Monoterpene Composition in Larix[1])

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Introduction

The field of phytochemistry has expanded rapidly during the past decade, due in large part to the increasing availability and operational ease of analytic equipment. In forest tree studies the terpenoids, and in particular the monoterpenes, have provided a much investigated class of biochemical compounds that show sufficient stability within individuals to be of taxonomic value. This same relative stability also suggests these compounds for physiological and genetic investigation. The work with Pinus by MIROV (for a summary see MIROV, 1961) has provided a particular stimulus to the use of resin analysis as a taxonomic technique. Recent studies have been conducted with several conifer genera (e.g.: Picea: VON RUDLOFF, 1962; Abies: ZAVARIN and SNAJBERK, 1965; Thuja: VON RUDLOFF, 1961; Pinus: MIROV, 1961; FORDE, 1964; ZAVARIN, et al. 1966; HANOVER, 1966; SQUILLACE and FISHER, 1966; SMITH, 1966; CALLAHAM, 195%; BANNISTER, et al. 1959; SAVORY, 1962; anid Pseudotsuga: HANOVER and FURNISS, 1966). From these and other studies, suggestions of seasonal variation, intra- and inter-population variation, and preliminary data on the mode of inheritance have became available. The biosynthesis of plant terpenes has been reviewed by NICHOLAS (1963), and by WEISMANN (1966). The status of this field may be summarized as one requiring additional work – although current theory supports the "biogenetic isoprene rule" (BERTHOLET, 1860; WALLACH, 1914; CHAYKIN, et al. 1958; RUZICKA, 1953) in relation to synthesis, and several ionic and radical mechanisms have been defined.

To tihe author's knowledge, the analysis of Larix resin as a taxonomic tool had not previously received intensive investigation. Therefore, this survey of the major monoterpene constituents in several *Larix* species was initiated. The investigation herein reported is part of a continuing research program with Larix at my laboratory. The study includes species that are among the fastest-growing conifers in the northern forests, and hybridization and mutation breeding studies in progress with these species will further define the inheritance of monoterpenes for the genus.

Material and Methods

The study material included trees from six species and one putative hybrid population. The species used were: Larix sibirica LEDEB.: L. Grnelini (RUPR.) LITVIN.; L. laricina (DUROI) K. KOCH., L. occidentalis NUTT.; L. leptolepis (SIEB. & Zucc.) GORD.; and L. decidua MILL. A putative hybrid population from a natural F, introgression of L. leptolepis and L. decidua was also sampled. The L. occidentalis resin was supplied by Dr. GEORGE BLAKE, University of Montana, from a natural stand; the other trees were growing in Central New York. The collections from L. laricina wer? also made from natural stands, the remaining New York trees were plantation grown from commercial seed sources. Ten mature trees were utilized for each species with the exception of L. occidentalis where only 5 sample trees were used. All trees were sampled at DBH at the south side of the tree. Resin collections were made in May and June; a second collection of L. *sibirica* resin was made in November to study seasonal variation. All samples were stored in glass vials under refrigeration prior to analysis. In three of the species (L. *decidua*, L. leptolepis, and L. *Gmelini)* trees were selected from two growth rate classes; five trees were selected as the faistest growing trees in each stand and the nearest average codominant trees were also sampled to provide a paired comparison of growth rate effects on monoterpene constituents. The remainder of the sample trees were chosen at random.

The resin analysis was conducted by gas chromatography. A Microtek DSS-172 dual column, dual hydrogen flame detector was utilized. Recording was conducted on a 1 mv recorder with disk integrator, and relative peak percentages were computed directly from integrator values. Sample determination were made with ¼ inch X 16 foot columns, 5% SE30 on 80190 Chromopart XXX. acid and base washed. In addition, each species was evaluated with carbowax 5% 20M on chromosorb-G 801100 mesh columns. Operating conditions were: inlet temperature 100° C, column temperaturc 75° C detector temperature 100° C, nitrogen flow (carrier gas) 25 cc/minute. The resin was dissolved in approximately equal volumes of acetone; 2 microliter samples were injected. Identification of monoterpenes was based on comparative retention times using standard solutions. Reference of all peaks to α-pinene was found to be the most reproduceable technique for retention time. Standard monoterpene solutions were also added to the unknown to aid in confirmation of a pratieular peak. Analysis of each compound must be considered tentative at this time, future studies are planned to include infra-red spectral analysis to confirm the identifications herein reported.

Results and Discussion

Results of the individual tree analysis are shown in *Table* 1, and the average for the six species in Figure 1. Monoterpene concentrations shown in Figure 1 suggest that three groups, with two species in each group, may be differentiated with relative ease.

Both quantitative and qualitative similarity was observed in L. decidua and L. leptolepis; each species had a preponderance of α-pinene (average over 80 percent) with β-pinene and limonene as the other major components. Concentration ranges of these three constituents overlapped and no significant between-species differences were observed. The small amounts of camphene and myrcene in botn species, and of A^3-carene in L. leptolepis, were not consistent enough to be useful in discriminating between the two.

The data obtained from a putative hybrid population (See Table 1) supported the species similarity. It must be noted that the putative hybrids were not derived from the parent

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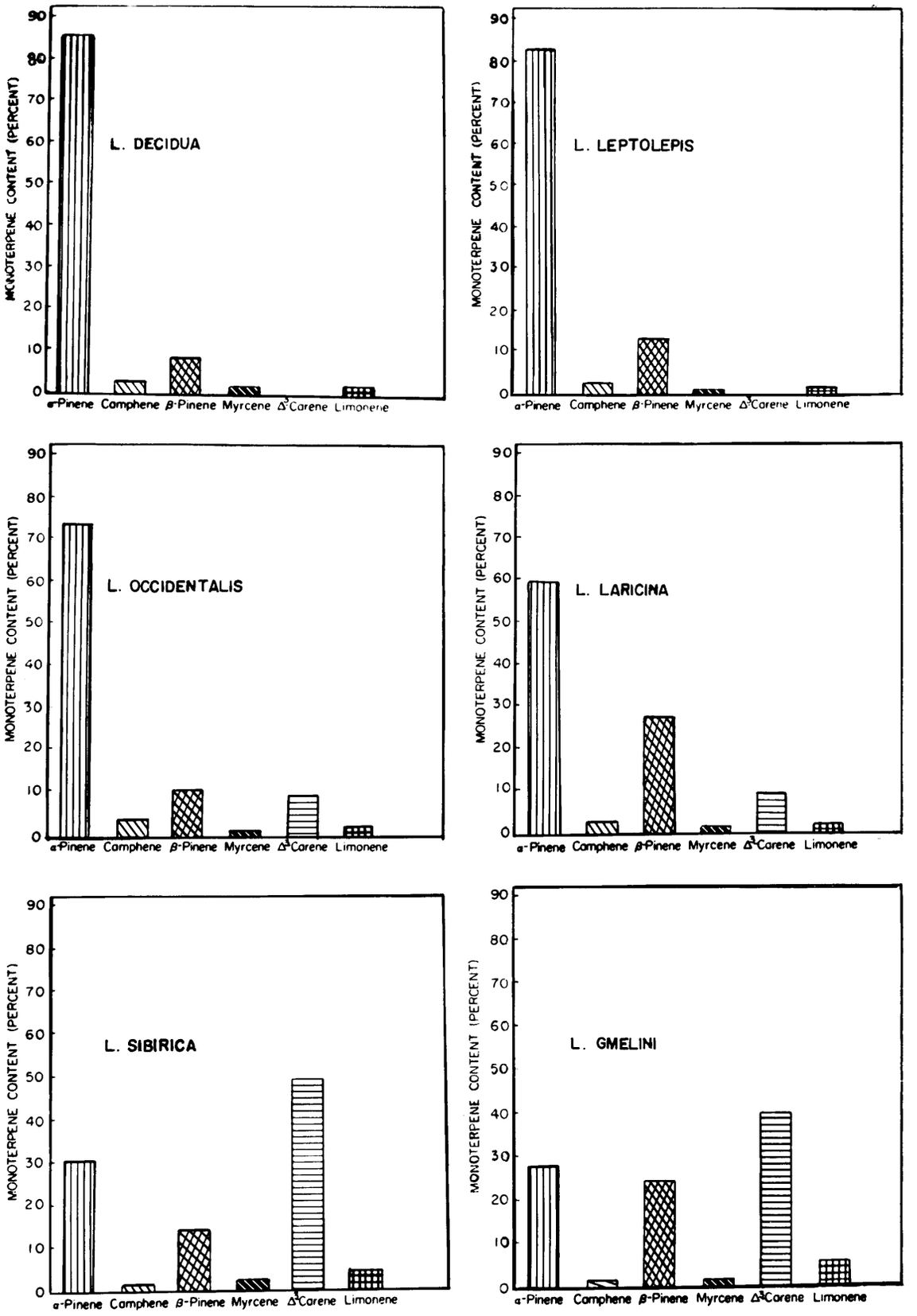

Figure 1. — Average monoterpene content for the six species investigated.

Table 1. — Monoterpene content for individual trees

Tree	α-pinene	Camphene	β-pinene	Myrcene	Δ³-carene	Limonene
			L. decidua			
A	84.8	2.3	9.8	Tr.		3.1
B	84.5	2.9	7.0	1.5		4.0
C	89.9	2.5	6.4	0.4		0.9
D	79.9	3.8	12.5	1.9		1.9
E	84.9	2.5	7.4	3.7		1.6
F	85.1	2.5	9.5	1.0		1.9
G	89.8	1.6	5.0	2.6		1.0
H	90.5	2.8	4.6	Tr.		2.1
I	90.2	3.2	5.2	0.8		0.6
J	78.4	1.8	16.8	1.2		1.8
x̄	85.8	2.6	8.4	1.3		1.9
SE	1.36	0.20	1.22	0.37		0.32
			L. sibirica			
A	26.0	1.0	12.7	2.0	52.7	5.5
B	23.4	0.7	13.7	2.8	55.5	3.8
C	33.4	1.6	16.4	2.2	42.5	3.9
D	37.1	1.1	16.6	1.8	40.1	3.2
E	34.7	1.7	14.1	1.8	44.6	3.0
F	45.3	1.6	15.9	1.1	34.2	1.9
G	26.0	1.0	12.5	2.8	53.1	4.6
H	21.8	0.6	13.7	0.9	61.0	2.1
I	26.6	1.2	14.0	3.3	49.5	5.4
J	25.6	0.5	11.9	1.7	56.9	3.3
x̄	30.0	1.1	14.2	2.0	49.0	3.7
SE	2.34	0.41	0.52	0.24	2.67	0.27
			L. eurolepis			
A	83.6	2.3	12.9			1.2
B	85.9	2.6	5.8		4.6	0.8
C	80.0	2.5	14.3	0.6	1.7	0.9
D	78.2	2.6	10.9	1.4	4.0	2.8
E	71.6	3.6	13.3	2.6	3.2	5.7
F	62.8	2.9	24.1	2.5		7.8
G	61.5	3.4	19.4	2.4	6.0	7.4
H	78.6	3.7	5.9		9.2	2.5
I	76.3	4.2	11.2	2.6		5.7
J	72.1	3.5	18.0	1.9		4.5
x̄	75.1	3.1	13.6	1.4	2.9	3.9
SE	2.57	0.20	1.82	0.36	0.99	0.84
			L. occidentalis			
A	79.3	3.2	12.7	0.7	2.4	1.6
B	65.2	3.1	6.9	0.6	22.9	1.2
C	76.6	5.1	14.7	1.1	0.0	2.5
D	63.4	4.0	12.4	1.8	15.6	2.6
E	82.8	1.7	7.7	Tr.	6.3	1.7
x̄	73.5	3.4	10.9	0.8	9.4	1.9
SE	3.87	0.56	1.52	0.29	4.28	0.27

Tree	α-pinene	Camphene	β-pinene	Myrcene	Δ³-carene	Limonene
			L. leptolepis			
A	85.4	2.1	10.7	Tr.		1.8
B	74.7	3.3	19.2	1.2		1.7
C	88.5	3.1	6.4	0.9		1.1
D	88.6	2.7	8.2	Tr.		0.5
E	87.7	2.1	9.5	0.7		Tr.
F	80.7	2.1	13.8	1.4		1.9
G	89.5	2.8	7.6	Tr.		Tr.
H	90.2	2.4	7.4	Tr.		Tr.
I	65.4	1.2	26.1	0.6	Tr.	6.7
J	76.8	1.2	20.7	0.5	0.4	0.4
x̄	82.8	2.3	13.0	0.5		1.4
SE	2.59	0.22	2.15	0.17		0.64
			L. Gmelini			
A	31.6	0.8	32.0	2.1	26.4	7.1
B	20.0	1.0	19.7	1.3	54.4	3.7
C	23.3	1.1	20.6	2.4	46.4	6.2
D	43.2	2.8	27.4	1.1	21.2	6.2
E	19.8	Tr.	9.3	0.7	66.5	3.6
F	17.2	0.4	17.0	1.4	60.0	4.0
G	44.4	1.7	33.3	2.3	10.4	7.8
H	21.6	0.5	29.3	2.1	40.2	6.2
I	28.9	0.5	28.6	1.3	33.6	7.1
J	23.1	1.4	27.1	2.9	37.3	8.2
x̄	27.3	0.8	24.4	1.8	39.6	6.0
SE	3.07	0.16	2.39	0.22	5.59	0.53
			L. laricina			
A	51.4	1.0	40.6	0.8	4.6	1.6
B	50.8	2.5	26.6	1.9	16.4	1.7
C	60.4	1.0	33.7	0.4	4.2	0.2
D	52.8	1.6	29.6	1.1	14.1	0.8
E	51.2	1.1	28.9	1.4	14.3	3.0
F	71.8	3.4	17.4	1.4	3.7	2.3
G	55.6	1.3	22.5	1.1	17.5	1.9
H	67.6	3.5	23.4	1.6	2.7	1.3
I	67.7	3.4	26.3	0.9	0.3	1.4
J	59.4	2.6	22.2	1.7	13.4	0.7
x̄	58.9	2.1	27.1	1.2	9.1	1.5
SE	2.48	0.34	2.08	0.14	2.07	0.23

Tr. = Trace; x = Mean; SE = Standard Error

populations herein reported and thus they include the potential for additional genetic variation. Nevertheless, the average monoterpene percentages for the hybrids were in good agreement with the parent-species values, with the exception of the Δ^3-carene concentrations. This compound was found at significantly higher concentrations in the hybrid and thus it may be anticipated that further sampling of *L. decidua* and *L. leptolepis* populations will show additional variance for that character. The added possibility that hybridity *per se* (or non-additive genetic variation) was responsible for the larger values does not seem consistent with our present biochemical knowledge of these compounds, but will require additional study for a final solution.

The close relationship of *L. sibirica* with *L. Gmelini* is shown by their similar monoterpene contents and distinguishing between these two species on this basis seems difficult. Both species have the same three major components; α-pinene, β-pinene and Δ^3-carene; and also the same minor constituents; camphene, myrcene and limonene. The amount of β-pinene was consistently higher (with the exception of one tree) for *L. Gmelini* on a tree-to-tree basis as were the average species values for limonene. The Δ^3-carene content (average for the species) was higher in *L. sibirica* but slight overlap occurred in the total range for the two species. Separation of these two species from *L. decidua* or *L. leptolepis* could be easily accomplished on the basis of terpene analysis, particularly in relation to quantitative amounts

Table 2. — Seasonal variation in monoterpene content in *L. sibirica*[1])

Tree	Date	α-pinene	Camphene	β-pinene	Myrcene	Δ³-Carene	Limonene
A	N	32.1	tr.	13.4	2.1	47.7	4.7
	J	26.0	1.0	12.7	2.0	52.7	5.5
B	N	21.5	tr.	13.1	2.2	59.4	3.6
	J	23.4	0.7	13.7	2.8	55.5	3.8
C	N	33.2	tr.	17.0	1.6	44.4	3.8
	J	33.4	1.6	16.4	2.2	42.5	3.9
D	N	34.4	tr.	15.7	2.3	43.8	4.2
	J	37.1	1.1	16.6	1.8	40.1	3.2
E	N	37.2	tr.	15.8	3.3	39.5	4.2
	J	34.7	1.7	14.1	1.8	44.6	3.0
F	N	44.7	tr.	15.6	3.2	31.2	5.2
	J	45.3	1.6	15.9	1.1	34.3	1.9
G	N	27.5	tr.	14.3	3.7	47.6	7.0
	J	26.0	1.0	12.5	2.8	53.1	4.6
H	N	23.3	tr.	12.7	2.7	56.6	4.8
	J	21.8	0.6	13.7	0.9	61.0	2.1
I	N	26.0	tr.	14.2	2.2	52.3	5.1
	J	26.6	1.2	14.0	3.3	49.5	5.4
J	N	31.3	tr.	13.1	3.0	47.8	4.7
	J	25.6	0.5	11.9	1.7	56.9	3.3
Correlation between collection dates							
r =		.916**	—	.786**	—.228^{NS}	—.844**	.190^{NS}
„t" test of differences between collection dates							
t =		.354^{NS}	—	.490^{NS}	1.858^{NS}	535^{NS}	2.152^{NS}

[1]) Collections made in November (N) 1966, and June (J) 1967. Correlation coefficients and t values significant at 1 percent level = *, at 5 percent level = **, non-significant = NS; trace amouts = tr.

of α-pinene and Δ³-carene. Such a distinction may be helpful in differentiating stands of European or Asiatic larch. Simak (1964) has discussed the separation of two groups of Euro-asiatic larch into: (1) the European larch group; and (2) the Siberian larch group. He was able to distinguish between these two groups on the basis of karyological techniques. Resin analysis may also be helpful in resolving this question; although additional studies among many provenances of the species will be necessary to define the variation range for terpene constituents.

The two species from the American Continent, *L. occidentalis* and *L. laricina*, form a third group on the basis of monoterpene analysis. Both have α-pinene, β-pinene and Δ³-carene as major resin constituents, with lesser amounts of myrcene, camphene and limonene. Separation of the American continent larches from the Euro-Asian groups may be made on the basis of Δ³-carene and α-pinene. The concentration of Δ³-carene was consistently higher for *L. Gmelini* and *L. sibirica*, while it is lacking or present at only small concentrations in *L. decidua* and *L. leptolepis*. In this respect and for other monoterpene constituents, *L. occidentalis* and *L. laricina* appear generally intermediate between the *L. decidua* — *L. leptolepis* group and the *L. sibirica* — *L. Gmelini* group.

An evaluation of seasonal differences was made with samples from *L. sibirica (Table 2)*. From this data it appears that while slight seasonal variation may be expected, the tree-to-tree differences are reasonably consistent. Statistical analysis of the *L. sibirica* data from the two collection dates showed no significant differences between dates when all trees were considered. A simple correlation between collection dates was significant for α-pinene (r — 0.916), β-pinene (r — 0.786) and for Δ³-carene (r = 0.844). The difference in seasonal values for myrcene and limonene were statistically significant at the .10 level when analyzed by the "t" test, but did not show positive correlation. The latter compounds were present in small amounts and may be subject to greater sampling error as well as increased environmental variance.

The correlation of diameter growth (last five-year increment) with monoterpene content is shown in *Table 3*. No significant correlations were observed; however, it should be noted that the comparison attempted may not properly define this relationship. More precise study of monoterpene biogenesis as related to physiological and genetic variance is needed before a final judgment can be reached.

In summary, the differences in monoterpene content between the American, European, and Asiatic larches were consistent enough to warrant additional investigation. A provenance evaluation of each species is needed, along with additional studies of inheritance and environmental control. The ultimate use of *Larix* resin analysis as a technique for hybrid identification appears promising for crosses between the three groups, but not for those within a group. The correlation between monoterpene content and other genetic or physiological factors such as growth rate, or insect and disease resistance will also be a subject for future investigations.

Abstract

A gas-chromatography analysis of resin for monoterpene constituents was conducted for six *Larix* species and one inter-species hybrid. The results indicate that three groups, with two species in each group, may be differentiated by this technique. These are: (1) *L. decidua* and *L. leptolepis;* (2) *L. Gmelini* and *L. sibirica*; and (3) *L. occidentalis* and *L. laricina*. The grouping was based principally on quantitative amounts of α-pinene and Δ³-carene. Seasonal variation was studied in *L. sibirica;* no statistically significant differences were observed between collection made in June and November. A simple correlation between growth rate and monoterpene content was non-significant for the three species studied in this manner. The taxonomic significance of the data, and the need for additional study are discussed.

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Table 3. — Correlation of growth rate and monoterpene content[1])

Species	α-pinene	Camphene	β-pinene	Myrcene	Δ³-Carene	Limonene
L. decidua	0.365	0.237	—0.389			—0,200
L. Gmelini	0.238		0.218	0.113	—0.250	0.161
L. leptolepis	—0.012	0.124	—0.022			

[1]) Simple correlation beween diameter growth and monoterpene content. Diameter growth was based on the most recent five-year increment; values were non-significant with 8 degrees of freedom.

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Versuche zur geographischen Variation bei der japanischen Lärche

Von HANS H. HATTEMER[1])

Vorbemerkungen

Im Jahre 1955 wandte sich Herr Prof. Dr. W. LANGNER, Direktor des Instituts für Forstgenetik und Forstpflanzenzüchtung in Schmalenbeck, mit der Bitte um Einsammlung des Saatguts für einen Herkunftsversuch mit der Japan-Lärche an Herrn Dr. IWAKAWA von der genetischen Abteilung der Japanischen Forstlichen Versuchsanstalt Meguro. Daraufhin wurden durch Herrn Dr. IWAKAWA die Erntebestände erkundet und das Saatgut bereitgestellt. Auf Empfehlung von Herrn Oberforstrat Doz. Dr. R. SCHMIDT, Gießen, stellte die Hessische Landesforstverwaltung auf Veranlassung von Herrn Landforstmeister ROSSMÄSSLER, die erforderlichen finanziellen Mittel für diese Arbeiten zur Verfügung. Im Jahre 1957 konnte in Schmalenbeck i. Holstein ein großer Teil des gelieferten Saatguts ausgesät werden. Weitere Saatgutproben gingen an Versuchsanstalten und Institute in mehreren Ländern.

Vf. ist Herrn Professor Dr. LANGNER sehr zu Dank verpflichtet für die großzügige Überlassung des Datenmaterials von Messungen an den verschiedenen Versuchen, für die vielfältige Unterstützung bei den Auswertungsarbeiten durch das technische Personal des Instituts und für die Bereitstellung eines Großteils der Geldmittel für die maschinelle Auswertung der Versuchsergebnisse.

Herrn Prof. Dr. K. STERN, Hann. Münden, der auch die Planung der beschriebenen Versuche besorgte, dankt Vf. Anregungen und Beratung bei den verschiedensten Problemen der Versuchsauswertung und der biologischen Interpretation der Befunde.

Die Auswertungsarbeiten erfolgten beim Institut für Forstgenetik in Schmalenbeck sowie am Lehrstuhl für Forstgenetik und Forstpflanzenzüchtung der Universität Göttingen in Hann. Münden und wurden durch Beihilfen des Bundesministeriums für Ernährung, Landwirtschaft und Forsten sowie der Deutschen Forschungsgemeinschaft unterstützt.

1. Einleitung

In den Jahren 1958 und 1959 wurden an verschiedenen Anbauorten in Japan, Europa und den Vereinigten Staaten Feldversuche mit den Absaaten 25 autochthoner Bestände *(Abb. 1)* von *Larix leptolepis* GORDON angelegt. Die Notwendigkeit solcher Herkunftsversuche wird seit dem Beginn forstgenetischer Forschung immer wieder betont und für *Larix leptolepis* von SCHOBER (1953, 1956) nachdrücklich herausgestellt. Über die Planung und Zielsetzung dieser Versuche berichtete LANGNER (1958). In der Bundesrepublik sind dies ein Baumschulversuch in Schmalenbeck (Holstein) und eine Serie von Versuchen kurzer oder mittlerer Laufzeit. Im Anschluß an LANGNER (1958) wird zunächst über die Ergebnisse des Baumschulversuchs berichtet. Hierbei wird auch auf die Ergebnisse anderer Baumschulversuche zurückgegriffen, die LANGNER von den Versuchsanstellern mitgeteilt wurden. Ein zweiter Teil dieses Berichts behandelt die Variation der aufgetretenen Frostschäden. Schließlich wird ein dritter Teil Ergebnisse über die Variation der Merkmale Baumhöhe, Brusthöhendurchmesser und Mortalität in der erwähnten Feldversuchsserie zum Inhalt haben; darin wird besonders auf die von Anbauort zu Anbauort wechselnden Versuchsergebnisse eingegangen werden.

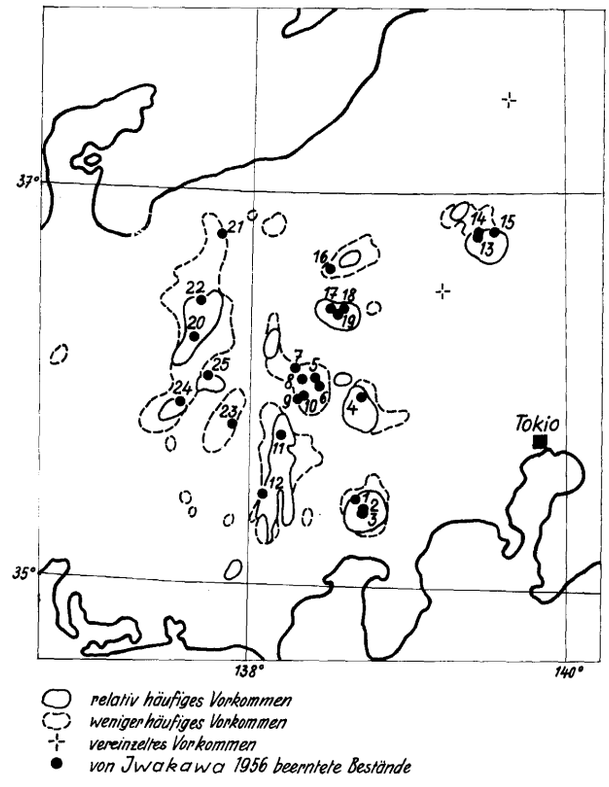

Abb. 1. — Geographische Lage der Erntebestände im natürlichen Verbreitungsgebiet.

[1]) Als Habilitationsschrift vorgelegt bei der Forstlichen Fakultät der Universität Göttingen in Hann. Münden am 21. 11. 1967. Derzeitige Anschrift des Verf.: Yale School of Forestry, New Haven, Connecticut 06511, U. S. A.