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Review article

Gene diversity in natural populations of oak species

A Kremer, RJ Petit

INRA, laboratoire de génétique et d'amélioration des arbres forestiers, BP 45, 33610 Gazinet, Cestas, France

Summary — This contribution reviews studies of nuclear and organelle gene diversity in oak species. Studies of allozymes were reported for 33 species belonging to the sections *Erythrobalanus*, *Lepidobalanus* and *Mesobalanus* of the genus *Quercus*. The extent and organization of gene diversity were investigated at 3 hierarchical levels: complex, species and population. Total diversity at the species and population level varies greatly among species (from 0.06 to 0.40). The range of variation among species is as large as that observed in other plant genera. Life history characteristics and evolutionary history are the main explanations for these results. Species with large and continuous distributions such as *Q petraea* and *Q rubra* exhibit high levels of gene diversity. Within a complex, most of the nuclear gene diversity is distributed within populations (74%). The remaining diversity is mainly due to species differentiation (23%), while the between-population component is low (3%). Organelle gene diversity has been investigated recently in 2 species complexes in the section *Lepidobalanus* (one in North America and one in Europe). Compared to nuclear genes, organelle gene diversity is strikingly different. Contributions of within-stand variation, species differentiation and population differentiation to total diversity, are respectively 13%, 11% and 76%. Trees of a given population generally share the same chloroplast genome. Moreover, trees of different species (with reported introgression) occupying the same stand exhibit a high degree of similarity.

***Quercus* / nuclear gene diversity / organelle gene diversity / gene differentiation**

Résumé — Diversité génétique dans les populations de chênes. *Cette contribution présente une synthèse des résultats obtenus sur la diversité génétique nucléaire et cytoplasmique chez les chênes. À l'heure actuelle, des données existent sur 33 espèces appartenant aux sections* Erythrobalanus, Lepidobalanus *et* Mesobalanus *du genre* Quercus. *Les analyses ont porté sur l'estimation du niveau de diversité et sur la répartition de la diversité entre les 3 niveaux : complexe, espèce et population. La diversité totale au niveau espèce et population montre une variation importante (entre 0,06 et 0,40). L'amplitude de variation entre espèces est aussi importante que celle observée dans d'autres genres. Les caractéristiques biologiques des espèces ainsi que leur histoire évolutive permettent d'interpréter ces résultats. Les espèces à large aire de distribution, telles que* Q petraea *et* Q robur *manifestent des niveaux élevés de diversité. Au niveau d'un complexe d'espèces, la majeure partie de la diversité réside à l'intérieur des populations (74%); la différenciation entre espèces à l'intérieur du complexe représente 23%, alors que la différenciation entre populations à l'intérieur d'une espèce ne représente plus que 3% de la diversité totale. La diversité génétique cytoplasmique a été étudiée récemment dans 2 complexes de chênes blancs de la section* Lepidobalanus *(le premier situé en Amérique du Nord, le second en Europe). Les résultats sont très différents de ceux obtenus au niveau nucléaire. Les contributions de la différenciation entre arbres (à l'intérieur des popu-*

lations), entre populations (à l'intérieur des espèces) et entre espèces sont respectivement de 13, 11 et 76%. Les arbres d'une même population partagent généralement le même génome cytoplasmique. Par ailleurs, les espèces proches, échangeant des gènes et occupant les mêmes peuplements, manifestent une similarité génétique élevée.

Quercus / *diversité génétique nucléaire / diversité génétique cytoplasmique / différenciation génétique*

INTRODUCTION

The genus *Quercus* comprises more than 300 species spread over Asia, North America and Europe (Camus, 1934–1954). On each continent, oak species are sympatric over large areas in which extensive gene flow among related species has been reported. Although morphological and ecological boundaries of species are usually well recognized, natural hybridization has been described in many combinations based on morphological evidence. This suggests that oaks are multispecies or large sets of broadly sympatric species exchanging genes (Van Valen, 1976).

Since introgression represents a potentially important source of genetic variation in natural populations, the multispecies level has to be considered in evaluating levels and organization of gene diversity. Questions related to the multispecies concept are: does interfertility between species provide higher levels of gene diversity than within species which do not normally experience introgression? How is diversity distributed among species and among populations within species? We address these questions by reviewing the scarce literature on gene diversity in oak species both at the nuclear and organelle levels.

In recent years, allozymes have been used to document nuclear variation in oaks, while restriction-site data on chloroplast DNA (cpDNA) have provided a preliminary insight into organelle polymorphisms. Because chloroplasts are maternally and clonally inherited, whereas nuclear genes undergo recombination and are biparentally inherited, the comparison of the organization of gene diversity in these different genomes is of particular interest and will be stressed in this review.

MATERIALS AND METHODS

Nuclear gene diversity

Reported studies and sampling strategies

Table I presents a general survey of gene diversity studies conducted so far on oak species, with particular emphasis on sampling schemes. Species are classified according to Camus's taxonomy (Camus, 1934–1954). Data are available on 33 species and originate from 13 references. These species belong mainly to sections *Lepidobalanus* (white oaks) and *Erythrobalanus* (red oaks) and are distributed over North America, Europe and Asia. No data are available on species belonging to sections *Macrobalanus* and *Protobalanus*. Sampling schemes are extremely variable and in some cases restricted to a few loci or populations. Among the 33 species only 8 assessed had more than 13 loci and 4 populations. For a few economically important species (*Q petraea*, *Q alba*, *Q rubra*, *Q macrocarpa*), investigations were conducted independently by different institutes, leading in some cases to substantial differences in the results. Therefore, species comparisons will only be made when the same techniques were applied.

Because oak stands are often composed of several interfertile species, gene diversity in nat-

ural populations should be analyzed at different hierarchical levels: complexes of species, species within complexes and populations within species. To evaluate gene diversity parameters, species were considered to form a complex when: 1) they belonged to the same botanical section, 2) their natural ranges were largely overlapping and 3) natural hybridization was indicated in the literature in all pairwise combinations. In defining a complex, we added an additional constraint – that the gene frequencies be obtained with the same techniques for all species forming the complex. Among the different species listed in table I, 4 complexes can be identified using the criteria reported above.

Q rubra *complex*

Two different studies (Manos and Fairbrothers, 1987; Guttman and Weight, 1989) have provided data on 6 and 10 species of red oaks, respectively. According to the aforementioned criteria and the *Quercus rubra* syngameon (Jensen, 1993), species were clustered in 2 complexes (4 species each): complex 1, comprised of *Q rubra*, *Q coccinea*, *Q ilicifolia* and *Q velutina* (Manos and Fairbrothers, 1987); and complex 2, comprised of *Q rubra*, *Q marilandica*, *Q phellos* and *Q velutina* (Guttman and Weight, 1989).

Q alba *complex*

This contains species studied by Guttman and Weight (1989) clustered in a complex according to the *Q alba* syngameon described by Hardin (1975): *Q alba*, *Q bicolor*, *Q lyrata*, *Q macrocarpa* and *Q stellata*.

Q douglasii *complex*

Two white oaks (*Q douglasii* and *Q lobata*) were selected among the 3 species studied by Millar *et al* (1992). They are sympatric over their entire distribution in California. Natural hybridization has been reported by Tucker (1990).

Q robur *complex*

Q petraea and *Q robur* species are sympatric over most of Europe and their introgression has been extensively documented (Rushton, 1979; Ietswaart and Feij, 1989). The data analyzed here originated from Müller-Starck *et al* (1992).

Estimation of gene diversity parameters

Gene diversity was investigated at 3 hierarchical levels (complex, species and population) by computing the following genetic parameters for each locus separately (Hamrick and Godt, 1990): 1) mean number of alleles *(A)*: number of alleles observed at a given hierarchical level (*ie*, species or populations); 2) genetic diversity (H_e); 3) effective number of alleles (A_e; $A_e = 1/(1-H_e)$).

Additional subscripts indicate the level at which these parameters were calculated; for example A_c, A_s and A_p are, respectively, the mean number of alleles at the complex, species and population levels. Genetic diversity was calculated at each different level by: $H_e = 1 - \Sigma\, p_i^2$; where p_i is the mean frequency of allele i over all units of the next lowest hierarchical level. Values of the genetic parameters were averaged over all loci analyzed.

The structure of gene diversity was analyzed using Nei's genetic diversity statistics (1973, 1977) in which the total diversity in a complex (H_T) was partitioned into 3 components: $H_T = H_S + D_{SG} + D_{GT}$; where H_S is the diversity within populations within species, D_{SG} is the component of diversity due to subdivision into populations within species, and D_{GT} is the component of diversity due to subdivision into species (within the complex).

These components were further calculated as ratios of total diversity (Chakraborty and Leimar, 1988; Kremer *et al*, 1991), which is different from the notation of Nei (1973): $G_S + G_{SG} + G_{GT} = 1$ and $G_S = H_S/H_T$, the coefficient of gene differentiation among individuals within populations; $G_{SG} = D_{SG}/H_T$, the coefficient of gene differentiation among populations within species; and $G_{GT} = D_{GT}/H_T$, the coefficient of gene differentiation among species within a complex. The proportion of gene diversity residing among populations irrespective of species is: $G_{ST} = G_{SG} + G_{GT}$.

Due to the extremely different sampling schemes used (table I), genetic parameters were not systematically calculated for every study. For documentation purposes, we report all the results on a species level, but restrict the analysis of organization of gene diversity to the cases where more than 13 loci were investigated. Because authors used different genetic parameters or estimation methods, most of the pa-

Table I. Sampling schemes and genetic parameters of nuclear gene diversity studies of oaks.

Species (complex No) [a]	*Sampling strategies*			*Gene diversity parameters*				*Ref* [g]
	No of loci	*No of pop*	*No of trees/pop*	A_s [b]	A_{es} [c]	H_{es} [d]	G_{SG} [e]	
Section *Cerris* (35 species [f])								
Q acutissima	6	6	5–30	2.50	1.60	0.336	0.07	1
Q serrata	6	4	5–30	3.17	1.64	0.310	0.12	1
Q variabilis	6	5	5–30	2.83	1.55	0.304	0.07	1
Section *Mesobalanus* (5 species [f])								
Q dentata	6	5	5–30	3.17	1.51	0.274	0.04	1
Section *Lepidobalanus* (152 species [f])								
European species								
Q ilex	3	16	23–158				0.07	2
Q petraea (5)	13	5	72–228	4.08	1.61	0.288	0.04	5
	15	32	120	3.20	1.54	0.288	0.02	3, 4
Q robur (5)	13	5	96–207	4.15	1.57	0.272	0.02	5
	15	2	120		1.50	0.264		3, 4
Asian species								
Q mongolica	6	6	5–30	3.50	1.63	0.319	0.05	1
Q aliena	6	4	5–30	3.00	1.70	0.341	0.09	1
North American species								
Q alba	16	2	19	1.63	1.20	0.100	0.03	6
(3)	18	1	37	2.33	1.57	0.276		7
Q bicolor (3)	18	1	12	1.77	1.55	0.255		7
Q douglasii (4)	21	7	20	3.19	1.22	0.150	0.01	8
Q gambelii	24	4	24	2.67	1.53	0.215	0.12	9
Q lobata (4)	21	7	20	2.67	1.13	0.083	0.03	8
Q lyrata (3)	18	1	14	1.72	1.51	0.234		7
Q macrocarpa (3)	18	1	24	2.44	1.72	0.314		7
	26	21	17–58	3.58	1.42	0.206	0.08	9
Q muehlenbergii	18	1	12	1.72	1.45	0.237		7
Q prinus	18	1	13	2.33	1.89	0.398		7
Q stellata (3)	18	1	31	2.00	1.43	0.196		7
Q virginiana	18	1	31	1.67	1.28	0.149		7
Section Erythrobalanus (136 species [f])								
Q agrifolia	18	15	20	1.83	1.08	0.061	0.07	8
Q coccinea (1)	16	2	16–21	1.50	1.08	0.058	0.05	6
Q falcata	18	1	25	2.11	1.49	0.211		7
Q ilicifolia (1)	16	3	15–29	1.56	1.23	0.116	0.04	6
Q imbricaria	18	1	21	2.39	1.56	0.262		7
Q laurifolia	18	1	24	1.94	1.24	0.146		7
Q marilandica	16	3	16–20	1.56	1.11	0.081	0.16	6
(2)	18	1	24	1.78	1.26	0.145		7
Q nigra	18	1	50	2.33	1.38	0.198		7
Q palustris	16	2	17–21	1.25	1.09	0.058	0.02	6
	18	1	29	2.17	1.29	0.151		7

Table I. *Continued*

Species (complex No) [a]		Sampling strategies			Gene diversity parameters				Ref [g]
		No of loci	No of pop	No of trees/pop	A_s [b]	A_{es} [c]	H_{es} [d]	G_{SG} [e]	
Q phellos	(2)	18	1	28	2.22	1.24	0.155		7
Q rubra	(1)	16	2	25–26	1.63	1.23	0.124	0.07	6
	(2)	18	1	19	2.11	1.30	0.172		7
		13	8	40–200	3.31	1.28	0.233	0.02	10
		4	9	100	5.25	1.66	0.319	0.04	11
		15	11	25				0.17	12
Q shumardii		18	1	35	2.17	1.24	0.141		7
Q velutina	(1)	16	3	17–21	1.56	1.21	0.123	0.17	6
	(2)	18	1	16	2.00	1.36	0.203		7
Mean, no of loci > 13					2.23	1.37	0.186	0.06	
Mean, all samples					2.41	1.42	0.211	0.07	

[a] Indicates the complex to which the species belongs (see tables III and VIII). [b] A_s is the mean number of alleles within a species. [c] A_{es} is the effective number of alleles at the species level ($A_{es} = 1 / [1-H_{es}]$). [d] H_{es} is the species gene diversity. [e] G_{SG} is the coefficient of gene differentiation among populations within species. [f] Number of species described in Camus' monograph (Camus, 1934–1954). [g] 1) Kim *et al*, 1993; 2) Lumaret *et al*, 1991; 3) Kremer *et al*, 1991; 4) Zanetto, 1989; 5) Müller-Starck *et al*, 1993; 6) Manos and Fairbrothers, 1987; 7) Guttman and Weight, 1989; 8) Millar *et al*, 1992; 9) Schnabel and Hamrick, 1990; 10) Schwarzmann and Gerhold, 1991; 11) Daubree, 1990; 12) Sork *et al*, 1993.

rameters were recalculated when allele frequencies were available.

Organelle gene diversity

Two separate studies were conducted independently on North American and European white oaks (*Q alba* and *Q robur* complexes), both of them based on chloroplast DNA (table II). The *Q alba* complex comprises *Q alba*, *Q macrocarpa*, *Q michauxii* and *Q stellata*. The *Q robur* complex comprises *Q petraea*, *Q pubescens* and *Q robur*. The theory of organelle gene diversity has recently been developed (Birky *et al*, 1989; Birky, 1991). If we postulate that there is no within-tree variation (*ie*, no variation among different chloroplasts of the same individual), the same *A*, *H* and *G* parameters for nuclear genes can be calculated for organelle genes. The data originated from restriction-site polymorphisms corresponding to restriction-site gains or losses. The polymorphisms were analyzed at the genotypic level, *ie* all haplotypes were considered to be different alleles of one locus. The genetic parameters were estimated following the procedures of Nei and Chesser (1983) and Nei (1987), recommended for low population sample sizes.

RESULTS

Levels of nuclear gene diversity

Complex level

At the complex level, oaks exhibited a high amount of genetic variation (table III). Over the 4 complexes, the average number of alleles was 3.55 and mean genetic diversity was 0.273. With one exception, the majority of loci in a complex were comprised of frequent alleles that were common to all species. The exception was the *Q alba* complex, in which different alleles were of-

Table II. Sampling strategies in organelle gene diversity studies.

Complex	*Number of:*				*Ref* [a]
	Species	*Polymorphisms*	*Populations*	*Trees/population*	
Quercus alba					
North American white oaks	4	8	17	1–19	13 [a]
Quercus robur					
European white oaks	3	3	91	4–18	3; 14

[a] 13) Whittemore and Schaal, 1991; 14) Petit, 1992; 3) Kremer *et al,* 1991.

ten fixed in different species (Guttman and Weight, 1989). The *Q alba* complex exhibited the highest overall diversity. White oak complexes (*Q alba*, *Q douglasii*, *Q robur*) showed higher diversity than the *Q rubra* complexes. Within the latter, there were striking differences between results originating from the 2 data sets; their causes can probably be attributed to different electrophoretic techniques used in different laboratories and different species included in each complex.

The 3 white oak complexes considered have a broad distribution in North America

Table III. Nuclear gene diversity parameters at the complex level.

Complex	*Complex No* [a]	A_c [b]	A_{ec} [c]	H_{ec} [d]	*Proportion of loci* [e]	*Ref* [f]
Q rubra						
Red oaks	1	2.00	1.59	0.127	0.94	6
	2	3.50	1.36	0.206	0.83	7
Q alba						
Northeastern American white oaks	3	3.61	1.94	0.402	0.44	7
Q douglasii						
Californian white oaks	4	3.48	1.45	0.241	0.67	8
Q robur						
European white oaks	5	4.39	1.60	0.280	1.00	5
Means		3.55	1.62	0.273	0.75	

[a] No corresponds to the number given in table I. [b] A_c is the mean number of alleles at the complex level. [c] A_{ec} is the effective number of alleles at the complex level: $A_{ec} = (1-H_{ec})$. [d] H_{ec} is the gene diversity at the complex level. [e] Proportion of loci having the same common allele shared by all species within a complex. [f] References are the same as those given in table I.

and Europe, except for the *Q douglasii* complex, which is restricted to California. No correlation between the number of species within a complex and the levels of gene diversity was found, but data were only available on 4 complexes.

Species level

Data on levels of gene diversity at the species level are summarized in table I. Because of the different sampling strategies, we restricted comparisons among species to data obtained with the same techniques. Manos and Fairbrothers (1987) analyzed gene diversity in 6 red oaks and one white oak, each represented by 2–3 populations in New Jersey. Guttman and Weight (1989) provided information on 8 white oaks and 10 red oaks. Although the sample size per species was small in the latter study (table I), the trees were collected across the range of each species; thus the data were appropriate for the species level. Five species were common to the 2 studies. When comparing the same species in the 2 different studies, the levels of gene diversity were always lower in the study of Manos and Fairbrothers, indicating the use of different electrophoretic techniques or different enzymes. Species comparisons of levels of gene diversity were therefore confined within each study.

Influence of taxonomy on genetic diversity (data from Guttman and Weight, 1989)

There were significant differences in the levels of diversity (A_{es} and H_{es}) between white (section *Lepidobalanus*) and red oaks (section *Erythrobalanus*) in eastern North America (table IV). White oaks exhibited higher levels of diversity than red oaks. Among the 80 pairwise comparisons between species of each section (table I), higher levels of H_{es} were found for white oaks in 66 cases.

Influence of life history characteristics on genetic diversity (data from Manos and Fairbrothers, 1987; Guttman and Weight, 1989)

We investigated variation of H_{es} in relation to several life history characteristics: mean northern latitude of distribution (NL), range of distribution (RD), seed size (SS), tree height (TH), crossability with other species (CR) and life habitat conditions (LHC). Quantitative data on RD, SS and TH came from Aizen and Patterson (1990), NL was estimated from distribution maps in Fowells (1965). Two habitat conditions were identified (Fowells, 1965): 1) wet soils, river banks and flood plains; and 2) dry uplands. Crossability of a given species is defined as the number of species which were reported to hybridize under natural conditions with the species studied. Data on CR were obtained from the review of American hybrids by Palmer (1948). For example *Q velutina* was reported to hybridize with 14 other species, whereas only 3 hybrids were mentioned for *Q prinus*.

Table IV. Nuclear gene diversity parameters at the species level. Comparison between North American white *(Lepidobalanus)* and red oaks *(Erythrobalanus)* (data from Guttman and Weight, 1989).

Section	*Number of species*	A_s [a]	A_{es}	H_{es}
Lepidobalanus White oaks	8	1.98	1.55	0.257
Erythrobalanus Red oaks	10	2.12	1.34	0.178
Student's *t*-test		NS	$P < 0.02$	$P < 0.02$

[a] For definitions of A_s, A_{es} and H_{es} see table I.

Significant correlations were found between H_{es} and NL, RD, SS and TH (table V). Because of the small number of species, correlation was sensitive to extreme values of H_{es} or other covariates. Therefore, different calculations were made by removing values for *Q prinus*, which exhibited extremely high values for H_{es} (0.398) and seed volume (10.5 cm^3). The relationships detected were stronger in the white oaks than in the red oaks. While the southern latitude of distribution is similar to all white and red oaks, the northern latitude varies according to the species. By construction, NL and RD are already correlated. Species distributed along the gulf of Mexico (*Q virginiana* for the white oaks and *Q laurifolia* for the red oaks) had low H_{es} values, respectively 0.149 and 0.146 (table I). On the other hand, widespread species (*Q alba* for the white oaks and *Q velutina* for the red oaks) exhibited higher H_{es} levels, respectively 0.276 and 0.203. Exceptions to these relationships in the red oaks (*Q imbricaria*) explain the lack of correlation within this section.

There was no significant relationship between crossability and levels of diversity. Nor was there any significant difference between the mean H_{es} values for the 2 categories of habitat conditions.

Population level

In making comparisons among species at the population level, only studies with 13 or more loci and 4 or more populations were included (table I). The results obtained show a large range of variation among species in H_{ep}, from 0.057 to 0.275. A closer analysis revealed that species with the highest level of gene diversity at the population level were characterized by evenness of allelic frequencies (table VI). In the case of *Q petraea*, for 33% of the loci, the frequency of the most common allele was lower than 0.7, whereas this pro-

Table V. Correlations between H_{es} and life history traits.

Section (no of species) [a]	*Northern latitude* [b]	*Range* [c]	*Acorn size* [d]	*Height* [e]	*Crossability* [f]	*Ref* [g]
Lepidobalanus (8)	0.60	0.05	0.86*	0.70	−0.24	7
Q prinus removed	0.93**	0.79*	0.69	0.86*	0.24	7
White oaks (7)						
Erythrobalanus (9)						
Red oaks	0.24	0.25	0.15	0.04	0.12	7
Erythrobalanus (6)	0.63	0.47	0.59	0.26	0.61	6
Red oaks						

Correlations were only computed for species whose data on life history traits were available. [a] Number of species per sample is given between parentheses. [b] Mean northern latitude of distribution (data obtained from Fowells, 1965). [c] Area of distribution (km^2) (data from Aizen and Patterson, 1990). [d] Acorn volume (cm^3) (data from Aizen and Patterson, 1990). [e] Tree height (m) (data from Aizen dand Patterson, 1990). [f] Crossability is the number of reported interspecific hybrids for a given species (data obtained from Palmer, 1948). [g] References are the same as those given in table I. * Correlation coefficient significant at the 5% level. ** Correlation coefficient significant at the 1% level.

Table VI. Nuclear gene diversity parameters at the population level.

Species	A_p [a]	A_{ep} [b]	H_{ep} [c]	*Allelic frequency profiles*			*Ref* [g]
				A [d]	B [e]	C [f]	
Section *Lepidobalanus* (white oaks)							
Q alba	1.47	1.19	0.097	0.06	0.13	0.81	6
Q douglasii	2.20	1.17	0.148	0.04	0.29	0.67	8
Q gambelii	2.14	1.37	0.204				9
Q lobata	1.70	1.09	0.081	0.05	0.10	0.85	8
Q macrocarpa	2.12	1.47	0.187				9
Q petraea	2.57	1.50	0.275	0.33	0.33	0.33	3,4
	2.78	1.56	0.278				5
Q robur	2.67	1.55	0.267				5
Section *Erythrobalanus* (red oaks)							
Q agrifolia	1.40	1.08	0.057	0.00	0.06	0.94	8
Q coccinea	1.34	1.08	0.055	0.06	0.00	0.94	6
Q ilicifolia	1.44	1.21	0.111	0.19	0.06	0.75	6
Q marilandica	1.54	1.09	0.068	0.06	0.13	0.81	6
Q palustris	1.22	1.09	0.057	0.06	0.06	0.88	6
Q rubra	2.47	1.45	0.229	0.16	0.34	0.50	10
	1.97		0.167				12
	1.50	1.23	0.116	0.19	0.06	0.75	6
Q velutina	1.42	1.15	0.100	0.12	0.19	0.69	6
Means	1.81	1.24	0.134				

[a] A_p is the mean number of alleles at a population level. [b] A_{ep} is the effective number of alleles at the population level. [c] H_{ep} is the within-population gene diversity. [d] Proportion of loci for which the frequency of the most common allele is lower than 0.7. [e] Proportion of loci for which the frequency is comprised between 0.7 and 0.9. [f] Proportion of loci for which the frequency is higher than 0.9. [g] References are the same as those given in table I.

portion was reduced to 5% in *Q lobata* and to 0% in *Q agrifolia*. Higher within-population diversities were more closely associated with differences in frequency profiles than with differences in numbers of alleles.

As noted in table I, the data of Manos and Fairbrothers (1987) show lower gene diversities than other studies on the same species. Again, this discrepancy may be due to methodological differences. If we discard the results of Manos and Fairbrothers, populations from species with large distribution ranges (*Q macrocarpa*, *Q petraea*, *Q rubra* and *Q robur*) exhibit considerably higher diversity than species with more restricted distributions (*Q agrifolia*, *Q douglasii*, *Q lobata*).

Levels of organelle gene diversity

Preliminary analyses of chloroplast polymorphisms in the European white oaks (*Q robur* complex) were made with 33 different restriction endonucleases and 2 large *Petunia hybrida* cp DNA probes representing 26% of the *Petunia* chloroplast genome on a sample of 6 trees belonging to 3 different species (*Q robur*, *Q petraea* and *Q pubescens*) (Petit, 1992). A similar approach was applied to the American white oaks (*Q alba* complex): 15 restriction endonucleases, 7 probes of the *Petunia* chloroplast genome (73% of the genome), and 45 trees of different origins (Whittemore and Schaal, 1991) were used. Six multirestriction-site genotypes were identified in the European oaks and 8 in the American oaks. With the exception of 3 cases, the different genotypes could be interpreted as single restriction-site gains or losses.

When the analysis was limited to the polymorphic sites of the genome, high levels of diversity were found at the species level (table VII). These values should not be compared to those obtained using allozymes, since they refer only to polymorphic sites in the chloroplast genome. In comparison to the species level, within-population diversity estimates were extremely low (table VII). Among the 91 populations analyzed in the *Q robur* complex, all trees within the same populations had the same haplotype except in 15 cases, where 2 different genotypes were found. Among the 17 populations of the *Q alba* complex, only 4 comprised more than one single haplotype.

Organization of nuclear gene diversity

Complex level

Over the 4 complexes, the proportion of genetic diversity among populations accounted for 26% of the total diversity (table VIII). A major part of that proportion was due to differentiation between species, rather than differentiation among popula-

Table VII. Organelle gene diversity parameters.

Species	*Sample size*		*Parameters at the species level*			*Parameters at the population level*			*Ref* [e]
	N_p [a]	N_t [b]	A_s [c]	A_{es} [c]	H_{es} [c]	A_p [d]	A_{ep} [d]	H_{ep} [d]	
Q petraea	62	8.1	4	3.02	0.669	1.16	1.07	0.062	13
Q pubescens	14	7.4	3	2.45	0.593	1.29	1.19	0.162	13
Q robur	25	7.8	3	2.16	0.538	1.12	1.05	0.045	13
Q alba	5	10.2	5	2.95	0.662	1.60	1.31	0.236	14
Q macrocarpa	6	6.0	4	3.17	0.685	1.16	1.06	0.056	14
Q michauxii	2	6.0	2	2.00	0.500	1.00	1.00	0.000	14
Q stellata	3	7.7	3	1.80	0.444	1.00	1.00	0.000	14

[a] N_p is the number of populations. [b] N_t is the mean number of trees per population. [c] Parameters A_s, A_{es}, H_{es} defined as in table I, but at the organelle level. [d] Parameters A_p, A_{ep}, H_{ep} defined as in table VI, but at the organelle level. [e] References are the same as those given in table II.

Table VIII. Subdivision of nuclear gene diversity at the complex level.

Complex	*Complex No* [a]	H_T [b]	G_S [c]	G_{GT} [d]	G_{SG} [e]	G_{ST} [f]	Ref [g]
Q rubra							
Red oaks	1	0.290	0.807	0.177	0.015	0.193	6
	2	2.32	–	0.198	–	–	7
Quercus alba							
Northeastern American white oaks	3	0.452	–	0.369	–	–	7
Quercus douglasii							
Californian white oaks	4	0.266	0.449	0.513	0.038	0.551	8
Quercus robur							
European white oaks	5	0.280	0.954	0.008	0.038	0.046	5
Means [h]		0.278	0.737	0.233	0.030	0.263	

[a] No corresponds to the number given in table I. [b] H_T is the total diversity within the complex. [c] G_S is the coefficient of gene differentiation among trees within populations. [d] G_{GT} is the coefficient of genetic differentiation among species within a complex. [e] G_{SG} is the coefficient of genetic differentiation among populations within a species. [a] G_{ST} is the coefficient of genetic differentiation among populations within a complex ($G_{ST} = G_{SG} + G_{GT}$). [g] References are the same as given in table I. [h] Mean values were computed based only on complexes 1, 4 and 5.

tions within species, except in the *Q robur* complex.

The proportion of variation due to the differences among species differed among the complexes. In the European white oaks (*Q robur* complex), differentiation between the 2 species was extremely low, while in the North American white oaks (*Q alba* and *Q douglasii* complexes), it accounted for more than 37% of the total diversity. Interestingly, values obtained for the red oaks were of the same magnitude in the 2 different studies, despite the important differences found for A_c, A_{ec} and H_{ec} (table III).

Differentiation among populations within species remained low in all cases (from 1 to 4%). The coefficient of differentiation among populations could not be calculated in the *Q alba* and *Q rubra* complexes of American oaks, since each species was represented by a bulk collection of trees sampled across the range of the species (Guttman and Weight, 1989). Due to this sampling scheme, G_S, G_{SG} and G_{ST} could not be estimated.

Species level

When data were available only on a species level (table I), differentiation among populations accounted only for a small proportion of the total diversity, in general less than 6%, regardless of the species considered.

Organization of organelle gene diversity

The 2 reported studies showed remarkably similar results (table IX). While the total diversity was rather high (0.664), it was geographically organized. The within-population component represented only 12% of the total diversity. Moreover, differentiation between species was similar (7%). As a result, interpopulation gene diversity is the major component of the total diversity.

Table IX. Subdivision of organelle gene diversity at the complex level.

Complex	H_T [a]	G_S	G_{GT}	G_{SG}	G_{ST}	Ref [b]
Quercus alba						
Eastern American white oaks	0.662	0.145	0.135	0.720	0.855	13
Quercus robur						
European white oaks	0.660	0.105	0.032	0.863	0.895	14
Means	0.661	0.125	0.083	0.791	0.875	

[a] Definitions of gene differentiation coefficients are the same as those given in table VIII, but at the organelle level.
[b] References are the same as those given in table II.

Whittemore and Schaal (1991) observed for the North American white oaks (*Q alba* complex) that, except for the most frequent one, all genotypes were geographically localized. That is, when species were sampled in the same locality, distinctive chloroplast genotypes were shared among them. Similar observations were made in white oaks in Europe (Petit, 1992). From a subsample of 13 pairs of populations (one *Q petraea* and one *Q robur*) originating from the same or contiguous stands, 9 presented the same genotype in each species.

DISCUSSION

Nuclear gene diversity

Oak species levels of nuclear gene diversity were among the highest found in long-lived woody species. Diversity on a species level (H_{es} = 0.186, table I) appears to be higher in the genus *Quercus* than in *Populus* (0.127), *Acacia* (0.125), *Abies* (0.145) or *Pinus* (0.157); of similar magnitude to *Eucalyptus* (0.187); but inferior to *Pseudotsuga* (0.201) or *Picea* (0.219) (Hamrick *et al*, 1992). Earlier reviews on gene diversity showed that long-lived, outcrossing, wind-pollinated species of the late stages of succession exhibited higher levels of gene diversity (Hamrick and Godt, 1990). Oak species possess all these characteristics. Moreover, the existence of large complexes comprising several interfertile sympatric species is an additional potential source of genetic variation, as shown by the high H_{ec} value on a complex level (0.275).

There is wide heterogeneity among species: levels of gene diversity vary between 0.058 *(Q palustris)* and 0.376 *(Q alba)*. A significant proportion of this variation appears to be associated with the range of distribution of the species, particularly the northern latitude of distribution and acorn size (table V). These characteristics, however, are not independent, as shown by Aizen and Patterson (1990). According to these authors, large-seeded acorns are preferentially dispersed by animals, particularly birds, and are more successful in site capture, as shown by the positive correlation between acorn size and early seedling growth. Thus, large-seeded oak species are considered to be better colonizers. These results support earlier con-

clusions drawn by Hamrick *et al* (1992) for tree species in general: that species with widespread distributions and widely dispersed seeds tend to have higher genetic diversities. Surprisingly, we did not find any relationship between crossability and level of gene diversity, perhaps because of imprecise estimates of crossability (table V).

In addition to life history traits, evolutionary history may contribute significantly to the current levels of genetic variation, as shown by the differences observed between the 2 major sections of the genus *Quercus* (table IV). Red oaks are less variable than white oaks. Causes of these differences may be attributed to the original gene pool of current species or to evolutionary forces. Combined data on molecular and morphological traits suggest that white oaks in northeastern America originate from multiple lineages covering different continents (Nixon *et al*, Cornell University, personal communication). Red oaks are restricted to North America and probably stem from a reduced gene pool compared to white oaks.

Species differentiation within a complex varies substantially among the different complexes. In the broadly sympatric European white oaks, species differentiation is even lower than geographic differentiation (among populations within species), whereas in the North American white oaks 37–51% of the total diversity within a complex is due to species differentiation. In general, most frequent alleles are common to the majority of species forming a complex. Time and rates of speciation and importance of gene flow between species constitute 2 complementary hypotheses for interpreting our observations. According to Axelrod (1983), oaks proliferated and differentiated rapidly during periods of extreme climatic changes during the middle to late Tertiary period. Rapid speciation is associated in most cases with low allozyme divergence (Crawford, 1989), while gradual speciation through geographic isolation results in considerable differentiation among species. On the other hand, natural hybridization is frequent within the genus *Quercus* (Rushton, 1993). Even if hybrid swarms are rare in oaks (Hardin, 1975), low gene flow among species may be sufficient to counteract allozyme divergence, unless allozymes are differentially selected in different species. There is some evidence that the extent of introgression in oaks depends upon site conditions. On sites optimal to parental species, selection against F_1 hybrids before they pass on their genes is thought to be important (Hardin, 1975). On sites less favorable to parental species, intermediate phenotypes are more frequent (Grandjean and Sigaud, 1987). Therefore, the past and present ecological opportunities to exchange genes may result in differences of genetic differentiation among species.

Population differentiation within oak species is in agreement with earlier reviews on gene diversity organization in plants which showed that the breeding system has a predominant influence on G_{ST} values (Hamrick and Godt, 1990). Oaks are largely outcrossing species with extensive gene flow among populations (Ducousso *et al*, 1993), thereby reducing differentiation between populations. On the average, G_{SG} (equivalent to G_{ST} in other papers) was 6% in oaks, with extreme values of 1–17% (table I). Sampling of populations was too low in most species to further analyze species variation of G_{SG} values.

Organelle gene diversity

Because the chloroplast genome was thought to be highly conserved within a species, studies on cpDNA have mainly focused on interspecific relationships. Nonetheless, large surveys over several popula-

tions have demonstrated the existence of intraspecific variation in cpDNA (Wagner *et al*, 1987 in *Pinus banksiana* and *Pinus contorta*; Neale *et al*, 1988 in *Hordeum*; Soltis *et al*, 1989 in *Tolmiea menziesii*; see Harris and Ingram, 1991, for a review). Combined inter- and intraspecific assessments of cpDNA polymorphisms in oaks show intriguing features in gene diversity organization.

Patterns of intraspecific variation are similar in sympatric species in both American and European white oaks. Different species share identical genotypes that are confined to geographic areas. This has been qualified as chloroplast 'capture' by Rieseberg and Soltis (1991). Other woody plant species showing similar trends are poplars (Smith and Systma, 1990) and willows (Rieseberg and Soltis, 1991). Chloroplast capture is attributed by these authors to active gene flow between species. Hybridization and introgression have been suggested to be important evolutionary forces in oaks (Burger, 1975; Van Valen, 1976). However, capture of a maternally inherited genome from a donor species by a receptive species requires, after hybridization, a series of unidirectional backcrosses. Preferential pollination between the pollen of the receptive species and the ovule of the hybrids is a prerequisite to the final inclusion of the chloroplast genome of the donor species into the receptive species. In European oaks, experiments with controlled crosses show that pollination of pedunculate oak *(Q robur)* by sessile oak *(Q petraea)* is more successful than that of the reciprocal cross (Steinhoff, 1993). Similar results were found in a natural stand comprised of both species (Bacilieri *et al*, 1993). Preferential backcrosses between hybrids and one of their parental species have been reported in a study of introgression between *Quercus prinus* L and *Quercus alba* (Ledig *et al*, 1969). Unidirectional gene flow resulting in chloroplast capture was also found in poplars (Keim *et al*, 1989; Smith and Systma, 1990). The role of the occurrence of chloroplast capture throughout the evolutionary history is still an open debate. Is ancient hybridization and introgression occurring concurrently with colonization, or is continuing gene flow responsible for the maintenance of low species differentiation of cpDNA polymorphism?

Within oak species, differentiation among populations accounts for the major portion of gene diversity as compared to within population variation. These results were expected from the neutral theory applied to organelle genomes (Birky *et al*, 1983, 1989; Birky, 1991). First, organelle genes are more sensitive to genetic drift than nuclear genes, since their effective population size is approximately one half that of nuclear genes in monoecious species. Second, if we postulate that organelle genes are only maternally inherited, their migration is lower than for nuclear genes. Increase of genetic drift and decrease of migration leads to greater fixation of genes within populations and, as a result, to important interpopulation differentiation. Biological features of fruiting and seed dispersal in oaks reinforce theoretical expectations of population differentiation. Fruiting in oak stands is extremely heterogeneous through time and space. As a result, some stands may originate from a restricted number of 'mother' trees. On the other hand, seed dispersion is limited (Sork, 1984). Even if transported long distances by jays or rodents (Darley-Hill and Johnson, 1981; Kanazawa, 1982; Miyaki and Kikuzawa, 1988), acorns can rapidly lose their viability either by predation or storage under unfavorable conditions.

CONCLUSION

The contrasting patterns of gene diversity organization between nuclear and organelle DNA may be unique to *Quercus*, due

essentially to the asymmetry of seed and pollen dispersal in this genus. Nuclear gene diversity is of similar magnitude and distributed as in most other woody plant genera. Although only scarce data exist for organelle genes, expectations for most tree species are that they should be less geographically structured. In most conifers, chloroplasts are predominantly paternally inherited (Neale and Sederoff, 1988) and cpDNA variation is expected to be more evenly distributed over the range of the species, as shown in *Pinus banksiana* and *Pinus contorta* (Wagner *et al*, 1987). In other angiosperm woody species, wider seed dispersal than in oaks will probably limit population differentiation of cp DNA. As more species are studied for organelle diversity, interesting comparisons will become possible between potential seed flow and cpDNA (or mitochondrial DNA) differentiation among populations.

Comparison of nuclear and organelle gene diversity on a range-wide basis will afford interesting insight into the evolutionary history of oak species, especially as regards recolonization after the last glaciations. Maternal lineages may be traced from suspected refugia to present distributions *via* cpDNA polymorphisms. Gametic disequilibria between nuclear and cytoplasmic genes in mixed stands will clarify the importance of hybridization as an evolutionary force in oak species.

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