a very wide variation in adaptability, growth, resistance to needle fungi and other characters. The recommendations resulting from provenance research were not always followed in practical forestry for seed import, even in the middle of the 1960s, this led to considerable losses (SCHENCK, 1939; KLEINSCHMIT, 1973).

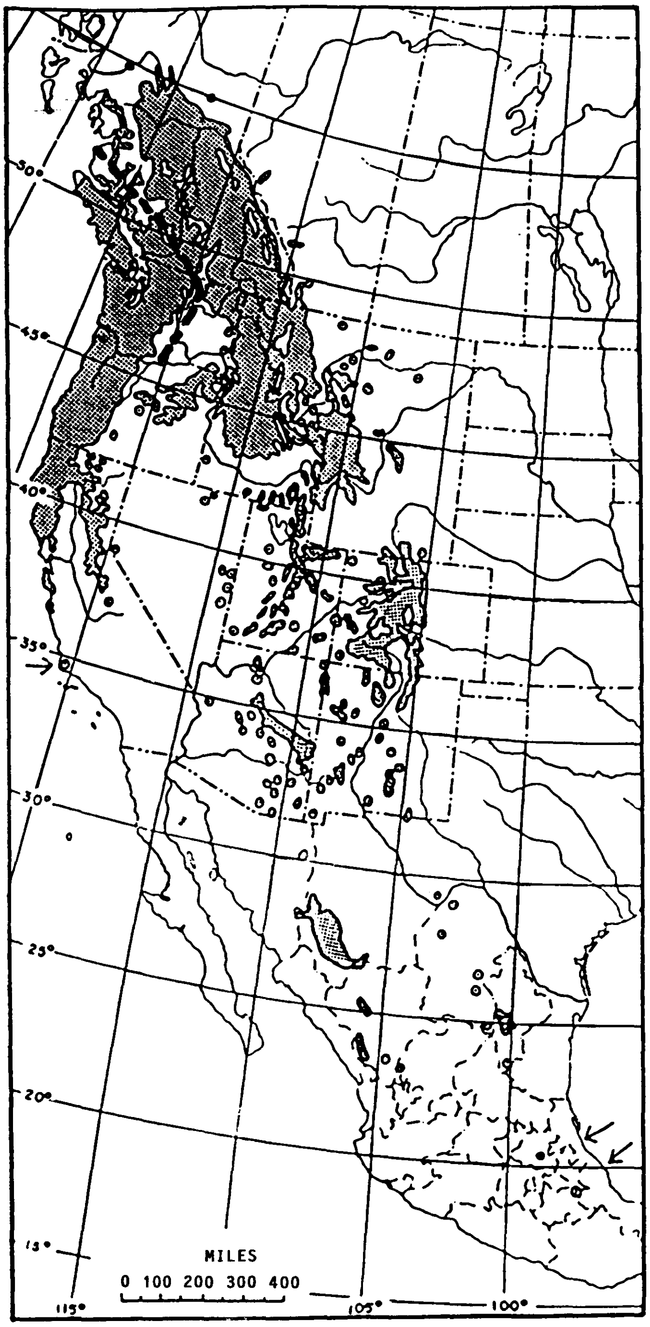
In September 1965, IUFRO Section 22 decided during a session in Pont à Mousson, France, to start a controlled seed collection of Douglas-fir and other Northwest American species in their natural range. A working party for seed procurement for provenance research was established and HELMUTH BARNER, head of the Tree Improvement Station in Humlebaek, Denmark was appointed as leader (BARNER, 1973).

To judge IUFRO's role in Douglas-fir improvement it is necessary to compare knowledge and activities before and after the establishment of the IUFRO collection.

2. Knowledge of Douglas-fir genetic structure before the IUFRO collection

Douglas-fir is one of 8 living *Pseudotsuga* species, but the only one with high economic value. Interspecific crosses with other *Pseudotsuga* species are not fertile with the exception of those with *P. macrocarpa*, where a low seed set was observed (ORR-EWING, 1966).

Douglas-fir is a monoecious species with an allogamous (crossbred) breeding system. Natural self pollination occurs (SORENSEN, 1971, 1973) at a rate of about 7% but



From FOWELLS, H. A.: Silvics of Forest Trees of the United States. Agriculture Handbook No. 271. 45 Dept. Agriculture, 1965, p. 547

Figure 1. — The range of Douglas-fir. The two varieties are seperated by a broken line.

strong natural selection reduces numbers of inbred seedlings.

The estimated mean number of lethal alleles is about 10 (SORENSEN, 1971; BISHIR and NAMKOONG, 1987). Self sterility was found in low frequencies (ORR-EWING, 1969, 1977). The reproductive cycle has been summarized by ALLEN and OWENS (1972) and OWENS (1973).

The extended natural range of Douglas-fir with the associated climatic changes must necessarily lead to considerable differences in selection pressure and as a consequence to genetically differentiated populations (*Fig. 1*). Douglas-fir extends over 2,500 km in its coastal range and over 4,500 km in the interior part of its range. Range of latitude is from 19 °N in Mexico to 55 °N in British Columbia, of longitude from 97 °W to 128 °W. In the coastal range Douglas-fir can be found at up to 750 m elevation in the north and 1,700 m in the south. East of the Cascades and the Sierra Nevada its range goes up to 3,300 m.

This has no consequences within the natural range as long population transfer does not occur over long distances. With the transfer of a species to a new habitat, as occurred with Douglas-fir planting in Europe, it soon became obvious, however, that it was extremely risky to regard Douglas-fir just as one species and not as a set of genetically subdivided populations with quite different adaptional behaviour. This is probably one of the explanations for the fact that the Europeans were much more interested in the seed of the IUFRO collections than the Americans.

Two distinct geographical varieties of Douglas-fir exist; the coastal or green form *P. menziesii* var. *menziesii* and the interior or blue form var. *glauca*. In the northern part of the range and the intermountain part, the intermediate form, var. *caesia*, shows seed and cone characteristics of both extremes in different intensity, so that it is difficult to draw a clear border line (ALLEN, 1960). Seedling studies showed distinct differences between coastal and interior sources (SORENSEN, 1967; IRGENS-MOELLER, 1958).

In the western coastal part of the natural range, Douglas-fir is a subclimax species that is less shade-tolerant than some of the associated species. Douglas-fir invades quickly after fire or storm (MUNGER, 1940). In the Rocky Mountains, Douglas-fir is, however, a climax species, which is replaced after fire by aspen or *Pinus ponderosa* but finally dominates these species. REHFELDT and LESTER (1969) argued that pioneer species should have high flexibility and variability with clinal patterns of variation. They have to colonize changing environments and associated continuous gene exchange. Climax species, which grow under more homogeneous environmental conditions, should express more ecotypic patterns of variation.

Pollen is the most important unit for gene exchange in tree populations. The Douglas-fir pollen grain is big and heavy — as compared to other conifers. In spite of this, transport occurs over long distances (SILEN, 1962; EDDELL and SCHMIDT, 1964). SILEN found 300 to 1,000 polllen grains per cm^2 in a non flowering seed orchard distant from Douglas-fir stands. In other seed orchards in British Columbia, Washington and Oregon, considerable amounts of outside pollen have been detected, varying from 100 to 1,000 pollen grains per cm^2, the pollen sources being up to 5 miles away. Even in areas with no Douglas-fir up to 20 km, 100 pollen grains per cm^2 were still present.

Since single Douglas-fir trees release pollen for 7 to 15 days and on the same site stands release pollen for up to 30 days, pollination can occur over an elevational range of up to 500 m (SILEN, 1963). The maximal pollen contribution will, however, originate from a similar elevation. For effective gene exchange, the geographic and orographic structures are also important. Equal elevation and extended monospecies forests are two factors which favour pollen exchange. Therefore different patterns of variation can be expected in Douglas-fir according to region.

A first provenance experiment with 120 open pollinated progenies from 13 Washington and Oregon sources collected from elevations between 20 m and 1,280 m was established in 1912 in 5 sites over Oregon and Washington at between 300 m and 1,500 m of elevation. At age 17, 2 provenances were superior at all locations. At age 50 this ranking had disappeared. With one exception, the local provenances were not superior in either growth or survival. Losses, however, increased with increasing elevational difference between site of origin and site of plantation. On the most exposed sites, there was a tendency toward superiority of local sources, but at protected sites the opposite was true (SILEN, 1964, 1966).

IRGENS-MOELLER (1968) was able to demonstrate a close relationship between length of growing season of trees of 3 provenances and climatic characteristics of the locations of origin. HERMANN and LAVENDER (1968) found differences in growth and phenology between provenances of different elevations along a transect across the Cascades which were correlated with elevation and other characteristics of locations of origin. Similar results were reported by MORRIS et al (1957). SORENSEN (1967) described significant differences between 8 provenances of an east-west-transect across Oregon and found 3 groups corresponding to elevation and exposition in Coast range, Cascades and Rocky mountains.

CHING (1965) planted 16 provenances from British Columbia, Washington and Oregon at the locations of origin. Significant differences in growth, survival and flushing were recorded. North-west Washington sources and provenances from Southern Vancouver Island performed thc best.

In a provenance experiment in Washington at age 7 WHEAT and WILSON (1965) found superior growth with coastal provenances as compared to *caesia* Douglas-fir from Interior British Columbia.

HADDOCK and SZIKLAI (1966) detected in coastal plantations that the best differentiation between B. C. coastal and interior sources was their growth potential, which decreased when provenance proceeded eastward.

GERHOLD (1965) tested juvenile growth of trees of 65 provenances covering the natural range with the exception of British Columbia and California. He described drastic differences in survival and height even from limited areas.

FERRELL and WOODWARD (1966) and PHARIS and FERRELL (1966) found a higher level of drought resistance among the inland sources than in the coastal ones. MILLER and GRAHAM (1963) found that wood of Rocky Mountain sources has lower permeability than that of coastal sources.

Altogether, the pattern of variation in the western part of the natural range is more clinal from north to south. From west to east changes are more drastic over short distances following mainly the orographic structure of the mountain range and elevation.

The description of the varieties "*menziesii*", "*caesia*" and "*glauca*" is a relatively rough scheme, which does not reflect the continuous changes and differentiation which occur in nature. Delineation is more or less arbitrary, especially in "caesia".

In 1958 GÖHRE and coworkers published a book "Die Douglasie und ihr Holz" which gives an excellent summary of the knowledge available at this time in Europe.

SCHÖNBACH (1958) pointed out the extreme variability in all characteristics observed within the three varieties "*menziesii*", "*glauca*" and „*caesia*" and discussed the possibilities of tree improvement, especially by selection and variety hybridization. Frost sensitivity is a limiting factor for growing Douglas-fir in eastern Germany and eastern Europe (LYR, 1958). This character was correlated with phenological traits like flushing and bud set, which were evaluated in provenance and progeny tests. SCHÖNBACH underlined the necessity of continuing provenance research including a high number of provenances on a broad basis. His proposals for breeding were physiologically well-based and in many aspects quite modern, e.g. compared with concepts recently presented for describing the genetic units by phenological traits (WHEELER et al., 1990).

The needle casts caused by *Rhabdocline pseudotsugae* and *Phaeocryptopus (Adelopus) gäumanni* are the most severe restrictions for growing interior Douglas-fir in Europe. *Rhabdocline pseudotsugae* was first observed in America in 1911 and caused severe damage in Scotland 1922 (STEPHAN, 1973). It subsequently spreads through continental Europe. Intensive research started in 1930 with important contributions by the father of the earlier president of IUFRO WALTER LIESE, (LIESE, 1932, 1935, 1936 e.g.), which showed that the coastal provenances were quite resistant. The northern interior provenances showed significant provenance and individual variation. The recent results were summarized by STEPHAN (1973, 1980), BERGER (1982) and SOUTRENON (1986). Highest sensitivity is observed in interior seed sources south of latitude 40 ^{0}N (Arizona, Colorado, New Mexico).

It is obvious that the knowledge of Douglas-fir pattern of variation was still quite incomplete prior to IUFRO provenance collection and testing. A rough knowledge existed of the geographical trends and especially about the suitability of provenances for the different parts of Europe (SCHOBER, 1959; LACAZE and TOMASSONE, 1967; NAN-

Table 1. — On Juli 1973; Douglas-fir samples had been distributed to 54 institutions in 30 countries as shown in the table below.

A	B	C
Argentine	1	56
Australia	3	45
Austria	1	18
Belgium	1	53
Canada	2	184
Czechoslowakia	1	25
Chile	1	56
Denmark	3	139
Finland	1	8
France	1	220
Germany, East	1	155
Germany, West	4	455
Hungaria	1	104
Iran	1	20
Ireland	1	32
Italy	2	128
Korea	2	7
New Zealand	1	1
Norway	1	51
Poland	2	158
S. Africa	1	3
Spain	1	91
Sweden	1	6
The Netherlands	1	161
Turkey	1	118
United Kingdom	3	166
USA	11	17
USSR	2	37
Venezuela	1	6
Yugoslavia	1	26
	54	2546

(from BARNER, 1973)
A = country; B = institutions; C = number of samples

son, 1978; Galoux, 1956; Lines and Mitchell, 1970). Some of the biochemical and genetic tools were not available at that time and testing was often un-systematic.

3. The IUFRO collection

The objectives of the collection were:

- scientific research on forest genetics and seed physiology;
- provenance research with the objective being to find the best yielding sources and to provide material for future breeding;
- preservation and establishment of gene resources in order to secure a continuous seed supply (Barner, 1973).

The natural range of the species was to be well-represented and the stands sampled indigeneous and typical of larger forest areas. However, certain isolated stands and marginal areas were included as well.

Collections were made mostly from 15 dominant trees per stand. The space between trees was kept to approximately 100 m to prevent possible effects of inbreeding. Every source was marked very carefully on a detailed map. The geographical longitude, latitude, elevation etc. were recorded on special collection data sheets.

Altogether, 182 Douglas-fir provenances with 326 kg of seed were collected and distributed to 54 institutions in 30 countries by 1973 (Barner, 1973, *Table 1*), and respectively to 59 institutions in 36 countries by 1978 (Fletcher and Barner, 1978).

This collection was possible due to the excellent assistance and cooperation of the US Forest Service and different other organizations and individuals in the United States of America and the financial loans of the Carlsberg Foundation and Den Danske Landmandsbank. When the senior author started his work as head of the Dept. for Forest Tree Breeding of the Lower Saxony Forest Research Institute in 1967, the first seed of the collection was just ready to be sown. This was a unique opportunity to fill gaps left by the series of earlier provenance studies, to serve as a basis for physiological and genetical research and to broaden knowledge view by the wider genetic basis of the samples and the broader ecological basis of the sites to be planted. At the same time, the collection was a start for the conservation and establishment of Douglas-fir gene resources.

The thorough and excellently organized collection by Helmuth Barner was not only an opportunity to extend provenance research with Douglas-fir on a sound and more systematic basis, but also to get into close international cooperation with other scientists working with the same species, to broaden the view and experience, to share ideas and to create friendship with colleagues all over the world. The open mind of Helmuth Barner and the fair and helpful supportive activities in the working party crossing all political borders was for many of us a most satisfying and stimulating experience.

The working party on Douglas-fir provenances organized 4 meetings alternating between Europe and Western North America:

1973 in Göttingen, Federal Republic of Germany;
1978 in Vancouver, British Columbia, Canada;
1985 in Vienna, Austria;
1990 in Vancouver, Washington, United States of America.

The proceedings of the meetings (IUFRO, 1973; IUFRO, 1978; IUFRO, 1987; and IUFRO, 1990) summarize on 1,207 pages the most important results of the IUFRO Douglas-fir collection and give additional information about the natural range, ancestral history, biosystematics based on biochemical and genetic research and on selection and breeding. It is of special interest that many findings within the natural range of the species based on more specific regional tests or on different approaches like terpene or allozyme patterns were incorporated into these proceedings, adding to the overall picture of Douglas-fir genetic variation, breeding strategy and breeding results.

The IUFRO activities gave rise to additional activities on a regional basis; much more research into provenance variation has been started since 1965 in America. Additional collections in more restricted areas have followed the IUFRO collection by different European countries for practical seed supply as well as for the establishment of broader breeding populations and of gene conservation areas.

In the following chapter the main findings since 1965 will be summarized according to the three objectives of the collection. Finally, future activities will be outlined.

3.1. Research on seed, cones, physiology and genetics

Cone and seed

The IUFRO collection has been used to study phenotypic variation in cone and seed characters. Sziklai (1973) used 124 IUFRO samples with 1,818 trees and 2 cones per tree to study cone and seed characteristics. Birot (1972) used 189 provenances to study 1,000 seed-weight. There was a clear trend for decreasing cone scale width with increasing latitude. In the interior part of the natural range, 1,000 seed weight decreased with increasing elevation; in the southern coastal region in contrast to this seed weight increased with increasing elevation. Seed morphology based on four characteristics allowed a clear separation between coastal and inland provenances.

Scagel and coworkers (1987) studied the variation of 10 seed and cone characteristics within and between provenances and varieties. A clinal variation was detected. However, most of the variation was within populations (67%). Glacial history and varietal classification accounted only for a minor part of total variation (6.8% resp. 6.9%). The latitudinal cline was strong when compared with the longitudinal. The strong within-population variation and the differing correlations among the variables indicated linkage disequilibrium. But non-selectionist explanations were considered equally. Nuclear volume and DNA content increased with increasing latitude. It was possible to locate provenances of unknown origin from Poland and Switzerland approximately based on these characteristics (Berney, 1972).

This study was further extended by Sziklai and De Vescovi (1978) and Sziklai et al. (1987). DNA content in Douglas-fir has adaptive significance. Northern coastal provenances had higher DNA content and larger chromosome width and volume, but there were no differences in chromosome length. The same differences were found between coastal and interior provenances. The chromosome morphology studies of 7 of the 8 living *Pseudotsuga* species show that *Pseudotsuga menziesii* deviates greatly from other species of the genus. *Pseudotsuga menziesii* is the only species with $n = 13$ chromosomes. All other species of the *Pinaceae* have $n = 12$ except *Pseudolarix amabilis* ($n = 22$). However, the different varieties of *Pseudotsuga menziesii* are morphologically poorly differentiated. SZIKLAI et al. (1987) postulate, that the additional chromosome originates from abnormal division of a metacentric chromosome and the ensuing production of 2 stable telocentrics (*Fig. 2*).

Frost sensitivity

The IUFRO collection has been used for a series of studies into frost hardiness, both under controlled conditions and in the field. DIMITRI (1973) established a close positive relationship between height, water content and winter-frost sensitivity. Considerable variation occurred within populations; interior British Columbia sources were the most resistant ones. LARSEN (1978) used an artificial freezing test with 60 IUFRO provenances. Interior B.C. provenances were resistant to early and winter frost but susceptible to late frost. Coastal provenances were generally more susceptible to early and winter frost but rather resistant to late frost. Latitude, distance from the Pazific Ocean and elevation above sea level explained 90% of the between-population variation in early frost resistance but only 18% of late frost resistance. Topography of the site of origin seems to be more important for variation in late frost resistance. Early and winter frost susceptibility are highly correlated. Phenological traits are closely correlated with frost sensitivity and are therefore very useful for indirect selection of frost hardiness. The same trends were observed by WEISGERBER (1978).

Coastal provenances showed a clinal variation with negative correlation between latitude and height growth, and a positive correlation with frost resistance from British Columbia to California (RECK, 1978; KLEINSCHMIT et al., 1974; MAGNESEN, 1973; HATTEMER and KÖNIG, 1975). There is, however, a clear distinction between coastal and interior provenances in morphological and phenological characteristics. The within-provenance variation exceeds between-provenance variation when regions like States are regarded for coastal respectively interior sources. Differentiation between Interior British Columbia and Coastal British Columbia is difficult when studying high elevation sources. Elevational differentiation in Washington and Oregon is not very clear up to 600 m. Under rough climatic conditions south provenances from Oregon and California show very low survival, due to their early and winter-frost sensitivity.

Phenology

Flushing and bud set of provenances are quite constant over years and over locations (O'DRISCOLL, 1978; LI and ADAMS, 1990; MICHAUD, 1987). They can be assessed early (NANSON, 1973) and have high adaptive importance. Bud set has a strong clinal pattern of variation. Flushing is more irregular, with an ecotypic variation similar to that of Sitka spruce (BURLEY, 1966; BIROT, 1982). Interior populations from the central dry and subboreal zone flush later than those of other interior sources. Populations from the coast in Washington and Oregon are generally late, but variation may occur at short distances.

Bud set is earlier in trees of northern and high elevation provenances (BIALOBOK and MEJNARTOWICZ 1970; BIROT and FERRANDES, 1972; LI and ADAMS, 1990). Early selection for bud set is less efficient than for bud burst. Lamma-shoot formation is less constant over years and over sites (WIDMAIER et al., 1987). This trait is less frequent in interior, northern and high elevation provenances (KRIEK, 1975; BIROT, 1982).

Genetic structure

Institut National de la Recherche Agronomique in France was the only institution in Europe that received single-tree seed lots of 26 provenances from Washington. This was a chance to estimate genetic parameters.

BIROT and CHRISTOPHE (1983) found the majority of variation in height growth of trees of 3 Washington provenances to be within families. Provenance and family contributed the same amount to overall variation at the nursery stage with decreasing family influence with increasing age. Heritability stabilized at 0.3 after age 1 from seed. For flushing, 62% of the variation was within families. Both provenances and families contributed 19% with high heritability values ($h^2 = 0.95$). Stem straightness, branch angle and forking showed little provenance influence; family influence was moderate ($h^2 = 0.08$ to 0.12) and residual variance comprised 85% of the total.

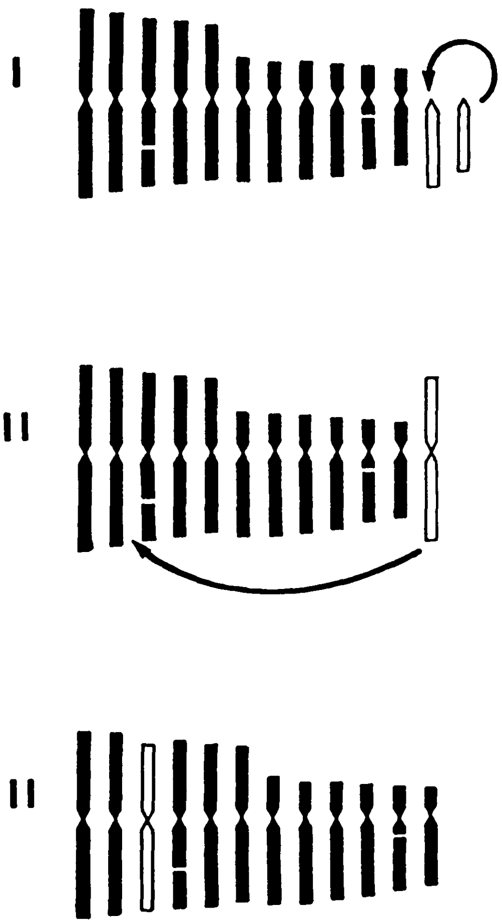
Heritability and genetic correlations were very different from one population to another, indicating that success of selection may be quite different for different populations. This means also that breeding strategy has to be adapted to the specific population (CHRISTOPHE and BIROT, 1979 1983).

Other studies in the Douglas-fir natural range contributed to support these results. In southwestern Oregon provenances, HAMLIN (1990) was able to show that the genetic structure of the populations differed among habitat types from distinct ecological habitats. The relative difference in population structure did nor appear to vary randomly, but was associated with the extent of habitat divergence. The relative degree of difference is dependent on the trait complex. The environments associated with the habitat appear to have influenced the interrelationships among traits.

CAMPBELL and FRANKLIN (1981) demonstrated that family mean values in a common garden test showed some adaptation to habitat type and elevation in a watershed. This explained 38% of the total variation as an average of 14 traits. Elevation was, however, the major source of variation. Residual variation, which includes individuals within families and error, was the major source in this study, as in many others comprising more than 60% of the total.

3.2. Provenance research for production and breeding

The main activities undertaken with the IUFRO collection concentrated on provenance research for production and breeding. The material was at the same time an excellent basis for the study of geographic variation and adaptability of the species. These studies, in combination with the regional studies in North America which have a more detailed sampling and more ecological information, give an excellent view of the pattern of variation in Douglas-fir, which is an important precondition for provenance transfer, conservation and breeding (e.g. CHING, 1965; SORENSEN, 1967, 1979, 1983; KUNG and WRIGHT, 1972; CAMPBELL and SORENSEN, 1973, 1978; CAMPBELL, 1974, 1979, 1991; CHING and HINZ, 1978; GRIFFIN, 1978; REHFELDT, 1978, 1983, 1989, 1990; ADAMS and CAMPBELL, 1980; CAMPBELL and FRANKLIN, 1981; SILEN and MANDEL, 1983; JAQUISH, 1990; KITZMILLER, 1990). This research is partly supported and refined by studies of biochemical and genetic characters of the species (HANOVER and FURNISS, 1966; VON RUDLOFF, 1972, 1973a and b; ZAVARIN and SNAJBERK, 1973, 1975; MUHS, 1974; YANG et al., 1977; VON RUDLOFF and REHFELDT, 1980; YEH and O'MALLEY, 1980; MERKLE and ADAMS, 1987; LI and ADAMS, 1988; u. a.).



From Sziklai et al., 1987

Figure 2. — Hypothesized meiotic disjunction and inferred reconstruction *of Pseudotsuga menziesii.*

Since the IUFRO experiments have been partly remeasured up to age 20, they form a broad basis for estimating juvenile-mature correlations and the potential for early selection. A growing body of information available on juvenile-mature correlations demonstrates that early selection can speed up breeding considerably and increase genetic gain (Bastien and Roman-Amat, 1988; Li and Adams, 1990).

The overall pattern of variation shows a clinal trend for most characteristics in the coastal part from north to south, but some characters, such as flushing, have a more ecotypic pattern. From west to east, changes are more drastic at a short distance following elevational gradients.

In the interior part of the natural range, the pattern of variation is much more ecotypic, due to the more drastic physiographic changes. Adaptation to heterogeneous environments can be viewed as physiological specialization for a relatively small portion of the environmental gradient. Populations separated by a relatively short distance along the environmental gradients tend to be different genetically. Height growth is related to elevation and geographic location, a phenomenon which explains the majority of the variance among populations (Rehfeldt, 1989).

Douglas-fir was found to be polymorphic at 37% of the loci with a range from 5.0% to 65.0%. Mean expected heteroygozity was 0.137 (range 0.021 to 0.239). Only 24% of the total genetic diversity was due to differentiation among populations, but for species with a wide geographical distribution this is among the highest values reported for conifers (Li and Adams, 1989).

All studies showed a relatively clear separation between coastal and inland varieties. The inland variety is separated into a northern and southern subgroup. Coastal provenances and northern interior provenances have a higher expected heterozygosity; the southern interior subgroup is much more differentiated. This can be due both to ancestral history and to the discontinuous distribution. In the interior part of the natural range the separation between northern and southern populations occurred more than 500,000 years ago. Differentiation between interior and coastal occured about 320,000 years ago. The introgression between coastal and interior Douglas-fir populations occured only after the last glaciation less than 10,000 years ago and the coastal Washington and British Columbia populations developed during the last 10,000 years, probably from refugia located in the Willamette Valley (Tsukada, 1982; Hermann, 1985, Li and Adams, 1989).

Allozyme variation follows a latitudinal cline in the interior variety but only a weak geographic trend was observed in the coastal part of the natural range. Rangewide patterns of allozyme variation are similar to those found in the terpene studies. There is one exception for the California Sierra Nevada populations which are more similar to the interior variety in cortical terpenes in the study of Zavarin and Snajberk (1973) but more similar to the coastal varieties in allozyme studies (Li and Adams, 1989).

Marginal population tend to have a lower genetic diversity. The isolated Mexican populations have the largest genetic distance from other populations and the lowest heterozygosity.

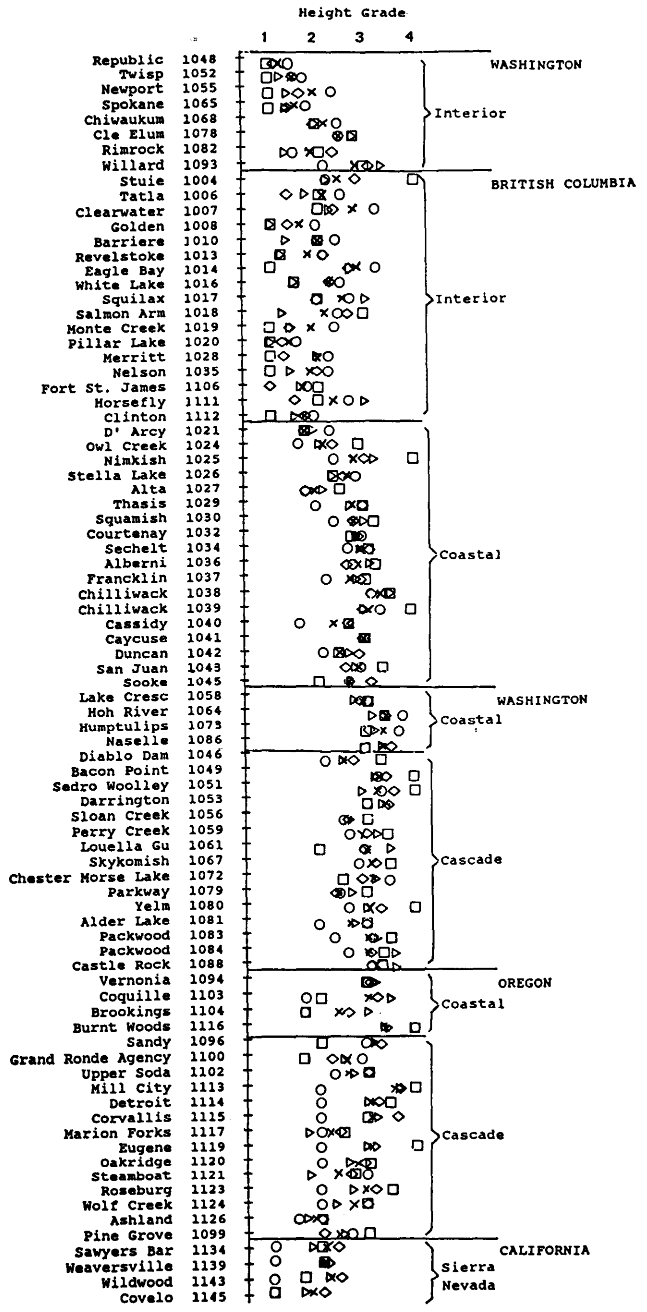
The coastal populations in Oregon, Washington and Vancouver Island have the highest heterozygosity. Expected heterozygosity decreases toward the north in British Columbia and toward the south in California.

One of the striking features is the considerable variation within populations found in most studies. This may partly explain the broad adaptability of trees of many Douglas-fir provenances. It is especially true for provenances from northern Oregon, Washington and southwest British Columbia west of the ridge of the Cascades (*Fig. 3*). These provenances gave good results in Denmark (Larsen and Kromann, 1983), the Netherlands (Kriek, 1975, 1978; de Vries, 1990), Belgium (Nanson, 1973, 1978), France (Michaud, 1987; Birot and Christophe, 1983; Rosette, 1986), Spain (Toval, 1987; Vega, 1990), Italy (Ducci and Tocci, 1987), Great Britain (Lines and Mitchell, 1970; Lines, 1978; Pearce 1978; Lines and Samuel, 1987; Fletcher and Samuel, 1990), Austria (Günzl, 1986; Nather, 1987), Turkey (Simsek, 1982), British Columbia (Illingworth, 1978; Fashler et al., 1987; Sziklai, 1990) and Germany (Schober, 1973; Kleinschmit et al., 1974, 1979; Weisgerber, 1978; Jestedt, 1979; Schober et al., 1983, 1984; Dittmar et al., 1985; Rau, 1985). Proceeding more to the north (Magnesen, 1978) or to the east in European plantation sites (Mejnartowicz, 1976; Birot and Burzynski, 1981; Burzynski and Gutowski, 1973) provenances from the transgression zone in British Columbia give improvement in growth, but not superiority except for a few sources from the wet belt of the Shuswap Lake region which may compare with the provenances from the Cascades in northern Washington.

Only in a continental climate such as that of Sweden (MARTINSSON, 1990), Finland (TIGERSTEDT, 1990) and Czechoslowakia (HOLUBCIK, 1976; SIKA, 1974; SIKA and PAV, 1990) are trees of interior British Columbia sources from the *caesia* region better under rough conditions. Coastal provenances have a low survival rate under these conditions. On the other hand, fungus diseases are less agressive in a continental climate. That is also true for high elevation sites.

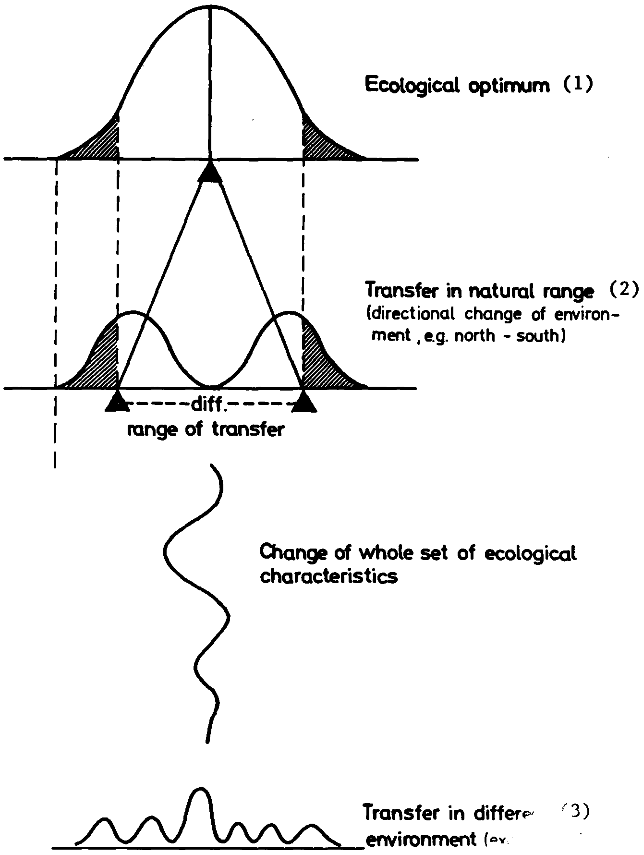
BREIDENSTEIN, BASTIEN and ROMAN-AMAT (1990) evaluated the IUFRO Data basis and arranged the plantation sites according to ecological groups:

1. Sites of North-eastern Europe with continental climate;



× All sites; ○ Group 1; ▽ Group 2; □ Group 3; ▫ Group 4; Grade 1 = lowest 25%; grade 4 = upper 25%

Figure 3. — Height grade performance means of all sites and groups. From BREIDENSTEIN and BASTIEN, 1990.



Tree populations maintain considerable variation within provenances on individual level (1). With the transfer to a new environment, a certain subset of these individuals is surviving. due to the natural selection. Within the natural range this is a more predictable part of the original population (2), with the transfer to a completely different environment the surviving part of the population is less predictable (3).

Figure 4. — Transfer of populations: surviving part.

2. Sites with relatively mild oceanic climate in north-western Europe and in southwestern British Columbia;
3. Sites exposed to rough oceanic climate, with precipitations and low mean temperatures, mainly in north-western British Columbia and Norway including a few particular locations in France and western Spain;
4. Warm European sites, south of 48 °N.

Figure 3 shows clearly, that the coastal and Cascade provenances from Washington are performing well over all plantation regions. Since there are quite drastic climatic differences between the regions, broad ecological adaptability must be a characteristic of these provenances. It is really surprising to find provenances like Hoh River, Humptulips, Naselle, Bacon Point, Seedro Wooley and Darrington always in the top ranking group under very different climatic conditions.

This leads us to consider within-provenance variation much more than has been done in most studies. Seed transfer of provenances from one region to the other can be considered from two different viewpoints:

1. Variation within-provenances and associated natural selection;
2. Individual adaptability (homeostasis).

The transfer of populations from one region to the other is necessarily associated with a process of natural selection (*Fig. 4*). Individuals less adapted to the new environment will be eliminated and the frequency of better adapted genotypes thus increases. This is one of the reasons for the relative improvement in ranking of Oregon sources in Germany (Schober et al., 1983, 1984) with increasing age after elimination of the sensitive individuals.

Since Douglas-fir populations have quite different variability and genetic correlations, as discussed earlier, it is not surprising to find provenances which can adapt better than others. The center of diversity for Douglas-fir seems to be in Washington, west of the ridge of the Cascades. Therefore a lot of additional seed collections following the IUFRO collection have been made there, e.g. by France, Germany, Austria and Belgium.

However, individual trees can also have a quite broad adaptability (physiological homeostasis) as we know from clonal tests (Michaud et al., 1990; authors unpublished results). This adaptability is superimposed on the individual pattern of variation of the respective provenances (*Fig. 5*). There are considerable differences in individual adaptability as expressed by stability parameters, which can be explained by differences in heterozygosity. Since expected heterozygosity is highest in the Pacific coastal region of Northern Oregon, Washington and Vancouver Island (Li and Adams, 1989) this could be an additional explanation for the broad adaptability of provenances from this region. These results also show the limitations of recommendations for seed transfer that are based only on climatic similarity between the place of origin and the plantation environments as proposed by von Wangenheim as early as 1787 and refined by Schenck (1939).

Seed transfer rules for Europe take on a new perspective, given the IUFRO results, with much more emphasis on genetic structure. Since the testing time for all the IUFRO material is still limited, it is necessary to combine these results with the results of the earlier provenance experiments. Some of the problems, e.g. with needle fungi and snow break, arise only at an advanced age of stand development, but they must be taken into account for a large scale application of results.

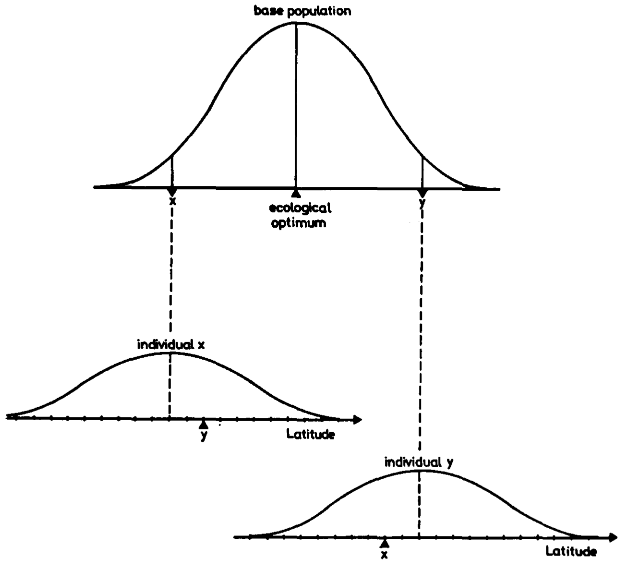
As a practical consequence of the IUFRO Douglas-fir provenance experiments, the European Community sponsored 4 missions in the natural range to check the present status of the original IUFRO stands and also to define around these stands potential seed collection areas for commercial purpose (Fletcher, et al., 1981, 1988, 1989). In addition, national regulations for Douglas-fir seed import have been influenced by the results of the IUFRO provenance experiments and the conclusions of these reports.

3.3 Future trends

Since most of the classical questions of provenance research have been answered for Douglas-fir, activities are more concentrated toward breeding and conservation. This change is also reflected in the titles of the proceedings, which was 1978 "Douglas-fir provenances", changed to "Breeding strategy for Douglas-fir as an introduced species" in 1985 and became "Douglas-fir Breeding and Genetic Resources" in 1990.

3.3.1. Breeding

Considerable investments in breeding have been made in western North America since the early 1960s. Over 40,000 selected plus trees and more than 800 ha of seed orchard emphasize the extent of this acclivity (Bordelon et al., 1987).



Adaptability exists as well on population level by genetic variation of individuals (*Fig. 4*) as on individual level by physiological homeostasis. A comparatively wide range of environments can be covered by individual trees (x, y) as known from clonal tests. Their competitive ability decreases when the plantation conditions deviate from the ecological optimum of the individuals, in pure plantations this is less important.

Figure 5. — Model for plasticity of individual genotypes.

In various European countries the IUFRO collection gave rise to many additional activities. Institutions in France, Belgium, Spain and Germany started a cooperative breeding program supported by EC with 10 Douglas-fir provenances, each represented by roughly 50 open pollinated progenies that were superior in the IUFRO experiment. The aim is to dvelop different breeding populations and to perform the testing on a broad basis in a coordinated way. Breeding zones must be defined all over Europe crossing administrative boundaries.

The necessity to include the differences between populations in the breeding strategy has been demonstrated and discussed by Christophe and Birot (1979, 1983).

Methods for vegetative propagation and for flower induction are being developed to improve flexibility in the breeding programs (Kleinschmit et al., 1976; Copes, 1977, 1983; la Goublaye et al., 1979; Bekkaoui and Franclet, 1986; Ritchie, 1991). In Douglas-fir, clonal propagation and testing have severe limitations due to topophysis effect. Only with juvenile seedlings is a rapid change from branch habit to orthotropic growth possible. Therefore, most efforts have been directed toward bulk propagation of tested juvenile material that has been sexually reproduced. This permits rapid utilization of superior material on a broad basis and is a good addition to seed orchard production technology.

For this purpose, flower induction with gibberellic acid and flower induction houses are increasingly used (Ross et al., 1985; Ebell 1970; Bonnet-Masimbert, 1982).

Hybridization, including the coastal and interior varieties, seems to be a promising approach, particularly for harsh climatic conditions (Braun and Schmiedel, 1985; Rehfeldt, 1986; Braun, 1988).

Seed orchard concepts have been reconsidered. Both clonal cutting seed orchards to prevent graft incompatibility and seedling seed orchards to combine testing and seed production have been established and are under test. The concept of the evolving seed orchard, which is open for new clones from the selection program as time goes on, was developed by NANSON (1986) and PAQUES and NANSON (1987) and is a good option for small-scale programs to make continuous use of the progress in the program. Graft compatible families were selected by COPES in Corvallis and made available to different European institutes to improve grafting success.

Modern methods like in vitro propagation (BOULAY, 1979; EVERS, 1985; MALA and CHALUPKA, 1987; MATSCHKE et al., 1991) and DNA markers (CARLSON et al., 1991) will improve propagation, identification and description of pattern of variation, but they will not basically change the concepts. Many technical and scientific problems still have to be solved before these methods can be applied.

Increasing ecological consciousness favours breeding strategies that maintain a broad genetic base and a high adaptability of the progeny. This is one reason why gene transfer will not drastically influence breeding strategy in most forest tree species.

3.3.2. Conservation

One of the problems with long term provenance research is the fact that the original stands have often disappeared by the time the test results are available. In addition, more and more interest is concentrated on relatively few sources that have turned out to be of outstanding interest for many different countries. Ex situ gene conservation is one option to solve these problems.

More than 1,000 ha of ex situ gene conservation plantations have been established in France, Germany and Belgium from controlled collection in American stands that were successful in the IUFRO Douglas-fir provenance experiment. These are partly treated as seedling seed orchards, and partly as production populations, but with the additional aim of using them as seed stands. These stands cover northern and central Washington west of the ridge of the Cascades with more than 30 provenances. 10 of these have been collected by single trees — 50 per provenance — in a joint program with France and Germany.

In situ conservation within the natural range of the species becomes a more urgent necessity with increasing utilization of natural stands and artificial stand establishment (National Research Council, 1991). An assessment and plan for Douglas-fir genetic resources have been elaborated for California only (National Council on Gene Resources, 1982).

Most of the European stands, which were the basis for the decision to plant Douglas-fir extensively, are included in the breeding and conservation work. It has been shown that these stands, which have already passed one cycle of natural and silvicultural selection, can adapt to the prevalent ecological conditions, especially with respect to phenological traits (BRAUN and SCHEUMANN, 1989; KLEINSCHMIT et al., 1974). These stands are often mixtures of provenances.

International cooperation as created on a broad basis by the IUFRO material will be an important precondition for further progress in future. However, efforts will have to be more individualized and regionalized, because of the different ecological preconditions and silvicultural concepts. Joint efforts for seed collection control, gene conservation and information exchange will be necessary on the broadest possible basis. IUFRO is an excellent basis for all these! One result of these activities could be the compilation of breeding programs existing outside of the natural range.

4. Conclusion

It is obvious that IUFRO has contributed considerably to Douglas-fir improvement, especially in Europe. Without IUFRO the state of Douglas-fir provenance research and breeding would not be as it is now. However it is clear too, that the contribution is not spectacular by itself. Many of the trends were visible before the IUFRO collection started and many contributions came from scientists outside of IUFRO activities. Here especially the excellent research carried out in the United States of America and in Canada must be mentioned.

The most important contribution of IUFRO was the decision to start a range-wide collection, to procure the same material to many countries, and by the organization of meetings acting as a catalyst to create a basis for open-minded cooperation and friendship, thus stimulating many research activities worldwide and improving research by interaction and support. This interaction was especially strong between Europe and United States of America. The Europeans, coming back for additional collections, received considerable support from colleagues in North America. Since IUFRO is an international non funding organization, it lives from the activities of its members. Therefore the borders to decide what is due to IUFRO and what due to the individual scientist are never clear. But cooperation will be even more important in future with increasing complexity and spezialization for which IUFRO is an excellent base.

Research in forestry is a matter of centuries. Every generation acts on a basis which was built by past generations and contributes only some bricks to the building. Many bricks have been added to the building during the past 25 years. IUFRO helped to arrange and form them in a proper way and to make the participation in this process more pleasant. The structure of the Douglas-fir building has now already clear contours. Many details, colour and equipment of the house will be added in the future. The importance of some of the bricks will only be clear later and some may be too weak to support the building and will have to be replaced.

Hopefully, those will not be bricks of scientists whose work is summarized in this paper.

5. Literature

ADAMS, W. T. and CAMPBELL, R. K.: Genetic adaptation and seed source specificity. Forest reproductive materials certification standards, Oregon, Washington. Seed Certification Service, Oregon State University and Wash. State Crop Improvement Ass. Publ., 78—85 (1980). —— ALLEN, G. S.: A method of distinguished coastal from interior Douglas-fir seed. University of British Columbia, Faculty of For., Res. Note 28, 3 (1960). —— ALLEN, G. S. and OWENS, N.: The life history of Douglas-fir. Environment Canada, Forestry Service, Cat. No. Fo 42—49 72, p. 138 (1972). —— BARNER, H.: Procurement of Douglas fir seed for provenance research. Proceedings IUFRO Meeting Working Party on Douglas-fir provenances, Göttingen, p. 82—89 (1973). —— BASTIEN, J. C. and ROMAN-AMAT, B.: Predicting Douglas-fir (*Pseudotsuga menziesii* (MIRB.) FRANCO) volume at age 15 with early traits. Silvae Genetica 39: 29—35 (1983). —— BEKKAOUI, F. and FRANCLET, A.: De l'amélioration de la multiplication végétative in vitro du Douglas. Annales de Recherches Sylvicoles, AFOCEL, Nangis, p. 63—79 (1986). —— BERGER, S. H.: Die Douglasienschütten: Eine zusammenfassende Betrachtung der bisherigen Erkenntnisse über *Rhabdocline pseudotsugae* SYD. and *Phaeocryptopus gaeumanni* (T. ROHDE) PETR. Diplomarbeit, Universität Göttingen, Forstliche Fakultät, pp. 109 (1982). —— BERNEY, J. L.: Studies on the probable origin of some european Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) plantations. M. F. Thesis Univ. of B. C., pp. 99 (1972). —— Bialobok, S. and Mejnartowicz, L.: Provenance differentiation among Douglas-fir seedlings. Arbor. Kornick. Rosz. XV (1970). —— Birot, Y.: Variabilité intraspécifique du poids de la graine chez le Douglas (*Pseudotsuga menziesii* (Mirb.) Franco). Silvae Genetica **21**: 205—225 (1972). —— Birot, Y.: Genetics of Douglas-fir. Meeting on Principles of species introduction. Lourizan, Spain, Oct. 4. to 8., pp. 49. (1982). —— Birot, Y. and Burzynski, G.: Analyse comparée d'un test de provenances de Douglas installé en France et en Pologne. Revue Forest. Franc. **33**: 116—126 (1981). —— Birot, Y. and Ferrandes, P.: Quelques aspects de la variabilité intraspécifique du Douglas (*Pseudotsuga menziesii* (Mirb.) Franco) introduit en zone mediterranéenne subhumide. Ann. Sci. Forest **29**: 335—351 (1972). —— Birot Y. and Christophe, C.: Genetic structure and expected genetic gains from multitrait selection in wild populations of Douglas-fir and Sitka spruce. Silvae Genetica **32**: 141—151 (1983). —— Bishir, J. and Namkoong, G.: Unsound seeds in conifers: Estimation of numbers of lethal alleles and of magnitudes of effects associated with the maternal part. Silvae Genetica **36**: 180—185 (1987). —— Bonnet-Masimbert, P. M.: Influence de l'état d'activité des racines sur la floraison induite par des gibberellines 4 et 7 chez *Pseudotsuga menziesii* (Mirb.) Franco. Silvae Genetica **31**: 178—183 (1982). —— Bordelon, M., Cook, B. and Mangold, R.: Seed orchards of Western Oregon, Western Washington, and Northern California. Oregon State Univ.; Dep. of Forestry, Corvallis, Oregon, USA; pp. 109. (1987). —— Boulat, M.: Propagation "in vitro" du Douglas par micropropagation de germination aseptique et culture de bourgeons dormants. Etudes et Recherches, Nr. 12, 67—75 (1979). —— Braun, H.: Ergebnisse der Hybridzüchtung bei Douglasie (*Pseudotsuga menziesii* (Mirb.) Franco). Beiträge für die Forstwirtschaft **22**: 1—7 (1988). —— Braun, H. and Scheumann, W.: Erste Prüfergebnisse von Bestandesnachkommenschaften unter besonderer Berücksichtigung der Frostresistenz. Beiträge für die Forstwirtschaft **23**: 4—11 (1989). —— Braun, H. and Schmiedel, H.: Ergebnisse der Anbauprüfung intraspezifischer Douglasienhybriden unter besonderer Berücksichtigung der Frostresistenz. Beiträge für die Forstwirtschaft **19**: 69—73 (1985). —— Breidenstein, I., Bastien, J. C. and Roman-Amat, B.: Douglas-fir range wide variation. Results from the IUFRO data base. Proceedings Joint Meeting Western For. Gen. Ass. and IUFRO Working Parties Olympia, Wash. **4**: 85, 14 (1990). —— Burley, J.: Genetic variation in seedling development of Sitka spruce (*Picea sitchensis* (Bong) Carr.). Forestry **39**: 68—94 (1966). —— Burzynski, G. and Gutowski, J.: Recent results of provenance experiments with Douglas-fir in the Federal Research Institute in Poland. Proceedings IUFRO Meeting Working Party on Douglas-fir provenances, Göttingen, p. 90—104 (1973). —— Campbell, R. K.: Use of phenologyfor examining provenance transfers in reforestation of Douglas fir. Journal of Appl. Ecology **11**: 1069—1080 (1974). —— Campbell, R. K.: Genecology for Douglas fir in a watershed in the Oregon Cascades. Evol. **60**: 1037—1050 (1979). —— Campbell, R. K.: Soils, seed-zone maps, and physiography: Guidelines for seed transfer of Douglas-fir in south-western Oregon. Forest Science **37**: 973—986 (1991). —— Campbell, R. K. and Franklin, J. F.: A comparison of habitat type and elevation for seed zone classification of Douglas-fir in western Oregon. Forest Sci. **27**: 49—59 (1981). —— Campbell, R. K.: and Sorensen, F. C.: Cold acclimatisation in seedling Douglas-fir related to phenology and provenances. Ecology **54**: 1148—1151 (1973). —— Campbell, R. K. and Sorensen, F. C.: Effect of test environment on expression of clines and delineation of seed zones in Douglas-fir. Theoretical and Applied Genetics **51**: 233—246 (1978). —— Carlson, I. E., Tulsieram, L. K., Glaubitz, I. C., Luk, V. W, K., Kauffeldt, C. and Rutledge, R.: Segregation of random amplified DNA markers in F_1 progeny of conifers. Theor. Appl. Genetics **83**: 194—200 (1991). —— Ching, K. K.: Early growth of Douglas-fir in a reciprocal planting. School of For. Oregon State Univ. For. Res. Lab. Res. Paper 3, pp. 20 (1965). —— Ching, K. K. and Hermann, R. K.: Biosystematics of Douglas fir. Proceedings IUFRO Meeting Working Party on Douglas-fir provenances, Göttingen, p. 23—36 (1973). —— Ching, K. K. and Hinz, P.: Cooperative provenance study of Douglas-fir in the Pacific North-West. Proceedings IUFRO Meeting of WP S. 2—02, 05, 06, 12, 14, Vancouver, Canada, p. 141—154 (1978). —— Christophe, C. and Birot, Y.: Genetic variation within and between populations of Douglas fir. Silvae Genetica 28: 197—206 (1979). —— Christophe, C. and Birot, Y.: Genetic structures and expected gains from multitrait selection in wild populations of Douglas fir and Sitka spruce. II. Practical application of index selection on several populations. Silvae Genetica **32**: 173—181 (1983). —— Copes, D.: Einfluß von Bewurzelungssubstrat auf Wurzelstruktur und Bewurzelungsprozent bei Douglasien-Stecklingen. Silvae Genetica **26**: 102—106 (1977). —— Copes, D. L.: Effects of annual crown pruning and serial propagation and rooting of stem cuttings from Douglas-fir. Can. J. For. Res. **13**: 419—424 (1983). —— Dimitri, L.: Research on frost resistance of Douglas-fir provenances. Proceedings IUFRO Meeting Working Party on Douglas-fir provenances, Göttingen, p. 140—149 (1973). —— Dittmar, O., Knapp, E. und Schulsen, B.: Ergebnisse des internationalen Douglasienprovenienzversuches 1961 im Pleistozän der DDR. Beiträge für die Forstwirtschaft **19**: 8—18 (1985). —— Ducci, F. and Tocci, A.: Primi resultati della sperimentazione IUFRO 1969 — 1970 su *Pseudotsuga menziesii* (Mirb.) Franko nell'Appenino centro-settentrionale. Annali dell' Instituto Sperimentale per la Selvicoltura — Arezzo. Estratto dal. Vol. XVIII, pp. 289 (1987). —— Ebeil, F.: Physiology and Biochemistry of Flowering of Douglas-fir. Proceed. Meeting IUFRO Working Party Vaparanta, Finl., p. 17—18 (1970). —— Eddell and Schmidt: Publication No. 1036. Canadian Dept. of Forestry, pp. 28. (1964). —— Evers, P.: Growth and morphogenesis of shoot initials of Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco, in vitro. Netherlands Journal of Agricultural Sci. **33**: 179—181 (1985). —— Fashler, A. M. K., El Kassaby, Y. A. and Sziklai, O.: Inter provenance variation in the IUFRO Douglas-fir provenance (progeny trial). Proceed IUFRO Meeting Working Party Breeding Strategy for Douglas fir as an introduced species, Vienna, 1985, p. 187—204 (1987). —— Ferrell, W. K. and Woodward, E. S.: Effect of seed origin on drought resistance of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco). Ecology **47**: 499—503 (1966). —— Fletcher. A. M. and Barner, H.: The procurement of seed for provenance research with particular reference to collections in NW-America. Proceedings IUFRO Meeting of WP S.2- 02, 05, 06, 12, 14, Vancouver, Canada, p. 141—154 (1978). —— Fletcher, A., Birot, Y. and Reck, S. G.: Douglas-fir case study. Field inspection EEC DG VI Internal report, pp. 32. (1981). —— Fletcher, A. and Bastien, J. C.: Douglas-fir seed sources field inspection; Southern Washington-Northern Oregon. EEC DG VI Internal report, pp. 12. (1988). —— Fletcher, A. and Bastien, J. C.: Douglas-fir seed sources field inspection; Southern Oregon-Northern California. EEC DG VI Internal report, pp. 11. (1989). —— Fletcher, A. M. and Samuel, C. J. A.: Growth and branching characteristics in the IUFRO origins of Douglas-fir 16 years after planting in Britain. Proceedings Joint Meeting Western For. Gen. Ass. and IUFRO Working Parties Olympia, Wash. 271:12 (1990). —— Flöhr, W.: Kennzeichnung, Varietäten und Verbreitung der Douglasie. In: Die Douglasie und ihr Holz. Ed.: K. Göhre. Akademie-Verlag, Berlin. p. 1—14 (1958). —— Galoux, A.: Le sapin de douglas et la phytogéographie. Trav. Sta. Rech. Eaux et Forêts, Groenendaal, Sér. B, 20, p. 131 (1956). —— Gerhold, H.: Douglas-fir growth and winter injury demonstration. Amer. Christmas Tree Growers Journal 9: 38-43 (1965). —— Göhre, K. Die Douglasie und ihr Holz. Akademie-Verlag, Berlin. pp. 595 (1958). —— Griffin, A. R.: Geographic variation in Douglas-fir from the coastal ranges of California. Silvae Genetica **27**: 96—101 (1978). —— Günzl, L.: Anbauerfahrungen aus den österreichischen Douglasien-Provenienzversuchen der letzten 20 Jahre. Allgemeine Forstzeitung, pp. 2 (1986). —— Haddock, P. G. and Sziklai, O. (1966): Seed collection zones for Douglas-fir in Canada. Proceed. Sixth World For. Congr. Madrid: p. 1467—1473 (1966). —— Hamlin, J.: Genetic structure of Douglas-fir populations from Southwestern Oregon. Proceedings Joint Meeting Western For. Gen. Ass. and IUFRO Working Parties Olympia, Wash. 4. 85, 1, pp. 16 (1990). —— Hanover, J. W. and Furniss, M, M.: Monoterpene concentration in Douglas-fir in relation to geographic location and resistance to attack by the Douglas-fir beetle. Proceed. Joint Meeting Second Genetics Workshop of the Soc. of Amer. For. and the Seventh Lake States For.. Tree Impr. Conf. Oct. 1965, St. Paul, Minn., p. 23—28 (1966). —— Hattemer, H. H.: and König, A.: Geographic variation of early growth and frost resistance in Douglas-fir. Silvae Genetica **24**: 97—106 (1975). —— Hermann, R. K.: The genus *Pseudotsuga*: Ancestral history and past distribution. For. Res. Lab. Coll. of. For., Oregon State Univ. Special Publ. 2b, 32p. (1985). —— Hermann, R. K.: Die Douglasie einst und heute. Allg. Forstzeitschrift **35**: 215—219 (1980). —— Hermann, R. K.: The genus *Pseudotsuga:* Historical records and nomenclature. For. Res. Lab. Oregon State University, Special Public. 2 a, pp. 29 (1982). —— Hermann, R. K. and Ching, K. K.: Palaeohistory of the genus *Pseudotsuga*. Proceedings IUFRO Meeting Working Party on Douglas-fir provenances, Göttingen, p. 13—22 (1973). —— Hermann, R. K. und Ching, K. K.: Bibliography of Douglas fir provenance studies 1907—1974. For. Res. Lab. Oregon State Univ. Res. Paper 25, pp. 30 (1975). —— Hermann, R. K. and Lavender, D. P.: Early growth of Douglas-fir from various altitudes and aspects in Southern Oregon. Silvae Genetica **17**: 143—151 (1968). —— Holubcik, M.: Prvé ryslecki medzinárochého proveniencného pokuso s douglaskou na Slovensku. Lesnicky Casopis, Rocn. **22**: 213—236

(1976). —— ILLINGWORTH, K.: Douglas-fir provenance trials in coastal British Columbia — Results to six years after planting. Proceedings IUFRO Meeting of WP S.2—02, 05, 06, 12, 14, Vancouver, Canada, p. 411—425 (1978). —— IRGENS-MOELLER, H.: Genotypic variation in the time of cessation of height growth in Douglas-fir. Forest Science 4: 325—330 (1958). —— IRGENS-MOELLER, H.: Geographical variation in growth pattern of Douglas fir. Silvae Genetica 17: 106—110 (1968). —— ISAAC, I. A. and DIMROCK, E. J.: Douglas-fir (*Pseudotsuga menziesii* (MIRB.) FRANCO) var. menziesii. In: Silvics of Forest Trees of the United States. U. S. Dept. of Agriculture, Agric. Handbook 271: 547—553 (1965). —— IUFRO: Meeting of Working Party on Douglas fir provenances, 3. to 5. Sept. Proceedings IUFRO Meeting Working Party on Douglas-fir provenances, Göttingen, p. 240 (1973). —— IUFRO: Meeting of Working Party on Douglas fir provenances, 21. 8. to 9. 9. 1978. Proceedings IUFRO Meeting of WP S.2—02, 05, 06, 12, 14, Vancouver, Canada. p. 141—154. (Proc. publ. by Province of British Columbia, Ministry of Forests, Vol. I, pp. 426) (1978). —— IUFRO: Meeting of Working Party on Breeding Strategy for Douglas-fir as an introduced species 10. to 15. 6. 1985, Vienna. Proceedings Schriftenreihe der Forstlichen Bundesversuchsanstalt Wien, Nr. 21, pp. 300 (1987). —— IUFRO: Meeting of Working Party Douglas fir Breeding and Genetic Resources 20. 8. to 24. 8., Olympia, Wash. Proceedings of Joint Meeting of Western For. Gen. Ass. and IUFRO Working Parties (published by Weyerhaeuser, Dougl.-fir), pp. 241 (1990). —— JAQUISH, B. C.: Geographic variation in ten-year height growth of Interior Douglas-fir in British Columbia. Proceedings Joint Meeting Western For. Gen. Ass. and IUFRO Working Parties Olympia, Wash. 4. 85, 12 (1990). —— JESTEDT, M.: Bisherige Erkenntnisse aus der Douglasien Provenienzforschung. Forst- und Holzwirt 34: 124—138 (1979). —— KITZMILLER, J. H. (1990): Genetic variation and adaptability of Douglas-fir in northwestern California. Proceedings Joint Meeting Western For. Gen. Ass. and IUFRO Working Parties Olympia, Wash. 4. 85, 13 (1990). —— KLEINSCHMIT, J.: Zur Herkunftsfrage bei der Douglasie. Der Forst- und Holzwirt 11: 209—213 (1973). —— KLEINSCHMIT, J., RACZ, J., WEISGERBER, H., DIETZE, W., DIETERICH, H. and DIMPFLMEIER, R.: Ergebnisse aus dem internationalen Douglasien-Herkunftsversuch von 1970 in der Bundesrepublik Deutschland. Silvae Genetica 23: 167—176 (1974). —— KLEINSCHMIT, J., SCHMIDT, J. and SAUER, A.: Versuche zur Stecklingsvermehrung von Douglasien. Forstarchiv 47: 226—231 (1976). —— KRIEK, W.: Douglas-fir IUFRO provenances in the Netherlands, 1968 to 1969 Series.. Ned. Bosb. Tijdschr. 47: 100—116 (1975). —— KRIEK, W.: Further development of Douglas-fir IUFRO provenances in the Netherlands 1966/1967 Series. Proceedings IUFRO Meeting of WP S. 2—02, 05, 06, 12, 14, Vancouver, Canada. p. 241—255 (1978). —— KUNG, F. H.: and W, J. WRIGHT.: Parallel and divergent evolution in Rocky Mountain trees, Silvae Genetica 21: 77—85 (1972). —— LACAZE, J. F. and TOMASSONE, R.: Contribution à l'étude de la variabilité du Douglas *Pseudotsuga menziesii* (MIRB.) FRANCO. Caracteristiques juveniles. Annales des Sciences Forestières 24: 85—106 (1967). — LA GOUBLAYE, DE T., NANTOIS, DE and FRANCLET, A.: Bouturage du Douglas: Rétablissement de l'orthotropie. Annales de Recherches Sylvicoles, AFOCEL, Nangis, p. 277—295 (1979). —— LARSEN, J. B.: Frost hardiness studies in Douglas-fir. Proceedings IUFRO Meeting of WP S. 2—02, 05, 06, 12, 14, Vancouver, Canada. p. 169—173 (1978). —— LARSEN, J. B. and KROMANN, K. H.: Douglas fir provenances in Denmark. Det forstlige Forsøgswaesen i Denmark 38: 349—375 (1983). —— LI, P. and ADAMS, W. T.: Range-wide patterns of allozyme Variation in Douglas-fir (*Pseudotsuga menziesii*). Canad. J. For. Res. 19: 149—161 (1989). —— LI, P. and ADAMS, W. T: Genetic variation and early testing of bud phenology in coastal Douglas-fir. Proceedings Joint Meeting Western For. Gen. Ass. and IUFRO Working Parties Olympia, Wash. 4.85:1 (1990). —— LIESE, I.: Zur Biologie der Douglasienschütte. Zeitschrif. für Forst- u. Jagdwesen 64: 680—693 (1932). —— LIESE, I.: Die Anfälligkeit der Douglasienrassen gegenüber der Douglasienschütte *Rhabdocline pseudotsugae*. Deutscher Forstwirt 17: 959—961, 973—975 (1935). —— LIESE, I.: Die Douglasienrassen und ihre Anfälligkeit gegenüber der Douglasiennadelschütte *Rhabdocline pseudotsugae*. Mitt. d. Dr. Dendrol. Ges. 43: 259—264 (1936). —— LINES, R.: The IUFRO experiments with Douglas-fir in Scotland. Proceedings IUFRO Meeting of WP S.2—02, 05, 06, 13, 14, Vancouver, Canada. p. 297—304 (1978). —— LINES, R. and MITCHELL, A. S.: Provenance: Douglas-fir. Report Forest Res. Forestry Comm., London, p. 63—64 (1970). —— LINES, R. and SAMUEL, C. J. A.: Results of the IUFRO Douglas-fir experiments in Britain at 10 years. Proceedings IUFRO Meeting Working Party Breeding Strategy for Douglas fir as an introduced species, Vienna, 1985. p. 31—47 (1987). — LYR, H.: Die Krankheiten der Douglasie. In: Die Douglasie und ihr Holz. Ed.: K. GÖHRE, Akademie Verlag, Berlin. p. 369—402 (1958). —— MAGNESEN, S.: Preliminary Report on the international short-term Douglas-fir (*Pseudotsuga menziesii*) provenance experiment in West Norway. Proceedings IUFRO Meeting Working Party on Douglas-fir provenances, Göttingen, p. 126—139 (1973). —— MALA, J. and CHALUPA, V.: Vegetativni rozmnozovani douglasky *Pseudotsuga menziesii* (MIRB.) FRANCO. Lesn. Praha 33: 525—532 (1987). —— MARTINSSON, O.: Research on Douglas-fir in Sweden. Proceetings Joint Meeting Western For. Gen. Ass. and IUFRO Working Parties Olympia, Wash. 4.85:6 (1990). —— MATSCHKE, J., HÜBL, S., KRETSCHMAR, U., SCHACHLER, G., HERTEL, H., NAUJOK, G., ZOGLAUER, K., DEMBUY, H. and ZOLT, U.: Grundlagenforschung für die in vitro Vermehrung der Lärche und Douglasie aus gelenkten Kreuzungen. Forschungsbericht, unpublished, pp. 99. (1991). —— MEYNARTOWICZ, L.: Genetic intestigations on Douglas-fir (*Pseudotsuga menziesii* (MIRB.) FRANCO) populations. Arboretum Kornickie, Rosz. 21: 126—187 (1976). —— MERKLE, S. A. and ADAMS, W. T.: Patterns of allozyme variation within and among Douglas-fir breeding zones in southwest Oregon. Can. J. For. Res. 17: 402—407 (1987). —— MICHAUD, D.: First results of American Douglas-fir provenance trials in France. Proceedings IUFRO Meeting Working Party on Breeding Strategy for Douglas-fir as in introduced species, Vienna, 1985. p. 3—23 (1987). —— MILLER, D. J. and GRAHAM, R. D.: Treatability of Douglas-fir from Western United States. Proc. American Wood Preserver's Association 59: 218—222 (1963). —— MORRIS, W. K., SILEN, R. R. and IRGENS-MOELLER, H.: Consistency of bud-bursting in Douglas-fir. Journal of Forestry 55: 208—210 (1957). —— MUHS, H. J.: Distinction of Douglas-fir provenances using Peroxidase-Isoenzyme-patterns of needles. Silvae Genetica 23: 71—76 (1974). —— MUNGER: Ecology, 451—459 (1940). —— NANSON, A.: International Douglas-fir provenance experiment in Belgium (Early results). Proceeding IUFRO Meeting Working Party on Douglas-fir provenances, Göttingen, p. 158—172 (1973). —— NANSON, A.: Belgian provenance experiments with Douglas-fir. Grand-fir and Sitka spruce. Proceedings IUFRO Meeting of WP S.2—02, 05, 06, 12, 14, Vancouver, Canada. p. 335—346 (1978). —— NANSON, A.: The evolving seed orchard: A new type. Proceed. IUFRO Meeting Williamsburgh, Virg., p. 554—556 (1986). —— NATHER, J.: Characterization of seed samples of Douglas-fir by short term investigation on bud set. Proceedings IUFRO Meeting Working Party Breeding Strategy for Douglas fir as an introduced species, Vienna, 1985. p. 265—273 (1987). —— National Council on Gene Resources: Douglas-fir genetic resources. An assessment and plan for California. National Council on Gene Resources, 2855 Telegraph Ave., Suite 216, Berkeley, Cal., pp. 274. (1982). —— National Research Council, Board on Agriculture: Managing Global Genetic Resources — Forest Trees. National Academy Press, Wash. D. C.. pp. 228 (1991). O'DRISCOLL, J.: Six year phenological study of thirty two IUFRO provenances of Douglas-fir Proceedings IUFRO Meeting of WP S.2—02, 05, 06, 12, 14, Vancouver, Canada. p. 265—296 (1978). —— ORR-EWING, A. L.: Inter- and intraspecific crossing in Douglas-fir, *Pseudotsuga menziesii* (MIRB.) FRANCO. Silvae Genetica 15: 121—126 (1966). —— ORR-EWING, A. L.: Inbreeding to the S_2 generation in Douglas-fir. Second World Consult. on Forest Tree Breeding, Wash. D. C.. pp. 13 (1969). —— ORR-EWING, A. L.: Female sterility in Douglas-fir. Silvae Genetica 26, 75—77 (1977). —— OSWALD, H. and PARDÉ, J.: Die Douglasie in Frankreich: Waldbau und Leistung. Allgemeine Forstzeitschrift, 438—441 (1984). —— OWENS, J. N.: The reproductive cycle of Douglas-fir. Pacific For. Res. Center, Can. For. Serv., B. C. Publ., pp. 21. (1973). —— PAQUES, L. and NANSON, A.: Douglas fir breeding in Belgium — breeding strategy and the evolving seed orchard. Proceedings IUFRO Meeting Working Party on Breeding Strategy for Douglas-fir as an introduced species. Vienna, 1985. pp. 145. (1987). —— PEARCE, H. L.: The IUFRO experiments with Douglas-fir in England and Wales. Proceedings IUFRO Meeting of WP S.2—02, 05, 06, 12, 14. Vancouver, Canada. p. 381—388. (1978). —— PHARIS, R. P. and FERREL, W. K.: Differences in drought resistance between coastal and inland sources of Douglas-fir. Canad. J. of. Botany 44: 1651—1659 (1966). —— POURTET, J.: Les repeuplements artificials. Ecole Nationale des Eaux et Forets, 14 rue Girardet, 5400 Nancy, France, pp. 242. (1951). —— RAU, H. M.: Der Douglasien-Provenienzversuch von 1958 in Hessen. Allg. Forst- u. Jagdzeitung 156: 72—79 (1985). —— RECK, S. G.: Height growth and frost resistance in Douglas-fir provenances tested in the northern part of Germany. Proceedings IUFRO Meeting of WP S. 2—02, 05, 06, 12, 14. Vancouver, Canada. p. 175—188 (1978). —— REHFELDT, G. E.: Genetic differentiation of Douglas-fir populations from the Northern Rocky Mountains. Ecology 59: 1264—1270 (1978). —— REHFELDT, G. E.: Genetic variability within Douglas-fir populations: Implications for tree improvement. Silvae Genetica 32: 9—14 (1983). —— REHFELDT, G. E.: Performance of Douglas-fir intervarietal hybrids after 10 years of field testing. Intermountain Res. Sta., USDA For. Serv. Res. Note 355, pp. 2 (1986). —— REH-

FELDT, G. E.: Ecological adaptations in Douglas-fir (*Pseudotsuga menziesii* var. glauca): A synthesis. Forest Ecology and Management 28: 203—215 (1989). —— REHFELDT, J.: Adaptability versus zone size. Continuous zones for the Rocky Mountains (USA). Proceedings Joint Meeting Western For. Gen. Ass. and IUFRO Working Parties Olympia, Wash. 4.85:11 (1990). —— RITCHIE, G. A.: The commercial use of conifer rooted cuttings in forestry. A world overview. New Forests 5: 247—275 (1991). —— ROSETTE, C.: Contribution à l'exploration de la variabilité intraspécifique du Douglas Mémoire de fin d'études de l'ENITEF, INRA. Station d'Amélioration des Arbres Forestieres, Ardon, F-45160 Olivet. (1986). —— ROSS, S. D., WEBER, I. E., PHARIS, R. P. and OWENS, J. N.: Interaction between gibberellic A 4/7 and root pruning on the reproductive and vegetative process in Douglas fir. I. Effects on flowering. Can. J. For. Res. 15: 341—347 (1985). —— RUDLOFF, E. VON: Chemosystematic studies in the genus *Pseudotsuga*. I. Leaf oil analysis of the coastal and Rocky Mountain varieties of the Douglas-fir. Can. J. Bot. 50: 1025—1040 (1972). —— RUDLOFF, E. VON: Geographical variation in the terpene composition of the leaf oil of Douglas-fir. II. Chemosystematic studies in the genus *Pseudotsuga*. Pure and applied Chemistry 34: 401—410 (1973a). —— RUDLOFF, E. VON: III. Population differences in British Columbia as determined by volatile leaf oil analysis. Can. J. For. Res., 443—452 (1973b). —— RUDLOFF, E. VON and REHFELDT, G. E.: Chemosystematic studies in the genus Pseudotsuga. IV. Inheritance and geographical variation in the leaf oil terpenes of Douglas-fir from the Pacific Northwest. Can. J. Bot. 58: 546—556 (1980). —— SCAGEL, R. K., DAVIDSON, R., EL KASSABY, Y. A. and SZIKLAI, O.: Variation of cone scale and seed morphology in Douglas-fir (*Pseudotsuga menziesii*). Proceedings IUFRO Meeting Working Party on Breeding Strategy for Douglas-fir as an introduced species. Vienna, 1985. p. 107—125 (1987). —— SCHENCK, C. A.: Fremdländische Wald- und Parkbäume. Vol. III. Berlin (1939). —— SCHOBER, R.: Ergebnisse von Douglasien-Provenienzversuchen in Deutschland, Holland und Dänemark. Allg. Forstzeitschrift 8: 145—152 (1959). —— SCHOBER, R.: Zur Gründung des Vereins der Forstlichen Versuchsanstalten Deutschlands vor 100 Jahren. Forstarchiv 43: 221—227 (1972). —— SCHOBER, R.: Ergebnisse von Douglasien-Provenienzversuchen in Deutschland. Proceedings IUFRO Meeting Working Party on Douglas-fir provenances. Göttingen. p. 12. (1973). —— SCHOBER, R., KLEINSCHMIT, J. and SVOLBA, J.: Ergebnisse des Douglasien-Provenienzversuches von 1958 in Nordwestdeutschland. Teil I. Allg. Forst- und Jagdzeitung 154, 209—236 (1983). —— SCHOBER, R., KLEINSCHMIT, J. and SVOLBA, J.: Ergebnisse des Douglasien-Provenienzversuches von 1958 in Norddeutschland. Teil III. Allg. Forst- und Jagdzeitung 155, 53—80 (1984). —— SCHÖNBACH, H.: Die Züchtung der Douglasie. In: Die Douglasie und ihr Holz. Ed.: K. GÖHRE. Akademie-Verlag, Berlin. p. 305—366 (1958). —— SCHWAPPACH, A.: Über den Wert der verschiedenen Formen der Douglasfichte. Mitt. d. Deutschen Dendrol. Ges. 16: 122—125 (1907). —— SIKA, A.: First results of the international provenances trial with Douglas-fir in Bohemia. Acta Musei Silediae, Opava, Ser. Dendrologia 23: 111—134 (1974). —— SIKA, A. and PAV, B.: Vyskovy rust dougla sky na provenienčnich plochách CR v ruznych fázich vyroje. Lesn. Praha 36: 369—380 (1990). —— SILEN, R. R.: Pollen dispersal consideration for Douglas-fir. Journal of Forestry 60: 790—795 (1962). —— SILEN, R. R.: Effect of altitude on factors of pollen contamination of Douglas-fir seed orchards. Journal of Forestry 61: 281—283 (1963). —— SILEN, R. R.: Regeneration aspects of the 50 year-old Douglas-fir heredity study. In: Proceedings Annual Meeting Western Reforestation Coordinating Committee. Spokane, Wash.. p. 35—39 (1964). —— SILEN, R. R.: A 50-year racial study of Douglas-fir in Western Oregon and Washington. US Forest Service, Western For. Gen. Ass. Proceedings 1965. (1966). —— SILEN, R. R. and MANDEL, N. L.: Clinal genetic growth variation within two Douglas-fir breeding zones. Journal of Forestry 81: 216—220 (1983). —— SIMSEK, Y.: Ergebnisse des internationalen Douglasien-Provenienzversuches von 1973/1974 in der Türkei. Manuskript (1982). —— SORENSEN, F. C.: Two year results of west-east transect provenance test of Douglas fir in Oregon. U. S. Dept. of Agric., For. Serv., Pacific N. W. For. and Range Exp. Sta. PNW-72:, pp. 8. (1967). —— SORENSEN, F. C.: Estimate of self-fertility in coastal Douglas-fir from inbreeding studies. Silvae Genetica 20: 115—120 (1971). —— SORENSEN, F. C.: Frequency of seedlings from natural self-fertilization in Coastal Douglas-fir. Silvae Genetica 22: 20—24 (1973). —— SORENSEN, F. C.: Provenance variation in *Pseudotsuga menziesii* seedlings from the *var. menziesii — var. glauca* transition zone in Oregon. Silvae Genetica 28: 96—103 (1979). —— SORENSEN, F.: Geographic variation in seedling Douglas-fir from the western Siskiyou Mountains of Oregon. Ecology 64: 696—702 (1983). —— SORENSEN, F. C. and FERRELL, W. K.: Photosynthesis and growth of Douglas-fir seedlings when grown in different environments. Can. J. Bot. 51: 1689—1698 (1973). —— SOUTRENON, A.: Sensibilité du Douglas vert et du Douglas bleu á la maladie foliaire provoqués par Rhabdocline pseudotsugae CEMAGREF, Informations Techniques, Cahier 61—4, pp.4. (1986). —— STEPHAN, R. B.: Über Anfälligkeit und Resistenz von Douglasienherkünften gegenüber *Rhabdocline pseudotsugae*. Silvae Genetica 22: 149—153 (1973). —— STEPHAN, R. B.: Prüfung von Douglasien-Herkünften auf Resistenz gegen *Rhabdocline pseudotsugae* in Infektionsversuchen. European Journal of For. Pathol. 10: 152—161 (1980). —— SZIKLAI, O.: Further information on the variation of Douglas-fir (*Pseudotsuga menziesii* (MIRB.) FRANCO) in its native habitat. Proceedings IUFRO Meeting Working Party on Douglas-fir provenances. Göttingen. p. 195—206 (1973). —— SZIKLAI, O.: Douglas-fir provenance-progeny test at Haney, B. C., Canada. Proceedings Joint Meeting Western For. Gen. Ass. and IUFRO Working Parties. Olympia, Wash. 4.85:9 (1990). —— SZIKLAI, O. and DE VESCOVI, M. A.: Further data on the variation of Douglas-fir. Proceedings IUFRO Meeting of WP S.2—02, 05, 06, 12, 14. Vancouver, Canada. p. 141—154 (1978). —— SZIKLAI, O. and DE VESCOVI, M. A.: Further data on the variation of Douglas-fir. Proceedings IUFRO Meeting of WP S.2 — 02, 05, 06, 12, 14. Vancouver, Canada. p. 51—64 (1978). —— SZIKLAI, O., EL KASSABY, Y. A. and SCAGEL, R. K.: Relationship of *Pseudotsuga menziesii* with other *Pseudotsuga* species inferred from karyotype reconstruction. Proceedings IUFRO Meeting Working Party Breeding Strategy for Douglas fir as an introduced species. Vienna, 1985. p. 127—142 (1987). —— TIGERSTEDT, P.: Adaptability of seed sources across geographic zones — 90 years of experiments in Finland. Proceedings Joint Meeting Western For. Gen. Ass. and IUFRC Working Parties. Olympia, Wash. 4.85:11 (1990). —— TOVAL, G.: Results in two test sites of provenances of the IUFRO collection of *Pseudotsuga menziesii* (MIRB.) FRANCO in Galicia. Proceed. IUFRO Meeting Working Party Breeding Strategy for Douglas fir as an introduced species. Vienna, 1985. p. 49—65 (1987). ——TSUKADA, H.: *Pseudotsuga menziesii* (MIRB.) FRANCO: Its pollen dispersal and late quaternary history on the Pacific Northwest. Japan. J. Ecol. 32, 159—187 (1982). —— VEGA, G.: Ten years' results of Douglas-fir IUFRO collection in North Spain. Proceedings Joint Meeting Western For. Gen. Ass. and IUFRO Working Parties. Olympia, Wash. 2.352 (1990). —— VRIES, S. H. G. DE: Use and improvement of Douglas fir in the Netherlands. Proceedings Joint Meeting Western For. Gen. Ass. and IUFRO Working Parties. Olympia, Wash. 4.37:8 (1990). —— WANGENHEIM, F. A. J. VON: Beytrag zur teuschen holzgerechten Forstwissenschaft, die Auspflanzung nordamerikanischer Holzarten mit Anwendung auf deutsche Forste betreffend. Göttingen (1787). —— WEISGERBER, H.: Height growth development and damage by spring frost of the IUFRO Douglas-fir provenance trial of 1970 in Hesse. Federal Republic of Germany. Proceedings IUFRO Meeting of WP S.2 — 02, 05, 06, 12, 14. Vancouver, Canada. p. 305—316 (1978). —— WHEAT, J. G. and WILSON, B. C.: Growth of three Douglas-fir varieties at Nisqualla, Washington. Journal of Forestry 63: 372 (1965). —— WHEELER, N. C., STONEZYPHER, R. W. and ZECH, K. S.: Physiological characterization of select families to aid in source movement decisions: supplementing long term performance trials. Proceedings Joint Meeting Western For. Gen. Ass. and IUFRO Working Parties. Olympia, Wash. 4.85:16 (1990). —— WIDMAIER, T, DAGENBACH, H. and HAUFF, U.: Lamma shoots and height growth of Douglas-fir. Proceedings IUFRO Meeting Working Party Breeding Strategy for Douglas fir as an introduced species. Vienna, 1985. 105—106 (1987). —— WORTHINGTON, N. P.: How much Douglas-fir will grow on an acre? Journ. For. 56: 763—764 (1958). —— YANG, I. C., CHING, T. M. and CHING, K. K.: Isozyme variation of coastal Douglas-fir. I. A. Study of geographic variation in three enzyme systems. Silvae Genetica 26: 10—18 (1977). —— YEH, F. C. and O'MALLEY, D. O.: Enzyme variation in natural populations of Douglas-fir, *Pseudotsuga menziesii* (MIRB.) FRANCO, from British Columbia. I. Genetic variation patterns in Coastal populations. Silvae Genetica 29: 83—92 (1980). —— ZAVARIN, E. and SNAJBERK, K.: Geographic variability of monoterpenes from cortex of *Pseudotsuga menziesii*. Pure Appl. Chem. 34: 411—433 (1973). —— ZAVARIN, E. and SNAJBERK, K.: *Pseudotsuga menziesii*: Chemical races of California and Oregon. Biochemical Systematics and Ecology, 121—129 (1975).