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Latitudinal Variation in Height and Phenology of Balsam Poplar

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Summary

Fifty clones from each of 4 provenances (Lat. 45° N to 53° N at Long. 90° W) were grown in 2 common garden tests at Lat. 48° N for 7 years and 5 years respectively. Provenance differences in height were mainly related to the period of shoot elongation, with the most southerly provenance (Lat. 45° N to 46° N) continuing elongation later and growing taller than northerly provenances. Clonal variation within provenances was also statistically significant, and broad-sense heritability estimates for height ranged from 0.04 to 0.19, depending upon degree of micro-site variation within provenance blocks. Variation in spring bud break was mostly attributable to differences among clones within provenances, was under moderate genetic control ($h^2 = 0.21$ to 0.47), and generally was not related to the amount of height growth.

Key words: Shoot elongation, bud break, genetic variance.

Introduction

Balsam poplar (*Populus balsamifera* L.) is a wide ranging, predominantly boreal species. In previous work with the species we have noted low genetic differentiation among latitudinal provenances (northern Wisconsin to Hudson's Bay) with respect to isozyme characteristics (FARMER et al., 1988a), preformed root primordia (FARMER et al., 1989), dormancy relations (FARMER and REINHOLT, 1985), relative growth rate and net assimilation rate (SCHNEKENBURGER and FARMER, 1989) and spring dehardening (WATSON, 1990). Most variation in stomatal density and transpiration rate is accounted for by clones within provenances, but leaf size decreases with an increase in latitude (PENFOLD, 1991). On the other hand, CHARRETTE (1990) observed a south-north increase in the rate of shoot growth cessation in response to short photoperiods. In most of the above characteristics there is substantial genetic variation within provenances. Here we report on the pattern of genetic variation in juvenile growth in the first phase of a long-term common garden experiment. In it we test the hypotheses that: (1) there is major latitudinal variation in shoot growth which is mainly due to provenance differences in photoperiodic response, (2) provenances from south of the test site will grow over a longer period at the test site than local or more northern material and (3) within-population genetic variance in growth will be as large as inter-population variance.

Methods

In 1982 and 1983, stem cuttings from approximately 50 juvenile trees (genets) were collected in each of the

following areas between Longitude 90° W and 91° W: northern Wisconsin (Lat. 45° N to 46° N), Thunder Bay, Ont. (48° N to 49° N), Pickle Lake, Ont. (50° N to 51° N), and the upper Severn River near Bearskin Lake (53° N to 54° N). Genets were selected at least 1 km apart to reduce the possibility of sampling more than 1 plant from a natural clone. Selection was thus not random, but neither was it biased with respect to observable tree characteristics. Cuttings were rooted in a greenhouse, then established in a nursery where several ramets of the resulting 50 clones per provenance were grown for 1 season.

In the spring of 1984 (year 1, the year of propagation), cuttings from these clones were rooted and grown in 750 ml SPENCER-LE-MAIRE containers filled with a peat-vermiculite mix. In July, they were transplanted in a field test the design for which is outlined in table 1 as test. I. The test site is an imperfectly drained 2.8 ha area in Thunder Bay (48° N) which prior to test establishment was occupied by a stand containing balsam poplar, willows (*Salix* sp.), aspen (*Populus tremuloides* MICHX.), black spruce (*Picea mariana* (Du Roi) K. Koch) and paper birch (*Betula papyrifera* MARSH.). Growth of natural balsam poplar and a lush ground cover of herbaceous species indicated that it was a suitable test site. The soil is loam to clay loam (20 cm to 30 cm) underlain by sands. Variation in elevation within the site is about 1 m.

The trees and shrubs were sheared in the winter of 1983 to 1984, and all debris was removed from the site. After regrowth was well underway in June 1984, the site was sprayed with glyphosate (12l/ha). Planting began about one month after treatment.

Each of the six replications in test I was a rectangle about 25 m x 100 m; 4 square provenance blocks were randomly located in each replication with the exception of 1 replication which contained only the 3 most southerly provenances. Three ramets of each of the 50 clones were randomly located within provenance blocks. Square spacing was 2 m x 2 m. After planting, vegetative competition (mostly grasses and sedges) was reduced for 3 years using hand equipment. Mortality was over 75% in some portions of 5 replications due to vegetative competition and poor drainage. These areas were deleted from the test; however no provenances were deleted from any replication and no clones were deleted from the test.

Total height was recorded annually for each plant from 1985 (year 2) to 1990. During the summers of 1986, 1987 and 1988, shoot elongation in a 10-clone sample from each provenance was observed. Measurements of terminal shoot length were made weekly on 2 ramets in each of 3 replications. These data were used to compute periodic rates (mm/day) for (1) the grand period of elongation in late

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Table 1. — Analysis of variance format and expected mean squares for balsam poplar common garden tests. Degrees of freedom are for 1990 measurements.

Source of variation	Degrees of Freedom		Expected mean squares
	Test I	Test II	
Replications (R)	5	2	$\sigma^2 + k\sigma^2_{RC} + k\sigma^2_{RP} + kpc\phi_R$
Provenances (P)	3	3	$\sigma^2 + k\sigma^2_C + krc\sigma^2_P$
Replication x Prov.	14	6	$\sigma^2 + k\sigma^2_{RC} + k\sigma^2_{RP}$
Clones/Prov. (C)	195	196	$\sigma^2 + k\sigma^2_C$
Repl. x Clones/Prov.	975	392	$\sigma^2 + k\sigma^2_{RC}$
Within (K)	654	823	σ^2

June (mid-season) and (2) a period in late July and August. An analysis of variance in rate took the form of those outlined in table 1. The date of bud break (leaves 1 cm out of bud on main stem) was recorded for all plants in three replications in the springs of 1985, 1986 and 1987.

In August 1986, 3 replications of the above design were planted as test II (Table 1) on an adjacent upland old field site. The first replication is on a uniform, deep well-drained loam; the other 2 are on sandy to sandy loam soils with rock outcrops. Most recently used for pasture, the site had been abandoned for at least a decade prior to planting. Site preparation included removing a few saplings of tamarack, mowing and spraying with glyphosate

in June 1986. Competition was reduced by mowing for 3 years after planting. Height was recorded every September from 1987 (year 2) to 1990.

Analyses of variance were completed using individual tree data and following the nested factorial design in table 1 which is described by MONTGOMERY (1976). Variance components were based on expected mean squares presented in table 1 after adjusting coefficients for inequalities in numbers of ramets within clones (SNEDECOR and COCHRAN, 1980). Broad-sense heritability (individual ramet basis) was estimated using pooled clone (σ^2_C), replication x clone (σ^2_{RC}) and within plot (σ^2_W) variances as follows:

Table 2. — Mean height (m) and analyses of variance in height of balsam poplar. Test I.

Item	Year 2	Year 3	Year 4	Year 5	Year 6	Year 7
Provenance						
Northern Wisconsin						
Mean	0.57	0.91	1.43	1.97	2.51	3.03
Range of clone means	0.34-0.80	0.53-1.23	0.82-1.79	1.42-2.68	1.75-3.10	2.13-4.06
Thunder Bay						
Mean	0.51	0.88	1.32	1.75	2.16	2.47
Range of clone means	0.32-0.75	0.57-1.28	0.94-1.67	1.28-2.29	1.54-2.81	1.28-3.23
Pickle Lake						
Mean	0.33	0.58	0.93	1.29	1.63	1.85
Range of clone means	0.14-0.56	0.34-0.93	0.62-1.22	0.85-1.73	0.92-2.18	1.16-2.57
Bearskin Lake						
Mean	0.33	0.59	0.94	1.22	1.51	1.73
Range of clone means	0.17-0.53	0.39-0.85	0.65-1.49	0.84-1.95	1.12-2.37	1.22-2.54
Source of variation	Mean Square	% of Variance	Mean Square	% of Variance	Mean Square	% of Variance
Replications	2.745	10	3.946	6	3.602	3
Provenances	8.821**	22	17.170**	20	31.787**	23
Repl. x Prov.	0.105**	<1	0.506**	3	0.687**	2
Clones/Prov.	0.091**	6	0.173**	4	0.294**	4
Repl. x Clones/Prov.	0.032	0	0.076	0	0.134	0
Within	0.043	62	0.109	67	0.193	68
Broad sense heritability		.09		.05		.05

**Statistically significant at the 0.01 level of probability.

Table 3. — Mean height (m) and analyses of variance in height of balsam poplar. Test II.

Item	Year 2		Year 3		Year 4		Year 5	
Provenance								
Northern Wisconsin								
Mean	0.85		1.08		1.57		2.27	
Range of clone means	0.72-1.04		0.91-1.27		1.29-1.88		1.73-2.70	
Thunder Bay								
Mean	0.56		0.77		1.10		1.49	
Range of clone means	0.34-0.72		0.58-0.97		0.83-1.43		1.11-1.86	
Pickle Lake								
Mean	0.53		0.77		1.04		1.39	
Range of clone means	0.25-0.74		0.40-1.04		0.70-1.38		0.93-1.85	
Bearskin Lake								
Mean	0.43		0.65		0.88		1.18	
Range of clone means	0.20-0.60		0.51-0.89		0.63-1.18		0.81-1.56	
Source of variation	Mean Square	% of Variance	Mean Square	% of Variance	Mean Square	% of Variance	Mean Square	% of Variance
Replications	22.832	36	36.516	43	114.86	51	310.314	49
Provenances	13.755**	30	14.273**	23	37.841**	23	102.696**	23
Repl. x Prov.	0.916**	6	1.226**	6	4.116**	7	16.274**	11
Clones/Prov.	0.071**	5	0.097**	5	0.174**	3	0.442**	3
Repl x Clones/Prov.	0.028	1	0.032	0	0.040	0	0.038	0
Within	0.024	22	0.034	22	0.064	15	0.168	14
Broad sense heritability								
	.18		.19		.19		.18	

**Statistically significant at the 0.01 level of probability.

Table 4. — Shoot elongation rates (mm/day) of balsam poplar during mid- and late-season. Test I.

Provenance	Period	Year 2	Year 3	Year 4
Northern Wisconsin	Mid-season	3	7	6
	Late-season	4	6	9
Thunder Bay	Mid-season	5	9	7
	Late-season	1	2	5
Pickle Lake	Mid-season	4	8	7
	Late-season	<1	1	1
Bearskin Lake	Mid-season	4	8	6
	Late-season	<1	<1	0

$$H^2 = \frac{\sigma^2_C}{\sigma^2_C + \sigma^2_{RC} + \sigma^2_W}$$

Results

In Test I, 53% of the ramets were alive in 1990, and an analysis of variance of arcsin transformations of survival percent for provenances indicated there were no significant provenance differences in survival. By 1990 (year 7), the Wisconsin provenance averaged 3.03 m in height (Table 2) almost twice the height of the northern provenances and 22% higher than the Thunder Bay provenance. This

ranking was established during the first full growing season (1985). By year 7, 28% of the total variance was accounted for by provenance. Changes in the scale of provenance variation with replication accounted for a significant replication x provenance interaction. While there was a wide range in clone means within provenances, by year 5 (Table 2) the clonal variance component accounted for only 2% to 3% of total variance. This resulted in low broad-sense heritability estimates (e. g. $h^2 = 0.04$ in year 7, Table 2).

Survival was higher (78%) on the upland old field site used for test II; one replication on a deep loam had 94% survival. The pattern of provenance variation in height was identical to that in test I (Table 3), but with the Wisconsin provenance performing relatively better than on the wetter site in test I. While there were major replication differences due to site quality, within plot variance (due to microsite variability) was less than in test I. This resulted in a higher broad-sense heritability estimate for height, ($h^2 = 0.18 - 0.19$) than in test I, though the percentage of total variance associated with clones was about the same in the 2 tests. As in test I, the range of clone means was wide (approximately 80 cm by year 5) within all provenances.

Shoot elongation of trees from the northern provenances ceased by early August while plants from Wisconsin continued growth until early September (Figure 1). To date, Wisconsin trees have not been damaged by frost despite their longer growing period. There were no significant differences in midseason shoot elongation rate among provenances or clones within provenance (Table 4), except

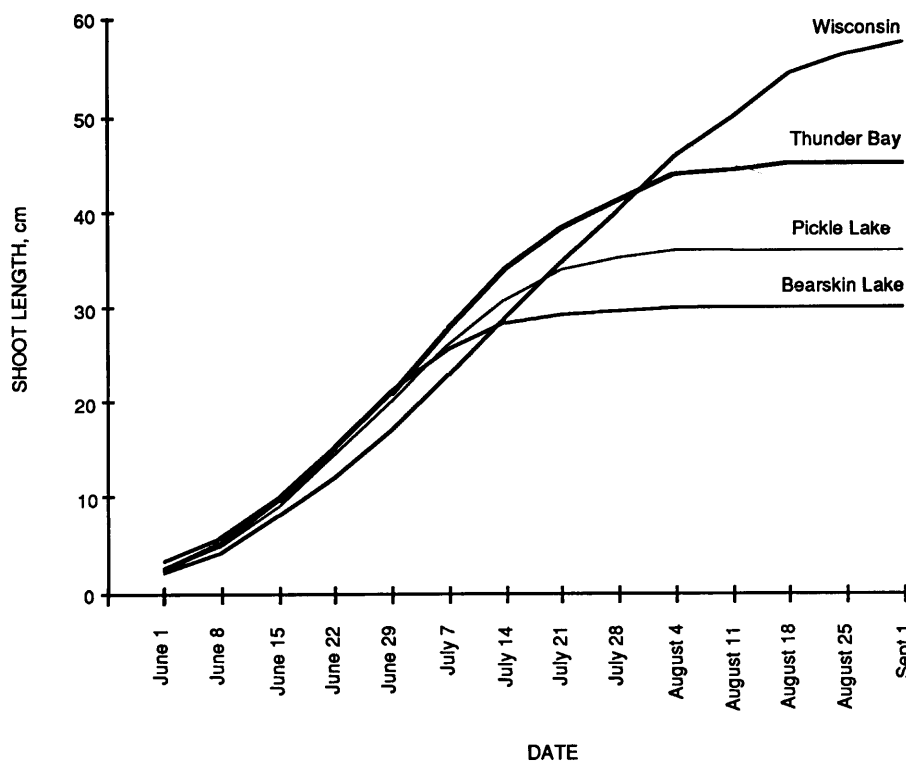


Figure 1. — Shoot elongation of balsam poplar provenances. Curves are based on 6 ramets from each of 10 clones per provenance measured in years 4 and 5.

for a 2 mm/day difference (significant at 0.05 level of probability) between Wisconsin and Thunder Bay provenances in 1986 (year 3). In late season, however, trees from Wisconsin had rates equal to or greater than their rates in midseason and significantly (0.05 level) greater than those of all the other provenances. In contrast, late season growth for the 3 northern provenances was significantly less than their midseason rates. Clonal variation in elongation rate was not statistically significant in the subsample of clones observed, though means were highly variable.

While there were some significant provenance differences in date of bud break (Table 5), except in year 4 they were small (<4 days). Trees from northern and southern provenances began growth earlier than local trees. Most of the genetic variance was accounted for by clones within provenances (18% to 39%, Table 5), and this is reflected in relatively high broad-sense heritability estimates. Correlation analysis using clone means revealed that there was no relationship between time of bud break and 7 year height in all but one provenance: the correlation coefficient for the Thunder Bay provenance was -0.30 and statistically significant. Coefficients of correlation between bud break dates among the 3 observation years ranged from 0.08 to 0.69.

Discussion

Provenance effects were similar in pattern to those now observed in many north temperate and boreal species (e. g. CLAUSEN et al., 1981; GARRETT et al., 1973; MORGENSTERN and MULLIN, 1990; FURNIER et al., 1991). Generally material moved south exhibits less growth than local material, and plants moved north of origin grow more than local trees. This type of response is directly related to latitudinal

differences in photoperiodic response, which has been demonstrated in other poplar (SYLVEN, 1940; PAULEY and PERRY, 1954). In many studies this relationship is modified by longitudinal differentiation and climatic variables not directly related to geographical coordinates. In our study the relationship is more straightforward since our latitudinal transect was uncomplicated by altitudinal or maritime climatic effects. Thus differences in the elongation period, rather than rates during the main period of growth, resulted in Wisconsin trees being 22% taller than local Thunder Bay trees by year 7 in test I and 52% taller by year 5 in test II. The difference increased over time in both tests. Substantially larger provenance differences were observed in some replications where site was less a limiting factor. For example, in replication I of test II Wisconsin trees were 82% taller on average than local trees. No frost damage was observed in the southern material during juvenility (<10 years) when trees would be expected to be most susceptible.

Though most of the genetic variance in height was related to provenance, the range of clone means within individual provenances was broad (i. e. commonly 60% to 70% of provenance means). However, relatively high within-plot variances resulted in broad-sense heritability estimates lower than those reported by FARMER et al. (1988b) for Thunder Bay material and by RIEMENSCHNEIDER et al (1992) for upper Great Lakes populations. Both of these studies were conducted under more uniform cultural and site conditions. RIEMENSCHNEIDER et al. (1992) further observed more within-population than among-population variance in material from Minnesota, Michigan and Wisconsin. In brief, our first 2 hypotheses related to early growth (see introduction) are supported by test data, while results are ambiguous with respect to the third.

Table 5. — Days from April 15 to budbreak date in balsam poplar. Test I.

Item	Year 2	Year 3	Year 4
Provenance			
Northern Wisconsin			
Mean	15 a***	14a	7c
Range of clone means	10 - 18	9 - 20	3 - 15
Thunder Bay			
Mean	16a	15a	13a
Range of clone means	10 - 23	10 - 22	4 - 20
Pickle Lake			
Mean	15a	15a	11b
Range of clone means	9 - 19	9 - 21	4 - 24
Bearskin Lake			
Mean	13b	12b	8c
Range of clone means	7 - 19	7 - 18	3 - 16

Source of variation	Mean Square	% of Variance	Mean Square	% of Variance	Mean Square	% of Variance
Replications	102.65	1	41.80	0	445.40	3
Provenances	246.77**	4	561.07**	7	1700.90**	14
Repl. x Prov.	23.62	<1	162.45	6	22.08	<1
Clones/Prov.	33.60**	23	41.01**	18	102.01**	39
Repl x Clones/Prov.	10.04	0	17.49	6	12.69	0
Within	10.97	70	14.64	63	16.90	44
Broad sense heritability		.25		.21		.47

**Statistically significant at the 0.01 level of probability.

***Provenance means with different letter suffixes are significantly different at the 0.05 level of probability.

In general provenance variation in bud break date followed a pattern which was observed in our study of balsam poplar dormancy (FARMER and REINHOLT, 1985) and in several northern studies (see WORRALL, 1983, for review), with trees from northern sources beginning growth earlier than local trees. Using data from his work with *Abies amabilis* and *A. lasiocarpa* WORRALL has interpreted this response in terms of genetic differences in threshold temperature and heat sum requirements. Our data differ from previous observations in that in 1987 (year 4), when bud break averaged 4 days earlier than in cooler years, the most northern and southern provenances began growth at about the same time. The relatively low correlations ($r = 0.4$ to 0.6) among clone means from year to year suggest that patterns of bud break vary somewhat with spring temperature regime.

While most of the variation in time of growth initiation was associated with clones within provenance (10 days to 12 days) these clonal differences had essentially no relationship to variation in shoot length. However, this variation in bud break time may have adaptive value in that it allows survival of some genotypes following hard late spring freezes, i.e., has a genetic buffering effect. WARSON (1990) has already observed that there is little genetic variation in frost resistance of balsam poplar during de-hardening, except that associated with differences in phenology.

The results of this study differ substantially from most of the previous findings noted above using the same population samples. It appears that, with the exception of

leaf size, only timing of shoot elongation, which adapts material to the local frost free period, exhibits much genetic differentiation among provenances. Within provenances there exists enough variation in this characteristic to allow rapid adaptation of populations to long-term changes in the frost free period and for survival under the year-to-year fluctuations (i.e. environmental uncertainty) typical of boreal conditions.

At present the low commercial value of balsam poplar precludes planting and the opportunity for increasing yield via selection. However, there is some interest in the hybrid of *P. deltoides* and *P. balsamifera* for intensive plantation culture under boreal conditions. In developing such hybrids, it should be useful to first select adapted parents which have shoot growth characteristics superior to average local stock. Results of this study suggest that a combination of provenance and individual clone selection prior to hybridization will be useful.

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Buchbesprechungen

Die Fichte. Band II/3: Waldbau — Ökosysteme — Urwald — Wirtschaftswald — Ernährung — Düngung — Ausblick. Von H. SCHMIDT-VOGT unter Mitarbeit von St. A. DYRENKOV (†), F. H. EVERS, H.-A. GUSSONE, J. I. MAN'KO, J. PARDE und H. THOMASUS. 1991 Verlag Paul Parey, Hamburg und Berlin. ISBN 3-490-09616-5. XXIII und 781 Seiten mit 497 Einzeldarstellungen in 342 Abbildungen und 105 Übersichten. 25,5 cm × 17 cm. Gebunden DM 296,—.

Der Abschlußband der umfangreichsten Fichtenmonographie liegt mit diesem Buch vor. Es ist das 4. Buch oder der 3. Teilband (II/3) des 2. Bandes und befaßt sich mit dem Waldbau in folgenden Kapiteln: Fichten-Wald-Ökosysteme, Fichten-Urwälder der Erde (Beschreibung vieler Ur- und Naturwälder, einschließlich Naturwaldreservate aus dem ganzen Verbreitungsgebiet der Fichten; dieses Kapitel enthält einen ca. 70 Seiten umfassenden Bildteil), Wirtschaftswald mit Fichte (u. a. Verjüngung der Fichte, Bestandespflege, Anlage und Bewirtschaftung von Fichten-Holzproduktionsanlagen, Umwandlung von Fichten-Reinbeständen in Mischbestände, Stabilisierung von Fichtenbeständen gegen Sturm und Schneebelastung und Behandlung geschädigter Bestände sowie waldbauliche Maßnahmen in erkrankten und immissionsbelasteten Fichtenwäldern), Ernährung und Düngung der Fichte (mit einem besonderen Abschnitt über die Kalkung und Nährelementzufuhr zur Minderung von Waldschäden). Im Ausblick geht der Autor u. a. auch auf die Auswirkungen der "neuartigen Waldschäden" und einer Klimaänderung ein.

Der Autor und seine Mitarbeiter haben ein sehr umfassendes Werk in der gleichen gründlichen Bearbeitung, wie es die 3 vorangegangenen Bände bereits gezeigt haben, vorgelegt. Insgesamt sind in allen 4 Bänden ca. 13 000 Veröffentlichungen ausgewertet worden. Damit stellt dieses Buch zusammen mit den anderen 3 Bänden ein einzigartiges Dokument des Wissens über die Fichten dar. Es ist gleichzeitig die Krönung des Lebenswerkes von Prof. SCHMIDT-VOGT, der wohl wie kein anderer sich dieser Baumart verbunden fühlte. Wir schulden ihm Dank und Anerkennung. Wir, das sind alle, die als Praktiker, Wissenschaftler, Naturschützer, Landesplaner oder Interessierte mit der Fichte zu tun haben.

Title: The Spruce. Volume II/3.

This 4th volume deals with the silviculture of spruce forests subdivided into 4 chapters: Spruce forest ecosystems, origin forests of spruces (descriptions of many virgin forests, including natural reserves of Europe, Asia, and North America with a special part of 70 pages containing pictures and profiles), management of spruce forests, and fertilization. (German, unfortunately no English summaries are given).

H.-J. MUHS (Grosshansdorf)

Eichenwälder im nordöstlichen Mexiko. Schriften aus der Forstlichen Fakultät der Universität Göttingen und

der Niedersächsischen Forstlichen Versuchsanstalt, Band 103. Von B. MÜLLER-USING. 1991. J. D. Sauerländer's Verlag, Frankfurt am Main. 263 Seiten mit 64 Abbildungen und 46 Tabellen. Kartoniert DM 49,—.

Wenn auch dieses Buch im Hinblick auf die Nutzbarmachung und die waldbauliche Behandlung der Eichenwälder, die im nordöstlichen Mexiko teils in Mischung mit Kiefernarten den überwiegenden Teil der Naturwaldfläche ausmachen, abzielt, so enthält es für den Forstgenetiker eine Fülle von Informationen über 15 dort häufig vorkommende Weiß- und Roteichenarten. Das Buch ist in 4 Kapitel gegliedert: Eichenwaldtypen der östlichen Sierra Madre, Dendrometrische Bearbeitung zweier Eichenarten (*Quercus laceyi*, *Q. rysophylla*) aus dem submontanen Eichenwaldgürtel, zur Entwicklungsrhythmik von Eichenbäumen und -keimlingen im Jahresverlauf, Verjüngungsdynamik und waldbauliche Behandlungskonzepte für Eichenwälder in Nordost-Mexico. Für jedes Kapitel bilden eingehende Studien und Untersuchungen die Grundlage, die der Autor während seines Aufenthaltes in Linares, Nordost-Mexiko, zusammen mit Postgraduierten durchgeführt hat. Dadurch erhält das Buch einen gut fundierten Charakter.

Title: Oak forest in north-eastern Mexico. The author gives a well based study about the types of oak forests in the eastern Sierra Madre, the dendronomic data about 2 oak species (*Quercus laceyi*, *Q. rysophylla*), developmental rhythmicity of adult oak trees and seedlings, dynamics of regeneration and silvicultural treatment of the oak forests. (German with English summary).

H.-J. MUHS (Grosshansdorf)

Alte liebenswerte Bäume in Deutschland. Von H.-J. FRÖHLICH. 1989. Cornelia Ahlering Verlag, Hamburg. ISBN 3-926600-02-0. DM 139,—.

Im Vorwort des Buches weist der Autor, Professor und Landesforstmeister a.D. darauf hin, daß der Baum hier mehr als Symbol denn als Objekt genetischer und züchterischer Arbeit gesehen werden soll. Die besondere Liebe des Autors zu alten Bäumen sowie der Aufruf zu ihrer Erhaltung hat dieses Buch entstehen lassen, das 193 alte Bäume meist mit mehreren, mehrfarbigen Bildern vorstellt. Im informativen Text versucht der Autor, die Lebensumstände des Baumes und seine Bedeutung aus der Geschichte zu ergründen. Manchmal sind Angaben über das Alter des Baumes möglich, in den meisten Fällen jedoch war der Autor auf Schätzwerte angewiesen. Als Beispiel sollen hier die wohl ältesten Bäume in Deutschland kurz skizziert werden.

Nr. 56: Femeeiche in Erle, 11 m hoch, 1250 cm Umfang, 8 m Kronendurchmesser ca. 1000 Jahre alt, hat mehrere Brände überlebt, ist hohl und muß gestützt werden.

Nr. 67: Gerichtseiche Gahrenberg im Reinhardswald, 18 m hoch, 850 cm Umfang, 18 m Kronendurchmesser und ca. 1300 bis 1400 Jahre alt.