

- VON WETTSTEIN, D.: The inheritance of the critical night length for budset in *Picea abies* (L.) KARST. Proceedings, IUFRO Joint meeting, S.02.04.1-3, Stockholm 439-448, (1974). — ERIKSSON, G., I. EKBERG, I. DORMLING, B. MATERN and VON WETTSTEIN, D.: Inheritance of bud-set and bud-flushing in *Picea abies* (L.) KARST. Theoret. Appl. Genetics 52, 3-19, (1978). — FARRAR, J. L.: Induced variation in the pattern of shoot extension in five seed sources of *Picea abies* (L.) KARST. 8th Northeastern Forest Tree Improvement Conference Proceedings, 14-20, (1961). — GÄRTNER, E.: Untersuchungen zur Beurteilung der Jugendentwicklung von Fichtenprovenienzen. Dissertation, München, (1975). — HOFFMANN, K.: Möglichkeiten der Beurteilung der Herkunft von Fichtensamen nach ihrer Höhenlage mit Hilfe eines Frühtestes. Arch. Forstwes. 14: 651-666, (1965). — HOLZER, K.: Die Augusttriebbildung als Höhenlagentest bei der Fichte (*Picea abies* (L.) KARST.). XIV. IUFRO Congress, Section 22, München, (1967). — HOLZER, K.: Zur Identifizierung von Fichtenherkünften (*Picea abies* (L.) KARST.). Silvae Genetica 24, 169-175, (1975). — KLEINSCHMIT, J. und SAUER, A.: Variation in morphology, phenology, and nutrient content among *Picea abies* clones and provenances, and its implications for tree improvement. Tree physiology and yield improvement. Eds. CANNELL, M. G. R. and LAST, F. T., London, (1976). — KÖNIG, A.: Einige Ergebnisse aus dem IUFRO-Fichtenprovenienzversuch von 1964/68 in der Bundesrepublik Deutschland. Allg. Forstztg. 92, (1981). — LOGAN, K. T. and POLLARD, D. F. W.: Mode of shoot growth in 12-year-old Black spruce provenances. Can. J. For. Res. 5, 539-540, (1975). — MAGNESEN, S.: Ecological experiments regarding growth termination in seedlings. III. Effect of daylength. Meddelelser Vestl. Forstl. Forsöksstasjon 52, 275-317, (1971). — MOLISCH, H.: Die Lebensdauer der Pflanze. Jena, 168 S., (1929). — NIENSTAEDT, H.: Chilling requirements in seven *Picea* species., Silvae Genetica 16: 65-68, (1967). — POLLARD, D. F. W. and LOGAN, K. T.: The role of free growth in the differentiation of provenances of Black Spruce *Picea mariana* (MILL.) B.S.P. Can. J. For. Res. 4, 308-311, (1974). — POLLARD, D. F. W. and LOGAN, K. T.: The effects of light intensity, photoperiod, soil moisture potential, and temperature on bud morphogenesis in *Picea* species. Can. J. For. Res. 9, 415-421, (1977). — ROSVALL-ÄHNEBRINK, G.: Practical application of dormancy induction techniques to greenhouse-grown conifers in Sweden. In: J. B. SCARRETT et al.: COJFRC Symp. Proc. 0-P-10, Can For Serv, Sault St. Marie, Ont., (1982). — SCHMIDT-VOGT, H.: Der Johannistriebtest als Hilfsmittel zur Feststellung der Bodenständigkeit von Fichtenbeständen in Hochlagen. In: Forstsamengewinnung und Pflanzenanzucht für das Hochgebirge. Hrsg. H. SCHMIDT-VOGT, München-Basel-Wien, (1964). — SEELIGER, R.: Topophysis und Zyklophysis pflanzlicher Organe und ihre Bedeutung für die Pflanzenkultur. Ang. Bot. 6: 191-200, (1924). — SAUER, A., J. KLEINSCHMIT and LUNDERSTAEDT, J.: Charakterisierung von Fichtenklonen (*Picea abies* KARST.) mit Hilfe morphologischer, physiologischer und biochemischer Methoden. I. Variation der untersuchten Merkmale. Silvae Genetica 22, 173-182, (1973). — SWEET, G. B. and BOLLMANN, M. P.: The terminology of pine shoot growth. New Zealand J. of For. Sci. 6, 393-396, (1976). — TRANQUILLINI, W., LECHNER, F., OBERARZBACHER, P., UNTERHOLZNER, L. und HOLZER, K.: Über das Höhenwachstum von Fichtenklonen in verschiedener Seehöhe. Mitt. d. Forstl. Bundes-Versuchsanst. Wien, Heft 129, 7-25, (1980). — UNUNGER, J.: Genetiska studier över tillväxtmönstret - fri och förutbestämd tillväxt - hos unga granplanter. Res. Notes 31, Swedish University of Agricultural Sciences, Uppsala, (1981). — WALTERS, J. and SOOS, J.: Some observations on the relationship of lammas shoots to the form and growth of Douglas-fir seedlings. Research Papers Faculty For. Univ. B.C. 40, 7 p., (1961). — WORRALL, J.: Provenance and clonal variation in phenology and wood properties of Norway spruce. Silvae Genetica 24, 2-5, (1975). — WORRALL, J. and MERGEN, F.: Environmental and genetic control of dormancy in *Picea abies*. Phys. Plant. 20, 733-745, (1967). — VON WÜHLISCH, G.: Untersuchungen über das prädestinierte und freie Triebängenwachstum junger Fichten (*Picea abies* (L.) KARST.) als Voraussetzung für einen Frühtest. Dissertation, Hamburg, p. 140, (1984). — VON WÜHLISCH, G.: Propagation of Norway-spruce cuttings free of topophysis and cyclophysis effects. Silvae Genetica 33, 215-219, (1984b). — VON WÜHLISCH, G.: Das freie Wachstum der Fichte und seine Verwendungsmöglichkeiten für Frühtests. Forum Genetik-Wald-Forstwirtschaft, Bericht über die 3. Arbeitstagung, Univ. Göttingen, 28-38, (1984c). — VON WÜHLISCH, G. and MUHS, H.-J.: Influence of age on sylleptical and proleptical free shoot growth of *Picea abies* (L.) KARST. Silvae Genetica 36, 42-48, (1986). — VON WÜHLISCH, G. and MUHS, H.-J.: Response to varying environments of predetermined and free shoot growth of Norway spruce seedlings (*Picea abies* (L.) KARST.). (In preparation), (1987).

Differences in the resistance of Douglas fir provenances to the woolly aphid *Gilletteella cooleyi*

By B. R. STEPHAN

Bundesforschungsanstalt für Forst- und Holzwirtschaft,
Institut für Forstgenetik und Forstpflanzenzüchtung,
Siekerlandstr. 2, D-2070 Grosshansdorf,
Federal Republic of Germany

(Received 8th January 1987)

Summary

Four year old plants of 165 Douglas fir provenances (*Pseudotsuga menziesii*) from the IUFRO seed collection 1966/69 have been evaluated for the resistance against the woolly aphid *Gilletteella cooleyi*. Large differences were found which correspond with the geographical groups within the species *Pseudotsuga menziesii*: northern coastal provenances (green form of Douglas fir) were infested severely, southern coastal provenances from southern Oregon and California were less attacked. Low attack was observed also in northern interior provenances (grey form of Douglas fir). Almost resistant were southern interior provenances (blue form of Douglas fir). The mean values of woolly aphid attack were strongly correlated with the percentage of infested trees within a provenance. — The results correspond very well with the differentiation of terpene types of Douglas fir by other authors.

Key words: Douglas fir, provenances, woolly aphid, resistance, terpene types.

Zusammenfassung

Vier Jahre alte Douglasien (*Pseudotsuga menziesii*) von 165 Herkünften aus der IUFRO-Einsammlung 1966/69 wurden auf ihre Resistenz gegenüber der Douglasien-Wollaus *Gilletteella cooleyi* bonitiert. Dabei ergaben sich Unterschiede, die weitgehend der geographischen Gruppierung innerhalb der Douglasien entsprachen: nördliche Küstenherkünfte (grüne Form der Douglasie) waren sehr stark befallen, südliche Küstenherkünfte aus Oregon und Kalifornien waren schwächer befallen. Geringen Wollaus-Befall hatten die nördlichen Interior-Herkünfte (graue Form der Douglasie). Als weitgehend resistent erwiesen sich die südlichen Interior-Herkünfte (blaue Form der Douglasie). Der

Dedicated to Prof. Dr. W. LANGNER on his 80th birthday.

mittlere Befallsgrad einer Herkunft war eng mit dem Prozentsatz befallener Bäume korreliert. — Zwischen dem Wollaus-Befall der Herkünfte in den verschiedenen geographischen Regionen und der von verschiedenen Autoren vorgenommenen Differenzierung von Douglasien-Rassen auf der Grundlage der Terpenzusammensetzung von Harzen besteht eine gute Übereinstimmung.

Introduction

In central Europe the Douglas fir woolly aphid (*Gilletteella cooleyi* GILL.) is a very common pest on needles of Douglas fir trees (*Pseudotsuga menziesii* (MIRB.) FRANCO). The main symptoms of a severe infestation are deformations and yellowing of needles, early needle cast, and reduced shoot growth (SCHWERTFEGER 1981). Particularly in spring and summer the insects can be recognized easily by their woolly white wax exudations. Mostly the trees recover again but young plants can suffer heavily and only little is known about growth reduction or mortality after annually repeated attacks.

The genus *Gilletteella* belongs to the insect family *Adelgidae* within the suborder *Aphidina* and has a complicated life cycle, which has been described in detail by STEFFAN (1972). There are two species, the heterocyclic *Gilletteella cooleyi* GILL. with the main host *Picea sitchensis* (BONG.) CARR. and the alternate host *Pseudotsuga menziesii*, and the anholocyclic, parthenogenetic *G. cowenyi* GILL. which occurs only on Douglas fir. The distinction of the two species is only possible by detailed life cycle studies. Therefore, the name of the holocyclic species *G. cooleyi* is used by most authors and also in the present paper.

Originally, *G. cooleyi* was endemic in north-western North-America (British Columbia, Washington, and Oregon), where Douglas fir and Sitka spruce have their common natural distribution area. The insect occurs especially in the coastal forests with high humidity. The parthenogenetic *G. cowenyi* was native in California in areas with only the alternate host Douglas fir (STEFFAN 1972). From North-America the aphid has been imported to Europe. In Germany it has been observed since about 1933 (TEUCHER 1954). During the last 50 years the woolly aphid spread to all artificial Douglas fir stands and is now a widely established pest (see also the review by KRUEL and TEUCHER 1958).

The first reports of a different susceptibility of the various Douglas fir forms came from Great Britain in 1920 (HENRY and FLOOD 1920), and were confirmed later also by observations on the European continent (see KRUEL and TEUCHER 1958). Summarizing, one can state that there seems to be racial and individual differences in the resistance of Douglas fir to the woolly aphid. The interior variety of Douglas fir (*Pseudotsuga menziesii* var. *glauca* (BEISSNER) FRANCO) is obviously more resistant than the coastal variety (*P. menziesii* var. *menziesii*). Studies with clonal material showed that resistance seems to be governed genetically (SYRACH LARSEN 1953, HEITMÜLLER 1954). Different resistance is also known on the level of provenances (SCHOBER and MEYER 1955, KRUEL and TEUCHER 1958, MEINARTOWICZ and SZMIDT 1978, and others). Most of these studies were conducted with a low number of provenances.

Therefore, the IUFRO seed collection of 1966 to 1969 offered a good opportunity to compare the behaviour of 165 Douglas fir provenances from the whole natural range against the woolly aphid. A few summarized results were given for the same IUFRO material by RECK (1978). The present paper gives the results of detailed evaluations of

the Douglas fir woolly aphid attack in 1973 under north German conditions.

Materials and Methods

Plant material: The IUFRO seed collections have been sown in 1970 and transplanted in 1972 in a nursery field trial near the institute. This trial was planted with 4 replications in a randomized block design.

Woolly aphid attack: The infestation of the 4 year old plants was evaluated in early July 1973. In that year a very heavy incidence of aphids was observed, which gave a good basis for a comparing investigation between the provenances. Each plant has been scored according to the following scale: 0 = no aphids; 1 = up to 10 aphids/plant; 2 = few aphids, not on all needles; 3 = many aphids on all needles, which are not yet deformed; 4 = very heavy infestation, needles already curled. No differences were made between the various stages of aphid development.

Evaluation: The comparison and analysis of the data was made on the basis of mean values of provenances. The number of plants per provenance varied between 4 and 92 with an average of 36 plants per provenance. This and the fact that not all provenances were present in all replications complicated the statistical analysis. Hence, the statistical comparison of Douglas fir regions, races or groups has been avoided with this material. But the general results are evident by themselves. A detailed analysis of race differences will be calculated in a later study in connection with the evaluation of further characteristics. In addition to the qualitative mean score of attack also the quantitative number of attacked trees was calculated, whereby only trees with score 0 were considered as unattacked.

Results

The investigation revealed in large differences between the 165 tested IUFRO provenances with respect to their infestation by the Douglas fir woolly aphid. The mean score values vary between 0 and 3.4 with an overall trial average of 1.2 (Table 1). The mean reaction of each provenance is shown by a 4 step scale in Figure 1. 70 (= 42%) provenances show no or a very weak woolly aphid attack below 1.4, in Figure 1 represented by open symbols. 95 (= 58%) provenances had a more severe infestation above 1.5, represented by solid symbols in Figure 1.

The distribution of the respective provenance symbols demonstrates a significant relationship with geographical regions (Figure 1). All provenances with a high woolly aphid attack are concentrated along the coast of British Columbia, Washington, and Oregon. These regions showed mean infestation values of 1.9, 2.2, and 2.2, respectively (Table 1). But the reaction is not completely uniform. Provenances along the Cascades, often from the eastern slopes, are sometimes less attacked than provenances from the coast range (see Figure 1). Coastal provenances of southern Oregon and California are obviously less attacked with mean values of 1.1 and 1.5, respectively (Table 1). A very low woolly aphid attack has been observed, with a few exceptions, also in provenances of the northern interior of British Columbia and Washington. The mean value was 0.8 (Table 1). Almost no aphids could be found on provenances from the southern interior of Utah, Colorado, Arizona, and New Mexico. Finally, the 4 provenances from Mexico remained also completely unattacked. The mean values of both regions were 0.1 and 0, respectively (Table 1).

Beside the mean infestation rate of provenances, expres-

Table 1. — Woolly aphid attack of Douglas fir provenances from different geographical regions. Range and mean are based on average values of provenances.

group	region	number of provenances	degree of attack		percentage of attacked trees	
			range	mean	range	mean
coast	Brit. Columbia, coast	11	0.4-2.5	1.9	28.0-100	89.1
	Brit. Columbia, Vancouver Island	15	1.3-2.8	2.2	94.4-100	98.9
	Washington, coast and western Cascades	41	1.1-3.4	2.2	65.3-100	96.4
	Oregon, north	20	1.0-3.2	2.2	83.3-100	97.0
	Oregon, south	4	0.9-1.5	1.1	77.8-85.9	82.4
	California	23	0.7-2.3	1.5	58.8-100	87.1
		Σ 114		\bar{x} 1.9		\bar{x} 91.8
northern interior	Brit. Columbia, interior	23	0.0-2.0	0.6	0.0-100	37.1
	Washington, north-east	3	0.2-0.6	0.4	13.5-34.2	23.4
	Washington, eastern Cascades	4	0.5-2.2	1.5	38.5-100	82.5
			Σ 30		\bar{x} 0.8	
southern interior	Utah, Arizona, Colorado, New Mexico	17	0.0-0.3	0.1	0.0-31.6	4.9
	Mexico	4	0	0.0	0	0.0
			Σ 21		\bar{x} 0.1	
total sum		165				
trial mean				1.2		63.5

sed by a mean score value, also the percentage of attacked trees within the respective provenances has been calculated. The mean values of each region and the range of percentage within the regions are given in Table 1. The provenances vary between 0% and 100% attacked trees with an overall average of 64%. Generally provenances with a high mean infestation value also have the highest percentage of attacked trees. It is not surprising that there exists a very strong correlation between these two factors with a mean rank correlation coefficient of $r = 0.87$ for the total trial, and coefficients of $r = 0.68$ for the coastal provenance group, $r = 0.95$ for the northern interior group, and $r = 0.99$ for the southern interior group.

Discussion

The results of this study confirm with a greater number of provenances earlier reports on differences in the resistance of Douglas fir against the woolly aphid (e.g. SCHÖBER and MEYER 1955, TEUCHER 1956, KRUEL and TEUCHER 1958, MEINARTOWICZ and SZMIDT 1978, RECK 1978). In this study a distinction is made between provenances from the coast, from the northern interior, and from the southern interior (Table 1). This grouping corresponds more or less with the distinction between the green, grey and blue forms of Douglas fir. Despite slight variations one can state that the green or coastal Douglas fir form is very susceptible to the woolly aphid. This is true for coastal provenances from British Columbia, Washington and northern Oregon. Provenances from southern Oregon and California were less attacked. Also the so called grey form of Douglas fir from the northern interior is obviously less susceptible. A very high resistance against the woolly aphid seems to be present in all blue forms of Douglas fir from the southern interior. Despite the woolly aphid resistance these blue forms are not suited for the central European forestry because of their generally slow growth (RECK 1978, and others) and

high susceptibility to the needle cast fungus *Rhabdochline pseudotsugae* (STEPHAN 1973).

The results show an interesting relation to studies of RUDLOFF (1972, 1973a, 1973b) as well as ZAVARIN and SNAJBERK (1973, 1975, 1976), and their distinction of races on the basis of chemotaxonomic characteristics. They used the composition of volatile needle oil and cortical oleoresin with respect to the terpenes as basis to differentiate chemical races in Douglas fir. The main results of these authors have been compiled by HERMANN (1981), whose classification is taken into account for the following explanations. His grouping and designation of the groups is also considered in Figure 1.

Chemical race A represents the coastal or green Douglas fir and is in general susceptible to the woolly aphid. The northern interior provenances belong to a transition group between A and B. The chemical race B is native in the Rocky Mountains of Idaho and Montana, and unfortunately not represented in this trial. Coastal provenances of southern Oregon and California belong to a transition group between A and D, the Sierra Nevada race according to ZAVARIN and SNAJBERK (1975). The latter one is also not represented in the trial. The border between the groups A and A/D extends approximately along the 43. degree of latitude which seems to be a precise border also between very susceptible northern coastal and less susceptible southern coastal provenances (Figure 1). Chemical race C represents the southern interior or blue Douglas fir with high resistance to the woolly aphid.

Up to now, nothing is known about the causal agents of the woolly aphid resistance in Douglas fir. But one can speculate that there is a relation between the chemical composition of a provenance or individual tree and its behaviour to the insect. In some cases, a causal relation between monoterpenes, single or in combination, and resistance to insect pests or fungal diseases could be demonstrated (SCHUCK 1982, BRIDGEN and HANOVER 1982). The

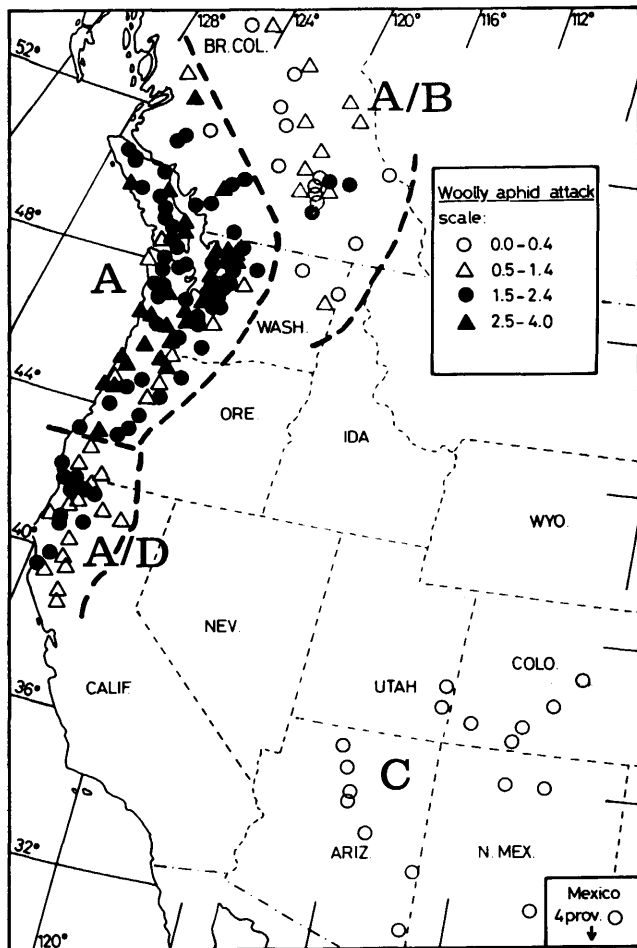


Figure 1. — Woolly aphid attack of 165 Douglas fir provenances in a nursery field trial in northern Germany. The provenance groups A, A/B, A/D, and C have been separated on basis of the classification by HERMANN (1981).

individual monoterpenes can be stimulating or inhibiting. This must be investigated for the individual case. So, for instance, it is interesting that the coastal or green Douglas fir is susceptible to the woolly aphid, but resistant against the fungal needle cast caused by *Rhabdocline pseudotsugae* (STEPHAN 1973). Contrary to this, the blue or southern interior Douglas fir is resistant to the woolly aphid but very susceptible for the *Rhabdocline* needle cast. The northern interior provenances show an intermediate behaviour.

The main differences in the terpene composition are that coastal provenances contain higher concentrations of sabinen and Δ^3 -carene, the northern interior provenances have a higher α -pinene content, and the southern interior ones a higher limonene and myrcene concentration (summary of papers from RUDLOFF, and ZAVARIN and SNAJBERK). But a causal relationship between resistance or susceptibility and these terpenes is not yet proven. The chemical

composition of the volatile needle oils and the oleoresin can be used not only as marker for a differentiation of Douglas fir races, but possibly also as a marker for an indirect selection of woolly aphid resistant Douglas fir provenances or individual trees.

Acknowledgement

The skilful technical assistance of Mrs. INGE SCHULZE is gratefully acknowledged.

Literature

BRIDGEN, M. R. and HANOVER, J. W.: Indirect selection for pest resistance using terpenoid compounds. In: HEYBROEK, H. M., STEPHAN, B. R. and WEISSENBERG, K. VON (eds.): Resistance to diseases and pests in forest trees. PUDOC. P. 161—168 (1982). — HEITMÜLLER, H.-H.: Beobachtungen über individuelle Resistenz gegen *Gilletteella cooleyi* GILL. an Douglasie. Zeitschr. f. Forstgenetik 3, 99—100 (1954). — HENRY, A. and FLOOD, M.: The Douglas-Firs. Proc. Royal Irish Acad. 35, Sect. B, No. 5, 120 (1920). — HERMANN, R. K.: Die Gattung *Pseudotsuga* — Ein Abriß ihrer Systematik, Geschichte und heutigen Verbreitung. Forstarchiv 52, 204—212 (1981). — KRUEL, W. and TEUCHER, G.: Die tierischen Feinde der Douglasie. In: GÖHRE, K.: Die Douglasie und ihr Holz. Akademie-Verlag, Berlin. S. 403—436 (1958). — MEINARTOWICZ, L. E. and SZMIDT, A.: Investigations into the Resistance of Douglas Fir (*Pseudotsuga menziesii* (MIRB.) FRANCO) Populations to the Douglas Fir Woolly Aphid (*Gilletteella cooleyi* GULL.). Silvae Genetica 27, 59—62 (1978). RECK, S. G.: Height growth and frost resistance in Douglas-fir provenances tested in the northern part of Germany. Proc. IUFRO joint meeting of working parties, Vancouver, Canada 1978, 175—188 (1978). — 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: Chemosystematic studies in the genus *Pseudotsuga*. II. Geographical variation in the terpene composition of the leaf oil of Douglas-fir. Pure and Applied Chemistry 34, 401—410 (1973a). — RUDLOFF, E. VON: Chemosystematic studies in the genus *Pseudotsuga*. III. Population differences in British Columbia as determined by volatile leaf oil analysis. Can. J. For. Res. 3, 443—452 (1973b). — SCHÖBER, R. und MEYER, H.: Douglasien-Provenienzversuche II. Allg. Forst- u. Jagdz. 126, 221—243 (1955). — SCHUCK, H. J.: Monoterpenes and resistance of conifers to fungi. In: HEYBROEK, H. M., STEPHAN, B. R. and WEISSENBERG, K. VON (eds.): Resistance to diseases and pests in forest trees. PUDOC. P. 169—175 (1982). — SCHWERDTFEGER, F.: Waldkrankheiten. P. Parey, Hamburg. 4. Aufl. 486 S. (1981). — SNAJBERK, K. and ZAVARIN, E.: Mono- and sesqui-terpenoid differentiation of *Pseudotsuga* of the United States and Canada. Biochem. Systematics and Ecology 4, 159—163 (1976). — STEFFAN, A. W.: Unterordnung Aphidina, Blattläuse. In: SCHWENKE, W. (ed.): Die Forstschädlinge Europas. Bd. 1. 162—386 (1972). — STEPHAN, B. R.: Über Anfälligkeit und Resistenz von Douglasien-Herkünften gegenüber *Rhabdocline pseudotsugae*. Silvae Genetica 22, 149—153 (1973). — SYRACH-LARSEN, C.: Studies of the diseases in clones of forest trees. Hereditas 39, 179—192 (1953). — TEUCHER, G.: Die Douglasienwollaus. Deutsche Akademie der Landwirtschaftswissenschaften zu Berlin. Merkblatt Nr. 15, 4 S. (1954). — TEUCHER, G.: Über die Anfälligkeit von Douglasien- und Stroben-Herkünften gegenüber der Douglasienwollaus (*Gilletteella cooleyi*) bzw. der Strobenwollaus (*Pineus strobi*) in Deutschland. 12th IUFRO Congress, Oxford 1956, IUFRO 56/24/18, 4 p. (1956). — ZAVARIN, E. and SNAJBERK, K.: Geographic variability of monoterpenes from cortex of *Pseudotsuga menziesii*. Pure and Applied Chemistry 34, 411—434 (1973). — ZAVARIN, E. and SNAJBERK, K.: *Pseudotsuga menziesii* chemical races of California, Oregon. Biochem. Systematics and Ecology 2, 121—130 (1975).