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Stand and Seed Source Variation in Peroxidase Isozymes of Quercus rubra L.[1])

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Summary

Variability in *Quercus rubra* foliar peroxidase isozymes was studied in 11 seed sources and 3 local stand collections. Analysis of isozyme frequency distributions by Berry's measure of distinctiveness, D^2, revealed significant differences for all but one (Michigan vs Pennsylvania) of the 55 pair-wise seed source comparisons. All sources could be tentatively differentiated from one another based on the presence or absence of one or more isozyme bands, or by large frequency differences between one or more isozymes.

Berry's D^2 also indicated the existence of significant differences in isozyme frequency distributions between trees (i. e. between four half-sib families) sampled in each of 3 Ohio red oak stands, as well as between stands.

Key words: northern red oak, isozymes, peroxidase, geographic variation.

Zusammenfassung

Bei 11 Provenienzen und 3 örtlichen Herkünften von *Quercus rubra* wurde die Variabilität der Blatt-Peroxydase-Isoenzyme untersucht. Eine Analyse der Häufigkeitsverteilung der Isoenzyme mit der Charakterisierungsmethode von Berry, D^2, zeigte signifikante Unterschiede für alle der 55 paarweisen Herkunftsvergleiche bis auf einen (Michigan gegenüber Pennsylvania). Alle Herkünfte konnten im Versuch voneinander durch das Vorhanden- oder Nichtvorhandensein eines oder mehrerer Enzymbänder oder die sehr unterschiedlichen Häufigkeiten bei einem oder mehreren Isoenzymen unterschieden werden.

Berry's D^2 zeigte außerdem die Existenz signifikanter Unterschiede in der Isoenzymhäufigkeitsverteilung sowohl zwischen Bäumen (z. B. zwischen 4 Halbgeschwisterfamilien), als Stichprobe aus je 3 *Quercus rubra* Beständen in Ohio, als auch zwischen Beständen, an.

Introduction

The analysis of genetic variation among and within forest tree populations traditionally has been approached by studying quantitative aspects of inheritance and natural variation for a wide variety of physiological and morphological characters (Libby *et al.* 1969). The application of electrophoretic techniques to such analyses overcomes many of the inherent disadvantages in traditional methods of characterizing genetic variability within and among tree populations by permitting precise determinations of allelic variation.

Many recent isozyme studies have focused on gymnosperms (e. g. Yeh and El-Kassaby 1980, Feret 1974, Mitton *et al.* 1977); considerably less work has been performed with hardwoods. Peroxidase inheritance patterns have been determined in *Ulmus* (Feret and Stairs 1971), *Populus* (Guzina 1978, Mitton and Grant 1980) and *Liriodendron* (Houston and Hood 1982). Kim (1979) has identified the mode of inheritance for leucine aminopeptidase and acid phosphatase isozymes in *Fagus*. Mitton and Grant (1980) also studied phosphohexose isomerase and glutamate dehydrogenase inheritance in *Populus*.

Developmental and inter-specific variability in several isozymes has also been reported for *Quercus* (Mayberry and Feret 1977, Tobolski 1978, Olsson 1975). Studies of intraspecific variation in enzyme systems of *Robinia* (Huang *et al.* 1977), *Betula* (Payne and Fairbrothers 1973), *Prunus* (Lewis and Cech 1969) and *Juglans* (Clarkson *et al.* 1974)

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demonstrated the power of the electrophoretic technique to distinguish between seed sources of forest trees. The elegant studies of the breeding system of several *Eucalyptus* species (Brown *et al.* 1975, Phillips and Brown 1977, Moran and Brown 1980) indicate the potential for this method for the isolation of gene markers, and the analysis of mating system and genetic population structure in North American hardwoods.

The study reported here represents a preliminary analysis of isozyme (peroxidase) variability among seed sources and local stand collections of *Quercus rubra* growing in Ohio. Techniques of selection for growth rate and form have not been notably effective in *Quercus* and other hardwood species. Basic information concerning the genetic structure of stands where selection is practiced could materially assist in the design of applied tree improvement programs.

Materials and Methods

Foliar tissues were collected from two different studies for analysis:

(1) NC-51 northern red oak provenance test

During the first week of July, fully expanded leaves were collected from 12 trees each of 11 different seed sources in the NC-51 northern red oak provenance test planted at Apple Creek, Ohio *(Figure 1).* Variability in growth and other characteristics in this study were reported by Kriebel *et al. (1976).* Sample trees were 11 to 13 years old. Leaf samples were stored at -20^0 C within two hours of collection.

(2) Ohio selected northern red oak stands

In addition to the provenance samples, seed was collected in the last week of September from four trees in each of three selected red oak stands in northwestern Ohio *(Figure 2).* The stands are part of a statewide genetic improvement program in this species. Each stand was a minimum of 100 years old, and ranged in size from 10 to 16 hectares. Seed trees were separated by a minimum of 50 meters.

After stratification for 90 days at 3^0 C, seed was sown (four per 3.8 liter pot) in a sand-soil-peat moss mixture (1:1:1) and seedlings grown in the greenhouse under a 14-hour photoperiod. Fully expanded leaves were sampled from 24 seedlings per family at 90 days after germination.

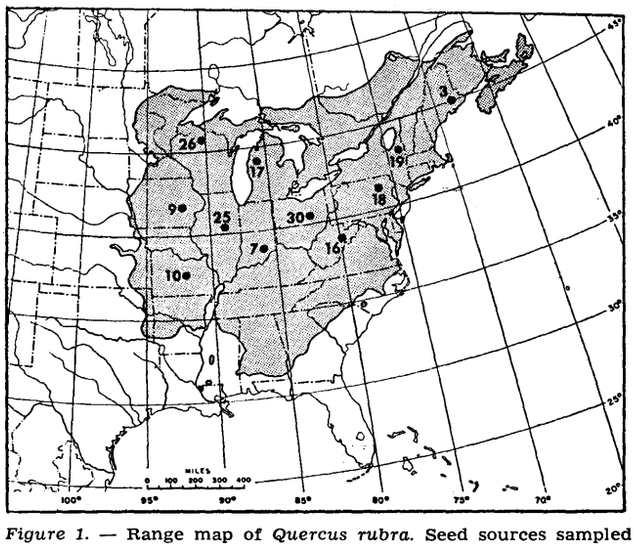

Figure 1. — Range map of *Quercus rubra.* Seed sources sampled in this study are designated by black dots and accompanying source numbers.

Figure 2. — Locations of Ohio *Quercus rubra* stands sampled in this study. Solid dots designate additional selected red oak stands utilized in Ohio's forest tree improvement program.

Peroxidase was extracted from 0.4 g tissue (F.W.) at 4^0 C by a 10-second homogenization in 3 ml 0.1M Tris-HCl buffer, pH 8.0, containing 0.006M ascorbate, 0.007M cysteine-HCl, 0.5M sucrose and 0.5 percent (v/v) Tween 80. Insoluble polyvinyl-pyrrolidone (0.4 g in 3 ml extract buffer) was added immediately after homogenization. After mixing, extracts were centrifuged at 12,000 × G for 15 minutes, decanted, and recentrifuged at 40,000 × G for 60 minutes. The clear supernatant was stored at -20^0 C until electrophoresis. Separations were performed anodally at 4^0 C on 7.5 percent polyacrylamide gels, pH 8.9, according to Davis (1964). A current of 3 ma was applied to each gel for 90 minutes; reservoir buffer was 0.1M Tris-glycine, pH 8.3. Gels were stained for peroxidase according to Scandalios (1964), and the R_f for each isozyme band was calculated relative to a bromophenol blue front marker. Two replicate samples were run for each extract. R_f values were repeatable to within $\pm$ 0.5 R_f units.

Analysis of peroxidase isozyme frequency differences within and among Ohio stands, and among seed sources, was accomplished using Berry's measure of divergence (D^2) (Berry 1963) as extended by Muhs (1974).

Results and Discussion

(1) *NC-51 Provenance Test*

Seventeen isozymes were characterized, of which 14 were subjected to analysis. Of these 14, each seed source had 8 to 12 *(Table 1);* no single isozyme was source-specific. Analysis by Berry's measure of distictiveness, D^2 *(Tale 2),* indicated no significant differences in frequency distributions of all isozymes (pooled) for only one (Michigan versus Pennsylvania) of the 55 pair-wise source comparisons. Samples from all other sources differed significantly from each other at the 0.05 or 0.01 level. In *all* cases,

Table 1. — Isozyme frequencies of foliar peroxidases in 11 seed sources of *Quercus rubra* L.

Seed Source (Map No.)	Isozyme Band (R_F x 100)													
	12	16	18	23	26	29	31	33	37	41	44	47	49	53
ME (3)[b]	0.92	0.08	0.25	0.50	1.00	0.50	---	0.25	0.50	---	0.50	---	0.33	---
IN (7)	1.00	0.25	0.25	0.58	0.75	0.25	---	---	0.08	---	0.92	0.67	---	---
IA (9)	0.83	0.33	0.50	0.50	0.75	0.33	---	---	0.17	0.17	0.67	---	0.42	---
MO (10)	1.00	0.17	0.42	0.67	0.92	0.50	---	---	0.17	0.67	0.08	0.67	---	---
WV (16)	---	1.00	---	---	0.50	0.50	0.75	0.25	---	0.17	---	0.67	0.50	---
MI (17)	---	1.00	0.42	0.25	---	0.75	0.83	0.08	---	0.50	---	---	0.75	0.58
PA (18)	---	1.00	0.33	---	0.25	0.50	1.00	0.17	---	0.33	---	---	0.83	0.58
NY (19)	0.67	0.92	0.08	0.25	---	0.92	0.75	0.25	---	0.50	0.50	0.50	0.33	0.17
IL (25)	1.00	---	---	0.25	1.00	0.58	---	---	0.50	0.58	0.42	0.42	0.08	---
WI (26)	---	1.00	0.17	0.33	0.67	---	0.92	0.67	---	0.25	0.33	0.75	---	0.08
OH (30)	1.00	0.83	---	0.17	0.58	0.67	0.83	---	0.42	---	0.83	---	0.50	0.67

[a] n = 12 trees/source.

[b] Source identification: ME (Maine), IN (Indiana), IA (Iowa), MO (Missouri), WV (West Virginia), MI (Mchigan), PA (Pennsylvania), NY (New York), IL (Illinois), WI (Wisconsin), OH (Ohio).

Table 2. — Berry's D^2 analysis of foliar peroxidase frequencies in 11 seed sources of *Quercus rubra* L.

Seed Source	(Map) No.	IN (7)	IA (9)	MO (10)	WV (16)	MI (17)	PA (18)	NY (19)	IL (25)	WI (26)	OH (30)
ME	(3)	0.5627**	0.1370*	0.7223**	2.1950**	2.7172**	2.2709**	1.5401**	0.4466**	2.3022**	1.0974**
IN	(7)		0.3862**	0.4356**	2.2973**	3.1457**	3.3760**	1.4632**	0.5581**	1.9438**	0.9466**
IA	(9)			0.5287**	1.8056**	1.8410**	2.0768**	1.2081**	0.5709**	1.9108**	0.9305**
MO	(10)				2.1136**	2.7306**	3.0618**	1.2885**	0.2379**	2.0721**	1.8364**
WV	(16)					0.8018**	0.5649**	0.7507**	2.3545**	0.5586**	1.8271**
MI	(17)						0.0805	0.6664**	3.3398**	1.4175**	1.6543**
PA	(18)							0.9565**	3.4040**	1.1790**	1.5218**
NY	(19)								1.8451**	1.0913**	0.9192**
IL	(25)									2.6446**	1.4780**
WI	(26)										2.1052**

* Significant at 0.05 level (d = 0.1153).
** Significant at 0.01 level (d = 0.1803).

however, sources could be tentatively differentiated from one another based on the presence or absence of one or more isozyme bands, or by large frequency differences between one or more isozymes.

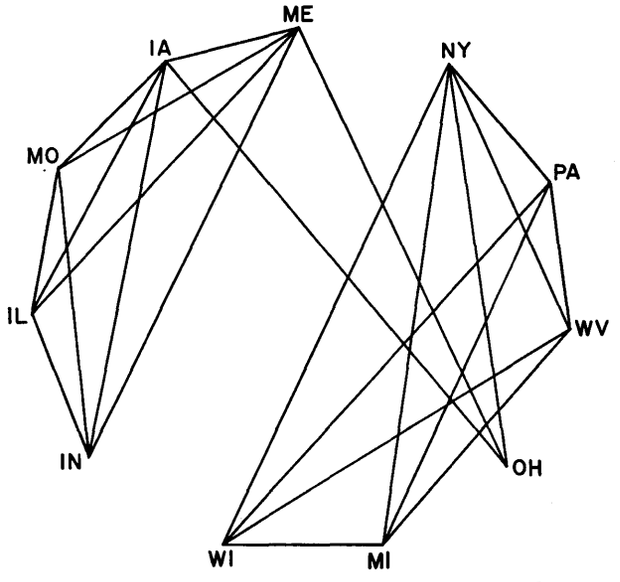

Figure 3. — Relationships between *Quercus rubra* seed sources based on relative size of Berry's D^2 values (*Table 2*). Lines connect source pairs for which the comparison yielded a D^2 value less than the mean D^2 for each source compared with all others. Non-reciprocal minimum D^2 value comparisons are not shown.

In this regard, inspection of isozyme distribution patterns indicated the existence of regional groupings of sources based on presence, absence, or frequency of occurrence of several isozymes. Isozymes 12 and 37 were not detected in samples from the north-central and Appalachian portions of the species range, while 16, 31, 33 and 53 were present in samples from the same areas, but absent or at low frequencies in those from the southwestern portion of the range.

If D^2 values are viewed as a relative measure of the difference between sources, then the smaller the D^2 value for a given comparison, the more similar are the sources. When each source is thus compared with all other sources, and grouped with those sources whose pairwise comparisons result in D^2 values less than the mean D^2 value for that source compared with all others, two distinct regional groupings result: (1) Maine, Iowa, Missouri, Illinois, Indiana, and (2) Wisconsin, Michigan, West Virginia, Pennsylvania, New York as depicted in *Figure 3*. This grouping is roughly equivalent to that determined by visual inspection of frequencies for isozymes 12, 16, 31, 33, and 53, but is formulated on the basis of comparisons involving all 14 isozymes studied. It also corresponds well to the regional grouping of provenances noted by Kriebel *et al.* (1976) for time of flushing in this species. The clusters noted in this study may have no biological significance however, as evidenced by the grouping of the Maine source with those from the southwestern portion of the species range. Alternatively, a relationship may exist, but is not apparent in

the context of this study. As indicated by *Figure 3*, Ohio could be placed in either group by this measure, having an isozyme complement that was partially characteristic of both groupings.

(2) *Ohio Selected Stands*

(a) Between trees within stands

Fifteen isozymes were characterized *(Table 3)* and analyzed by Berry's D^2. This measure indicated the existence of significant differences in isozyme frequency distributions between trees (i.e. between half-sib families) for 10 to 15 isozymes in each stand. Comparisons of the four families in each stand based on mean D^2 values for all isozymes (pooled) are presented in *Table 4*. Only one overall family comparison (2 vs 4 in stand 2A) was not significant, demonstrating the high level of variability extant in the stands for this character. Excluding those isozymes which were not present in a stand, only four (12, 16, 18, and 44 in stand 1A) demonstrated no significant differences across all family comparisons. All others had at least one significant comparison ($\bar{X}$ = 3.3) for each of the 15 isozymes.

Isozyme presence/absence and/or relative frequency may also have some potential for distinguishing between individual seed lots. In several cases (e.g. isozymes 16 in stand 2A, 20 in stand 14A, 26 and 46 in stands 2A and 14A, 41 in stand 14A, etc.), families could be identified or tentatively differentiated from other families in the stand sample by these measures. Given the cyclic nature of red oak flowering and seed production however, a determination of year-to-year variation in isozyme frequency distribution patterns in progenies from the same tree would be advisable. The lower D^2 estimates indicate the population represented in stand 1A may be less variable genetically than those of the other stands.

(b) Among Ohio stands

Data for the four families in each stand were pooled for these analyses *(Table 5)*. Only one isozyme, 35, was not significantly different in all stand comparisons by Berry's D^2. All others demonstrated at least two significant differences. Some isozymes appeared to be stand-specific (e.g. 37 and 53), while others were present at medium to high frequencies in one or two stands and missing or at low frequencies in the others (e.g. 23 and 33). Mean D^2 values were significant at the 0.01 level for all three comparisons.

No clear geographic pattern was evident for isozyme distribution. In terms of relative size of average D^2 values (disregarding statistical significance), stand 1A was more closely related to 14A (the two most widely separated stands) than to 2A. Pairwise comparisons for 1A vs 2A and 2A vs 14A produced very similar D^2 estimates, As was

Table 4. — Analysis of *Quercus rubra* foliar peroxidase frequencies within three Ohio stands by Berry's measure of distinctiveness (D^2).

Stand	Family Comparison 1 vs 2	1 vs 3	1 vs 4	2 vs 3	2 vs 4	3 vs 4	Avg.
1A	0.3196**	0.5285**	0.3365**	0.1159**	0.1015**	0.3404**	0.2904
2A	1.9546**	1.7947**	1.7283**	0.5774**	0.0312	0.4176**	1.0840
14A	0.7056**	0.9763**	1.6165**	0.6965**	0.3559**	0.9351**	0.8810

** Significant at 0.01 level (d = 0.0865).

Table 5. — Analysis of *Quercus rubra* foliar peroxidase frequencies among three Ohio stands by Berry's measure of distinctiveness (D^2).

Isozyme (R_f x 100)	Stand Comparison 1A vs 2A	1A vs 14A	2A vs 14A
12	1.0758**[a]	0.1826**	0.3347**
16	0.6575**	0.9410**	0.0039
18	0.0421	0.7758**	0.3911**
20	0.3683**	0.0078	0.6079**
23	2.4759**	-0.0195	2.5907**
26	0.7441**	0.1136*	0.2373**
29	1.3155**	0.0055	1.7171**
33	3.5464**	0.0479	4.6013**
35	-0.0185	-0.0155	-0.0202
37	0.9326**	-0.0108	0.7471**
41	0.0038	0.7111**	0.4675**
44	1.4161**	0.7818**	0.0709*
47	0.0711*	0.0711*	-0.0208
49	1.1501**	-0.0167	1.2937**
53	1.3232**	-0.0208	1.3232**
$\bar{D}^2$ =	1.0069**[b]	0.2370**	0.9564**

[a] * = significant at 0.05 level (d = 0.0591).
** = significant at 0.01 level (d = 0.1171).
[b] ** = significant at 0.01 level (d = 0.0216).

Table 3. — Isozyme frequencies of *Quercus rubra* L. foliar peroxidases in three Ohio stands.[a]

Stand No.	Family No.	Isozyme Band (R_f x 100) 12	16	18	20	23	26	29	33	35	37	41	44	47	49	53
1A	1	1.00	----	----	0.46	0.79	1.00	0.62	0.38	0.12	----	----	0.50	----	0.08	----
	2	1.00	----	0.04	0.08	0.92	0.96	0.46	----	0.25	0.25	0.08	0.75	0.17	----	----
	3	1.00	0.04	----	0.17	1.00	0.83	0.29	----	0.54	0.38	0.38	0.54	----	----	----
	4	1.00	----	----	0.50	0.92	0.92	0.46	----	----	0.25	0.12	0.62	0.38	0.04	----
	$\bar{X}$	1.00	0.01	0.01	0.30	0.91	0.93	0.46	0.09	0.23	0.22	0.15	0.60	0.14	0.03	0.00
2A	1	0.04	0.92	----	0.21	----	0.17	0.75	1.00	0.67	----	----	0.04	----	0.96	0.12
	2	1.00	----	0.12	----	0.54	0.67	1.00	0.79	----	----	0.25	----	0.12	0.33	0.67
	3	1.00	0.04	----	0.08	----	0.79	1.00	0.96	0.17	----	0.12	0.29	0.58	----	0.17
	4	0.96	----	0.08	----	0.29	0.71	1.00	0.83	----	----	0.46	----	0.33	0.42	0.25
	$\bar{X}$	0.75	0.24	0.05	0.07	0.21	0.58	0.94	0.90	0.21	0.00	0.21	0.08	0.26	0.43	0.30
14A	1	1.00	0.33	0.58	0.88	0.88	0.29	0.04	----	0.04	----	0.92	----	----	----	----
	2	1.00	0.08	0.25	0.46	1.00	0.96	0.21	----	0.38	0.12	0.42	0.38	0.46	----	----
	3	0.79	0.67	0.25	----	0.96	1.00	0.50	0.08	----	0.25	0.92	----	0.17	0.08	----
	4	1.00	0.17	----	0.17	0.83	1.00	0.79	0.04	0.38	0.33	----	0.33	0.42	----	----
	$\bar{X}$	0.95	0.31	0.27	0.38	0.92	0.81	0.38	0.03	0.20	0.18	0.54	0.18	0.26	0.02	0.00

[a] N = 24 seedlings/family, 96 seedlings/stand.

the case for trees (families) within stands, variation appeared to be at random. This variation pattern is not unlike that noted by KRIEBEL *et al.* (1976) for growth rate in red oak, in which genetic control of this complex trait appears to be more closely related to stand and family than to geographic area within the species distribution.

As only 12 trees per source were sampled in the provenance study, it is probable that not all of the genetic variability in this character was identified. A more intensive sampling of a limited area (three Ohio stands) of the species range identified two more isozymes (20 and 35) while failing to detect isozyme 31. Isozymes not identified in the Ohio source of the provenance study (18, 33, 41 and 47) were present in low (0.26) to very high (0.90) frequencies in the three Ohio stands. A detailed analysis of genetic population structure in this species will require more intensive sampling of local populations, and more importantly, the inclusion of additional isozyme systems.

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Buchbesprechungen

Pareys Buch der Bäume. Nadel- und Laubbäume in Europa nördlich des Mittelmeeres. Von ALAN MITCHELL und JOHN WILKINSON. Aus dem Englischen übersetzt und bearbeitet von Prof. Dr. PETER SCHÜTT, München. 1982. 272 Seiten mit 2440 Einzeldarstellungen, davon 2400 farbig. Verlag Paul Parey, Hamburg und Berlin. Kartoniert DM 32,— (ISBN 3-490-19418-7).

Unter den zahlreichen Büchern zur Bestimmung von Gehölzen hat die vorliegende Neuerscheinung im Taschenbuchformat den großen Vorteil, daß alle behandelten Arten, Varietäten und Formen in sehr guten farbigen Zeichnungen abgebildet sind. Mit diesem Buch dürften nahezu alle in Europa nördlich des Mittelmeeres anzutreffenden Baumarten mit Ausnahme von Raritäten sicher anzusprechen sein. Da die Originalausgabe für England unter dem Titel "The trees of Britain and northern Europe" konzipiert wurde, findet man viele Arten beschrieben, die zwar auf den britischen Inseln gedeihen, in Mitteleuropa aber nur selten zu finden sind. Entsprechende Anmerkungen und Ergänzungen wurden vom Bearbeiter der deutschen Ausgabe, P. SCHÜTT, eingefügt. Der Text gliedert sich in eine allgemeine Einführung über Biologie, Anzucht, Verwendung und Alter der Bäume. Es folgen kurze Bestimmungsschlüssel bis zu den Gattungen. Im Hauptteil werden in systematischer Reihenfolge die einzelnen Baumarten behandelt, wobei sich Abbildung und Text gegenüberstehen. Die zahlreichen Detailzeichnungen der Blüten, Früchte und Blätter, der Rinde bei bestimmtem Baumdurchmesser und des Aussehens des belaubten Baumes im Freistand ermöglichen eine rasche und sichere Bestimmung der betreffenden Baumart. Zum besseren Größenvergleich sollten allerdings in einer Neuauflage bei Blättern, Nadeln oder Früchten die entsprechenden Abbildungsmaßstäbe angegeben werden, wie dies bei den Koniferenzapfen bereits der Fall ist. Der beschreibende Text enthält Hinweise auf die Heimat des Baumes und auf spezifische Unterscheidungsmerkmale zu anderen Arten sowie Anmerkungen zur Kulturfähigkeit, eine Beurteilung des Gartenwertes und andere interessante Einzelheiten. Im abschließenden Teil des Buches findet man einen Bestimmungsschlüssel für Laubbäume im Winter, die Wintersilhouetten von 40 laubabwerfenden Baumarten, Verzeichnisse der deutschen und wissenschaftlichen Namen sowie eine Anleitung zur Ermittlung der Baumhöhe. — „Pareys Buch der Bäume" ist eine gelungene Neuerscheinung, die jedem dendrologisch Interessierten empfohlen werden kann.

B. R. STEPHAN

Illustrierte Flora von Mitteleuropa. Von GUSTAV HEGI. Band I, Teil 2: Gymnospermae, Angiospermae, Monocotyledoneae 1. Herausgegeben von FRIEDRICH MARKGRAF, bearbeitet von F. MARKGRAF und H. ZOLLER. 3., völlig neubearbeitete Auflage. 269 Seiten, 283 Abbildungen, 8 Farbtafeln. Verlag Paul Parey, Berlin und Hamburg. 1981. Ganzleinen DM 168,—.

Hegi's Illustrierte Flora von Mitteleuropa ist seit Erscheinen der ersten Bände ab 1906 ein Standardwerk der floristischen Literatur. Seit vielen Jahren sind Neuauflagen einzelner Bände in Bearbeitung bzw. bereits abgeschlossen. Der 1. Band mit den Pteridophyten, Gymnospermen und *Monocotyledoneae* bis einschließlich den Gräsern wurde 1936 in 2. Auflage herausgegeben. Die 3.