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Review article

Reproduction and gene flow in the genus *Quercus* L

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Summary — In this paper we review the characteristics of the floral biology, life cycle and breeding system in the genus *Quercus*. The species of this genus are self-incompatible and have very long life spans. The focus of our review is on the effects of gene flow on the structuration of genetic variation in these species. We have examined the influence of gene flow in 2 ways: 1) by measuring the physical dispersal of pollen, seed and vegetative organs; and 2) by using nuclear and cytoplasmic markers to estimate genetic parameters (F_{is}, N_m). These approaches have shown that nuclear (isozyme markers) as well as cytoplasmic (chloroplastic DNA) gene flow is usually high, so that very low interspecific differentiation occurs. However, intraspecific differentiation is higher for the cytoplasmic DNA than for the nuclear isozyme markers.

floral biology / life cycle / breeding system / gene flow / oak

Résumé — Système de reproduction et flux de gènes chez les espèces du genre *Quercus*. *Les caractéristiques de la biologie florale, du cycle de vie et du système de reproduction ont été analysées pour les espèces du genre* Quercus. *Ces espèces sont auto-incompatibles et à très longue durée de vie. Les effets des flux de gènes sur la structuration de la variabilité génétique ont aussi été étudiés de 2 manières. D'une part, grâce aux mesures de la dispersion du pollen, des graines et des organes végétatifs, et, d'autre part, en utilisant des paramètres génétiques* (F_{is}, N_m) *obtenus à partir des marqueurs nucléaires et cytoplasmiques. Il apparaît que les flux géniques nucléaires (isozymes) et cytoplasmiques (ADN chloroplastique) sont en général importants, d'où une faible différenciation interspécifique. Néanmoins la différenciation intraspécifique est plus forte lorsqu'elle est estimée à partir des marqueurs cytoplasmiques que lorsqu'elle l'est à partir des marqueurs nucléaires.*

biologie florale / cycle de vie / système de reproduction / flux de gènes / chêne

INTRODUCTION

Plant populations show a significant amount of organization in the genetic variation they contain (Wright, 1951). Such organization is significantly influenced by joint action of mutation, migration, selection and genetic drift. In this context, gene flow among plant populations may represent a significant factor influencing the maintenance of genetic organization in plant species populations (Slatkin, 1987). Gene flow is generally considered to be both small enough to permit substantial local genetic differentiation (Levin and Kerster, 1974), and large enough to introduce variability into widely separated populations (Loveless and Hamrick, 1984). This is particularly important in outbreeding, perennial and iteroparous species, such as forest trees.

In the present paper, the influences of the mating system and factors operating on gene flow at different stages of the life cycle are reviewed in various species of the genus *Quercus*.

REPRODUCTIVE SYSTEM

Floral biology

Species of the genus *Quercus* (the oaks) are predominantly monoecious with distinct male and female flowers borne on 2 types of inflorescences; very occasionally they bear hermaphroditic flowers or inflorescences (Scaramuzzi, 1958; Stairs, 1964; Tucker, 1972; Bonnet-Masimbert, 1978; Tucker *et al,* 1980). The characteristics of male and female flowers are summarized below.

Staminate flowers

Male flowers are grouped in catkins which develop in the axils of either the inner bud scales or the first leaves, in the lower part of the branches produced in the same year. Staminate inflorescences are initiated in late spring, flowers develop in early summer and meiosis occurs in the following spring, giving rise to binucleate pollen grains immediately prior to the emergence of catkins (Sharp and Chisman, 1961; Stairs, 1964; Tucovic and Jovanovic, 1970; Hagman, 1975; Bonnet-Masimbert, 1978; Merkle *et al,* 1980). For a given tree, if weather conditions are suitable, catkin growth is achieved 1–2 weeks after bud opening, and pollination is completed in 2–4 days (Sharp and Chisman, 1961; Stairs, 1964; Vogt, 1969; Lumaret *et al,* 1991). In deciduous oaks, leaf expansion ceases during the release of pollen, which allows freer movement of pollen (Sharp and Chisman, 1961).

Pistillate flowers

Female flowers appear in the axils of leaves produced in the same year. They are produced on a short stalk and become visible a few days after the emergence of the male catkins (Sharp and Sprague, 1967). Inflorescence primordia are difficult to distinguish from lateral bud primordia before late summer, hence the exact time of the initiation of pistillate inflorescences is difficult to determine. As hermaphrodite flowers are known to occur occasionally, Bonnet-Masimbert (1978) has hypothesized that their initiation may occur in late spring, when the staminate inflorescences develop. Female flowers develop in late winter or early spring (Bonnet-Masimbert, 1978; Merkle *et al,* 1980). Each flower is included in a cupule, which is regarded as homologous to a third-order inflorescence branch (Brett, 1964; McDonald, 1979). During elongation of the stalk, 3–5 styles emerge from the cupule and become reddish and sticky when receptive (Corti, 1959; Sharp and Sprague, 1967; Rushton, 1977). Stigma receptivity for a single flower may last up to 6 d and 10–14 d for the pistillate inflorescence as a whole (Pjatniski, 1947; in Rushton, 1977). Stigma receptivity for a given tree was found to be roughly 15 days in *Q ilex* L (Lumaret *et al*, 1991). In annual acorns, *eg* in the white oaks section of the genus, meiosis and fertilization of ovules occur 1 or 2 months after pollen deposition. In biennial acorns, *eg* in most of the American red oak section, the delay is about 13–15 months (Helmqvist, 1953; Arena, 1958; Sharp, 1958; Corti, 1959; Stairs, 1964; Brown and Mogensen, 1972). In several species, such as *Q coccifera* L and *Q suber* L, annual and biennial, or even intermediate acorns, occur on distinct individual trees (Corti, 1955; Bianco and Schirone, 1985). One embryo sac is usually initiated per spore and this develops in the nucellus. Rare cases of polyembryony, due to the development of more than 1 embryo sac per nucellus, or to the occurrence of 2 nucelli per ovule, have been reported (Helmqvist, 1953; Corti, 1959; Stairs, 1964). At fertilization, the pollen tube enters the ovule through the micropyle (Helmqvist, 1953) after which 1 of the 6 ovules in the ovary develops into a seed. This ovular dominance occurs during early embryo growth (Stairs, 1964). Mogensen (1975) reported that 4 types of abortive ovules occur in *Q gambelii* Nutt, with an average of 2.7 ovules per ovary that do not develop into seed due to lack of fertilization. In other cases, ovule abortion was due to zygote or embryo failure, or the absence of an embryo sac or the occurrence of an empty one. For these reasons, Mogensen (1975) proposed that the first fertilized ovule either suppresses the growth of the other fertilized ovules or prevents their fertilization. After fertilization, the acorns mature within about 3 months, then fall (Sharp, 1958; Corti, 1959). Each year, even when a good acorn crop occurs, a large amount (70% or more) of fruit abscisses (Williamson, 1966; Feret *et al*, 1982).

The occurrence of a period of stigma receptivity longer than the period of pollen production for an individual tree may diversify the number of potential partners for a given tree (Lumaret *et al*, 1991).

Life cycle

Life span and vegetative multiplication

Several species which possess vegetative multiplication produce rejuvenated stems from root crown, trunk or rhizomes, so that it becomes impossible to ascertain the age of a given individual. It is, nevertheless, likely that such oaks are long-lived species (Stebbins, 1950; Muller, 1951). For example, *Q ilicifolia* Wangenh and *Q hinckleyi* Muller have short-lived stems (20–30 yr and 7–9 yr respectively) but they mainly reproduce *via* sprouts (Muller, 1951; Wolgast and Zeide, 1983). This capacity for stump sprouting may be present in juveniles and, although decreasing with the age of the trunk, may enable oaks to maintain their populations even in the absence of acorn production (Muller, 1951; Jones, 1959; Neilson and Wullstein, 1980; Andersson, 1991).

Age and reproduction

The age of first acorn production varies with the species, but also with latitude, life span, tree density (a low density favors earlier reproductive maturity) and site

(Sharp, 1958; Jones, 1959; Shaw, 1974). The age of first reproduction also occurs earlier for trees in coppiced sites than those from seed origin, and range from 3 growing seasons old for the short-lived sprouts of *Q ilicifolia* (Wolgast and Stout, 1977b) to 30–45 years for the long-lived species *Q petraea* (Matt) Liebl (Jones, 1959). Acorn yield is often correlated with tree size, although, fecundity decreases with increasing diameter (Sharp, 1958; Iketake *et al,* 1988).

Sex allocation

As oaks are monoecious, individual trees may show biased reproductive effort favoring one or the other of the sexes. Variability in flowering abundance among trees within the same year has been reported for *Q alba* L (Sharp and Chisman, 1961; Feret *et al,* 1982), *Q acuta* Thumb (Iketake *et al,* 1988), *Q pedunculiflora* C Koch (Enescu and Enescu, 1966), *Q ilex* (Lumaret *et al,* 1991) and *Q ilicifolia* (Aizen and Kenigsten, 1990). Between-year variation in flower abundance for a given tree, *eg* variation in catkin density in *Q cerris* L and *Q ilex,* has also been reported (Hails and Crawley, 1991; Lumaret *et al,* 1991). In the latter case, variation in male and female investment concerned 15–20% of the individuals.

Acorn production by individual trees

Variation in acorn production among individual trees has been well documented and appears to be a general rule in oak species. In each year of a 14-year study on *Quercus alba,* massive variation in acorn yield was observed among the trees (Sharp and Sprague, 1967). In *Q ilicifolia,* Wolgast (1978b) found, for a given year, interindividual variation in the production of immature acorns by trees growing in the same stand to be greater than stand-to-stand or site-to-site variation. Many other similar examples have been reported (*eg* Jones, 1959; Feret *et al,* 1982; Hunter and Van Doren, 1982; Forester, 1990; Hails and Crawley, 1991).

For interannual variation, Forester (1990) and Hails and Crawley (1991) have observed that fruit set in *Q robur* L is mainly a characteristic of individual trees. Similarly, Sharp (1958) has reported that, in white oaks, each tree is fairly consistent in acorn production, at least in years of good acorn crops. In addition, for *Q ilicifolia* individuals transplanted to a common site, individuals of different origins were not found to have the same productivity (Wolgast, 1978a). In *Q pedunculiflora* (Enescu and Enescu, 1966) and *Q alba* (Farmer, 1981), substantial clonal control over seed yield has been reported. However, in several species of the red oak section, acorn production can fluctuate widely for a single tree over a number of years (Sharp, 1958; Grisez, 1975).

Mean acorn production at single sites

For single sites as a whole, a consistent abundance of flowers from year to year is usually observed, in marked contrast to the marked fluctuations in acorn production known to occur (Sharp and Sprague, 1967; Grisez, 1975; Hails and Crawley, 1991). The occurrence of mast years in acorn production seems to depend upon many factors and is a problem that remains distinct from the interannual variation in seed production that occurs for individual trees. Thus, in red-oak populations, acorn crops can be consistent from one year to the next, because of variation between individuals each year and variation within individuals between years (Sharp, 1958; Grisez, 1975). Because each year's flowers are initiated independently of the environmental fluctuations occurring during flowering the next spring (Bonnet-Masimbert, 1978; Crawley, 1985), there is some unpredictability in fruit set. It will depend upon the success of pollination and compatibility of male and female gametes (Farmer, 1981; Stephenson, 1981; Sutherland, 1986), on the amount of resources and water available at the time of flowering and fruiting (Corti, 1959; Sharp and Chisman, 1961; Wolgast and Stout, 1977a), and will be susceptible to many environmental conditions, such as soil fertility (Wolgast and Stout, 1977b), attack by parasites and weather cues (Wood, 1938; Bonnet-Masimbert, 1973; Neilson and Wullstein, 1980; Feret *et al,* 1982; Crawley, 1983).

Two strategies have thus been described for oaks. In the long-lived species *Q robur,* Crawley (1985) has found that trees initially allocate resources to vegetative development, and once survival has been ensured, commence acorn development. In the short-lived *Q ilicifolia,* Wolgast and Zeide (1983) have shown that, at the juvenile stage, environmental stress which is not too severe can increase seed production, whereas good conditions tend to augment vegetative growth. In *Q ilex* and *Q pubescens,* acorns have been found to be lighter in years of low production (Bran *et al,* 1990). A further explanation for between-year variation in acorn production is that the trees have an "interval clock" (Sharp, 1958; Sharp and Sprague, 1967; Feret *et al,* 1982; Forester, 1990). The occurrence of unpredictable mast–fruiting years may also control populations of seed predators (Forester, 1990; Smith *et al,* 1990). Several examples of variation in the population dynamics of acorn parasites are known in relationship to the abundance of fruit production (*eg* Smith KG, 1986a,b; Smith KG and Scarlett, 1987; Hails and Crawley, 1991). Relationships have also been demonstrated between acorn size and their dispersal ability, their tolerance to parasite attacks and the vigor of young seedlings (McComb, 1934; Jarvis, 1963; Fry and Vaughn, 1977; Aizen and Patterson, 1990; Forester, 1990; Scarlett and Smith, 1991).

Breeding system

Incompatibility within and between species

From both direct experimental tests of self-pollination and crosses between half-sibs (Lumaret *et al,* 1991; Kremer and Daubrée, 1993) and indirect estimates of outcrossing rates from electrophoretic data (Yacine and Lumaret, 1988; Aas, 1991; Schwartzmann, 1991; Bacilieri *et al,* 1993; Kremer and Daubrée, 1993), it has been shown that oak species are highly self-incompatible. Hagman (1975) has stated that, in oaks, this incompatibility is due to a gametophytic control of the pollen-tube growth in the style. Interspecific crosses are not rare within the same systematic section and several cases of hybridization between sections have been reported (Cornuz, 1955-1956; Van Valen, 1976). Dengler (1941; in Rushton, 1977) and Rushton (1977) have shown that controlled crosses between *Q robur* and *Q petraea* may be successful but with variation according to the year.

Phenology

Oak trees flower during the spring in temperate regions and during the dry season in paleotropical areas (Sharp, 1958; Shaw, 1974; Kaul *et al,* 1986). It has been shown in Spain that up to 85% of *Q ilex* trees have a second flowering period during late spring or autumn (Vasquez *et al,* 1990). Only a few studies of individual tree phenology have been completed. They have shown: 1) that, among the trees of a given location, perfect synchronization from bud opening to the flowering stage does not occur; and 2) that interannual variation in flowering time may involve up to 30% of the individuals (Sharp and Chisman, 1961; Rushton, 1977; Fraval, 1986; Du Merle, 1988; Lumaret *et al,* 1991).

The success of natural crosses ultimately depends upon synchronization in flowering phenology between trees and the pattern of resource allocation to reproductive functions. In addition, there are no stable reproductive groups of individuals from one year to the next which could lead to homogamy. Such characteristics lead to a diversification of the effective pollen cloud received by each tree for a given year, and for a single tree in different years (Copes and Sniezko, 1991; Lumaret *et al,* 1991).

GENE FLOW

Levin and Kerster (1974) have defined 'potential gene flow' as the deposition of pollen and seeds from a source according to the distance. In contrast, 'actual gene flow' refers to the incidence of fertilization and establishment of reproductive individuals as a function of the distance from the source. The potential gene flow is a measure of physical dispersal, whereas to measure actual gene flow, appropriate genetic markers, *eg* isozymes and restriction fragment length polymorphism are required.

The physical dispersal (potential gene flow)

The variance in parent–offspring dispersal distribution (σ^2) has been separated into its different components by Crawford (1984) and Gliddon *et al* (1987). These authors consider this parent–offspring dispersal as consisting of 2 distinct phases, *ie* gametic and zygotic dispersal. In plant species which show significant amounts of vegetative growth, it is necessary to consider this growth as a component of dispersal. Combining these several components Gliddon *et al* (1987) have proposed the following formula:

$$\sigma^2 = \frac{t}{2}\,\sigma_p^2 + \sigma_v^2 + \sigma_s^2$$

where t is the proportion of pollen and/or ovules outcrossed, σ_p^2 is the variance in pollen dispersal from flower to flower, σ_v^2 is the variance in dispersal of flowers from the plant base and σ_s^2 is the seed dispersal variance from the flower to the site of seed germination. Each of these dispersal components is reviewed below.

Pollen dispersal

Little information exists concerning oak-pollen dispersal. The velocity of pollen-grain movement is negatively correlated with grain diameter (McCubbin, 1944; Levin and Kerster, 1974). Oak species have relatively small pollen grains (Olsson, 1975; Rushton, 1976; Solomon, 1983a,b). Niklas (1985) has shown that a higher release point allows more horizontal movement. The pollen dispersal parameters calculated for several species in table I show that the oak species *(Q robur)* has a relatively high pollen-dispersal potential. The local-mate-competition model developed by Lloyd and Bawa (1984) and Burd and Allen (1988) predicts that taller individuals reduce local-mate competition and have less saturating fitness curves due to a wider dispersal of their pollen and a higher male investment. All these models predict a large dispersal distance for the main oak species (*Quercus petraea, Q alba, Q rubra,* etc) and a relatively low

Table I. Weight, size, velocity and distance of pollen dispersal according to the model of Dyakowska and Zurzycki (1959).

Species	*W*	*S*	*V*	*D*
Dactylis glomerata	1.9	33.3	3.1	174.2
Picea abies	93.2	162	6.8	22.2
Pinus sylvestris	30.1	59	3.7	267.8
Alnus sp	9.4	24.6	2.8	546.7
Coryllus avellana	9.5	24.2	2.9	267.8
Quercus robur	18.1	24.8	4	199.0

W: weight in 10^{-9} g; S: size in μm; V: velocity in $cm \cdot s^{-1}$; D: distance in km.

pollen dispersal for the small species *(Q inkleyi).*

Several factors may act to reduce pollen dispersal, *eg* a high vegetation density, precipitation and leaf cover (Tauber, 1977). Except for the evergreen oaks, flowering begins prior to leaf expansion. Dispersal over short distances depends upon pollen production which is very variable and, in contrast, is constant for long distance (Tauber, 1977). All this information predicts a variable and high pollen-dispersal potential.

Seed dispersal

Seed dispersal is easier to observe than pollen dispersal and has thus been the subject of much research by scientists in many different disciplines (*eg* plant geneticists, plant biologists, animal behaviorists). The possession of acorns, *ie* heavy nuts dispersed by gravity, has led to the suggestion that oaks are K-selected species with low mobility (Harper *et al,* 1970). In the absence of biotic dispersal vectors, large seeds, such as acorns, move shorter distances than smaller ones (Salisbury, 1942; Harper *et al,* 1970). However, the rapid post-glacial migration of oak species has raised questions concerning how acorns are actually dispersed, since it has frequently been observed that distances of up to 300 m per year may occur (Skellam, 1951; Gleason and Cronquist, 1964; Webb, 1966; Johnson and Webb, 1989). The minimum seed-dispersal distances necessary for such range extension are equal to 7 km/generation (Webb, 1986). Mammals and birds which eat and thereby disperse acorns vary in their caching behavior: thus transport distance is highly variable.

In North America, at least 90 species of mammals are involved in acorn predation and dispersal (Van Dersal, 1940). These mammals are comprised of 2 groups, each of which has contrasting roles in acorn utilization and dispersal. First are the small mammals (*eg* mice, voles, squirrels and gophers), which trap food locally, and the larger non-caching animals (*eg* deer, hare, wild boar and bear). Mice are known to move acorns only over tens of metres from the source trees (Orsini, 1979; Sork, 1984; Jensen and Nielsen, 1986; Miayaki and Kikuzawa, 1988). Rodents appear to be the most important seed predators (Mellanby, 1967; Vincent, 1977; Vuillemin, 1978; Orsini, 1979; Jensen, 1982; Kikuzawa, 1988) and can reduce the effect of dispersal (Jensen and Nielsen, 1986). Seed-dispersal distances for squirrels may be several times larger, reaching 150 m for seeds of *Juglans nigra* dispersed by *Sciurus niger* (Stapanian and Smith, 1978), but is often less than 40 m. The habit of embryo excision in white oaks limits seed dispersal compared to the red oak (Wood, 1938; Fox, 1982).

The second category of animals moves acorns greater distances but destroys the ones they eat. Birds that feed on acorns fall into 3 groups: 1) those which do not cache acorns and destroy them (turkeys, ducks, pheasants, pigeons); 2) those which disperse and cache acorns above the ground (woodpeckers, parids, nuthatches); and 3) birds which routinely cache acorns in the soil. The first 2 groups offer virtually no opportunity for effective dispersal, although a very small number of seeds may be dispersed by these birds (Webb, 1986). The third group appears to be exclusively made up of the American and European jays. Recent research on these birds (Bossema, 1979; Darley-Hill and Johnson, 1981; Johnson and Adkisson, 1985, 1986; Johnson and Webb, 1989) provide new insight into long-distance dispersal of oaks and may help explain the patterns of vegetation–climate equilibria observed to occur after the last glaciation. Darley-Hill and Johnson (1981) found for the blue jay that the mean distance between maternal trees and their seed deposition sites was 1.1 km with a range of 100 m to 1.9 km and which could reach 5 km (Johnson and Paterson: in Darley-Hill and Johnson, 1981). Nuts were dispersed individually within a few meters of each other and were always covered with debris or soil. Covering improved germination, rooting and early growth by protecting the acorns and the radicle from desiccation and solar insulation, and scatter hoarding decreased the concentration of seeds under the parental trees and thus reduced the probability that the seeds would be eaten by other predators (Griffin, 1970; Barnett, 1977; Bossema, 1979; Forester, 1990). The occurrence of numerous oak seedlings in jay hoarding sites and the tendency for jays to hide acorns in open environments improves the chance of survival and indicates that jays facilitate the colonization of open area by oaks. Bossema (1979) concluded that for several reasons, jays and oaks can be considered as co-adapted features of symbiotic relationship.

The oak forest settlement could occur in 2 phases: 1) the arrival of colonizers following long-distance dispersal by jays; 2) population settlement following short-distance dispersal by small mammals and jays.

Vegetative dispersal

Vegetative dispersal in the genus *Quercus* can occur in two ways (Muller, 1951). The first is stump sprouting. This phenomenon is very common among oak species (*eg, Quercus rubra, Q virginiana* and *Q ilex)*. The second is rhizomatous sprouting, different types of which have been described depending upon: 1) rhizome length: from 4–20 cm for short rhizomes *(Quercus hinckleyi)* and from 0.3 m to > 1 m for long rhizomes *(Q havardii);* and 2) the origin of the rhizomes, which may either be juvenile rhizomes (terminating in a tree-habit, 1–6 m in *Q virginiana)* or rhizomes from mature trees (*Q toza* or *Q ilex).*

Even with a short rhizome, an individual can cover large areas (3–15 m in diameter) due to prolific sprout production.

In contrast to pollen and acorn dispersal, vegetative propagation is not an important component of gene flow. It can, however, participate in the maintenance of genetic variability within a population (Lumaret *et al,* 1991).

Theoretical approach (actual gene flow)

For most species, the actual movement of genes has been observed to occur over distances much smaller than those determined according to the mobility of these genes; second, a strong natural selection can overcome the homogenizing effects of gene flow and can produce local differentiation (McNeilly and Antonovics, 1968).

Several indirect approaches are available to assess actual gene flow: 1) the correlation between variables at different spatial locations (Moran's index) which measures the genetic structuration within a population and is independent of any assumption regarding population structure; 2) Wright's fixation index, F_{is} and its derivatives. F statistic quantifies the deviation of the observed genotypic structure from hardy–Weinberg proportions in terms of the heterozygote deficiency within a population for the F_{is} and between populations for the F_{st} and gives an estimation of genetic structuration. A deviation of the F_{is} from this expected value can be caused by the combined effects of random drift, selection, mating system, founder effects, assortative mating and the Wahlund effect. N_m which is the mean number of migrants exchanged among populations is calculated using the following formula (Slatkin, 1987): $N_m = (1/F_{st}-1)/4$, $(G_{st} = F_{st})$.

As indicated in table II, Wright's fixation index calculated by using enzyme markers, indicates a situation close to random mating for *Quercus ilex* (Yacine and Lumaret, 1989) and *Quercus rubra* (Schwarzmann, 1991) or a slight deficit of heterozygotes for *Q macrocarpa* and *Q gambelii* (Schnabel and Hamrick, 1990) *Q rubra* (Sork *et al*, in press) and *Q agrifolia, Q lobata* and *Q douglasii* (Millar *et al*, in press). This observed deficit of heterozygotes could not be explained by the selfing rate which is very low for all the studied species. This result has been explained by: 1) structuration within a stand (Sork *et al*, 1993) which induces Wahlund's effect; and 2) assortative mating (Rice, 1984).

As indicated in table III, gene flow between populations or between different species of oak is greater than that observed between populations of many other plant species (Govindaraju, 1988) and limits the possibility of differentiation because the number of migrants (N_m) is greater than one (Levin and Kerster, 1974). For the nuclear genome, the observed differentiation among populations is weak (Yacine and Lumaret, 1989; Schnabel and Hamrick, 1990; Kremer *et al*, 1991; Müller-Starck and Ziehe, 1991; Schwarzmann, 1991; Millar *et al*, in press; Sork *et al*, 1993). The strong structuration obtained

Table II. F_{is} data for different oak species.

Species	F_{is}	*No of pop* [a]	*No of loci*	*Ref*
Q ilex	–0.008	16	3	Yacine and Lumaret (1989)
Q rubra	–0.008	8	13	Schwarzmann (1991)
Q macrocarpa	0.026	21	26	Schnabel and Hamrick (1990)
Q gambelii	0.014	4	24	
Q agrifolia	0.087	15	12	Millar *et al* (in press)
Q lobata	0.098	7	15	
Q douglasii	0.108	7	15	
Q rubra	0.128	11	14	Sork *et al* (1993)
Northern pop	0.202	4	12	
Southern pop	0.077	7	12	

[a] pop = population.

Table III. Number of migrants per generation (N_m) among populations (pop) and between species in several oak species. The review is based on studies using nuclear markers (nucl) with biparental inheritance (*eg*, isozymes) and chloroplastic DNA (cp DNA) with maternal inheritance.

Species	N_m	*Marker*	*Reference*
Intra-specific			
Q rubra	27	Nucl	Schwarzmann (1991)
Q ilex	3.17	Nucl	Yacine and Lumaret (1989)
Q macrocarpa	3.03	Nucl	Schnabel and Hamrick (1990)
Q gambelii	1.85	Nucl	
Q agrifolia	3	Nucl	Millar *et al* (in press)
Q lobata	8	Nucl	
Q douglasii	25	Nucl	
Q rubra			Sork *et al* (1993)
Northern pop	2.99	Nucl	
Southern pop	1.07	Nucl	
Q petraea	10.60	Nucl	Kremer *et al* (1991)
Interspecific			
Q rubra 'complex'	2.65	Nucl	Manos and Fairbrother (1987)
Q alba 'complex'	0.48	cp DNA	Whittemore and Schaal (1991)
Q petraea and *Q robur*	2.62	Nucl	Kremer *et al* (1991)

by the chloroplast DNA (Whittemore and Schaal, 1991) and the low structuration observed by isozymes supports the fact that seeds are less mobile than pollen.

Chloroplast DNA variation in oaks does not reflect the species boundaries, but is concordant with the geographical location of the population. These results suggest that genes are exchanged between species, even between pairs of species that are distantly related and show limited ability to hybridize. The genotypes distributed in American (Whittemore and Schaal, 1991) and European (Kremer *et al*, 1991) oaks are thus not part of a completely isolated gene pool, but are actively exchanging genes.

The conclusion obtained from estimating the potential gene flow, *ie* that the gene flow is very high within and even between oak species, is thus further confirmed by assessment of the actual gene flow.

DISCUSSION

The life history traits of oak species (mating system, phenology, wind pollination, jay–oak co-evolution, incompatibility, sex allocation, acorn production and life span) lead to significant gene flows. This phenomenon is confirmed by the molecular markers which give the highest values obtained in the plant world.

Species occupying disturbed or transient habitats usually have a greater dispersability than those in more advanced or stable habitats (Levin and Kerster, 1974). This generality appears to hold for different oak species. For example, if we compare *Quercus robur* and *Q petraea*, it can be seen that in the former, physiological characters such as a high light requirement (Jones, 1959; Horn, 1975; Wigston, 1975; Duhamel, 1984) high pollen dispersal due to small pollen diameter, and wide acorn dispersal due to their being the European jay's preferred food (Bossema, 1979), convey a high colonizing ability. *Q petraea,* however, is the species which is more commonly found in climax communities due to its shade tolerance and its ability to replace *Q robur* during successional forest development (Rameau, 1987).

During its lifetime, a population passes through different stages: colonization, establishment, succession and extinction. Although one local population may thus be in disequilibrium, the collection of local populations (*ie* a metapopulation) may be at equilibrium (Levins, 1971; Olivieri *et al,* 1990). During these phases, the inter- and intrapopulation gene-flow intensity and pattern varies (Thiébaut *et al,* 1990). First, during the colonization stage, the trees are scattered and the pollen (Tauber, 1977) and acorns travel over large distances (Bossema, 1979; Darley-Hill and Johnson, 1981). The slight differentiation observed in the northern populations of *Q rubra* (Sork *et al,* 1993) confirms this because since the last glaciation, the number of generations has been low and structuration has not yet had time to develop. Second, during the later stages, pollen and seed dispersal are low and differentiation is more marked. The southern populations of red oak, where the number of generations is higher, show such a pattern.

The concept of a biological species advocated by Mayr (1942, 1963) as a group of organisms that are actually or potentially interbreeding is not applicable to the genus *Quercus* because it relies on a total isolation between species. Using morphological, ecological or physiological characters, several authors (Burger, 1975; Hardin, 1975; Van Valen, 1976) have discussed this problem. A model more appropriate to oaks is that which considers species as adaptative peaks, in which interspecific gene flow is balanced by selection for one or several groups of co-adapted and linked alleles (Whittemore and Schaal, 1991). This theory could explain how sympatric species are able to remain distinct despite considerable gene exchange.

The pattern of gene flow, the assessment of selection pressure and the demography of natural populations could be used to determine the limits and the amplitude of seed-collection zones and genetic resource reserves. Slatkin (1978) has developed a model which Govindaraju (1990) has applied to 2 species of pine. Such a model could also be used for the different oak species.

Falk (1990) suggests that the loss of dispersability (*ie* gene flow) could induce the decline of a species and may explain the situation of several endangered oak species *(Q inckleyi, Q tardifolia).* On the contrary, maintaining gene flow mainly improves the chance of survival for species facing habitat fragmentation (deforestation, urbanization) and global change. The activity of jays in transporting and hoarding acorns provides one hopeful sign that the main oak species may be able to shift location relatively quickly.

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