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Original article

An overview of ecology and silviculture of indigenous oaks in France

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Summary — There are nine species of oaks in French forests: *Quercus petraea, Q robur, Q pubescens, Q pyrenaica, Q ilex, Q rubra, Q suber, Q coccifera* and *Q cerris.* Among them, five are of major economic and ecological importance, either because of the quality and value of their wood or because of their geographic extension, or both. Two of these species are widespread in the hills and plains of the Atlantic and of the mid-European domains: *Q petraea* (sessile oak), and *Q robur* (pedunculate oak). Four are present in the Mediterranean region: *Q pubescens* (pubescent oak), *Q ilex* (holm oak), *Q suber* (cork oak) and *Q coccifera* (kermes oak). Pubescent oak is also present in the Atlantic and mid-European regions provided the local soil and climate conditions are favorable. The last species is of very limited extent and will not be considered further in this review. First, we will analyze the distributions of these species in France, as they result from the vegetation dynamics in Europe and the long-lasting action of man. Second, their synecology will be described, based on the empirical knowledge accumulated by botanists and phytoecologists. We will then describe the vegetation series to which they are related. We will next consider the results of ecophysiologal studies of the species, carried out in many laboratories in France and in other European countries. Finally, we will review the sylvicultural practices applied to oak forests, their productivity under different local conditions and the diverse products they yield.

France / oak / *Quercus* / taxonomy / ecology / ecophysiology / sylviculture

Résumé — Essai de synthèse sur l'écologie et la sylviculture des chênes indigènes en France. *Il y a en France neuf espèces de chênes :* Quercus petraea, Q robur, Q pubescens, Q pyrenaica, Q ilex, Q rubra, Q suber, Q coccifera, *et* Q cerris. *Parmi celles-ci cinq sont d'une importance économique et écologique certaine, soit du fait de la qualité et donc de la valeur de leur bois, soit du fait de leur extension spatiale, soit pour ces deux raisons à la fois. Deux de ces espèces sont largement répandues à l'étage collinéen des domaines atlantique et médio-européen, ce sont le chêne sessile* (Q petraea) *et le chêne pédonculé* (Q robur). *Trois autres sont bien répandus dans le domaine méditerranéen : le chêne-liège* (Q suber) *d'une part, le chêne vert (ou yeuse)* (Q ilex) *d'autre part et enfin le*

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chêne pubescent (Q pubescens) *; ce dernier pénétrant largement dans les domaines atlantique et médio-européen à la faveur de conditions pédoclimatiques favorables. Les autres espèces ont soit une distribution limitée* (Q pyrenaica)*, soit ne sont pas des arbres mais des arbustes* (Q coccifera)*. Il ne sera question ici que des premiers qui seuls jouent un rôle dans la foresterie française. On aborde d'abord la répartition géographique en France de ces espèces, telle qu'elle résulte de l'histoire des flores en Europe et de l'action séculaire des hommes, puis leur synécologie et les unités de végétation auxquels ils participent. On s'intéresse ensuite à leur écophysiologie et aux différentes sylvicultures, auxquelles ces espèces ont été ou sont encore soumises.*

France / chêne /* Quercus *// taxonomie / écologie / écophysiologie / sylviculture

INTRODUCTION

There are nine species of oaks in French forests: *Quercus pedunculata* L, *Quercus petraea* (Matt) Liebl, *Quercus pubescens* Willd (*Q toza* Bast), *Quercus pyrenaica* Willd (*Q toza* Bast), *Quercus cerris* L, *Quercus rubra* L and *Quercus ilex* L, *Quercus suber* L, and *Quercus coccifera* L, which represent 30% of the forested area and are thus the most important species in France.

Oaks in France have been the subject of many publications referring to their botanical (Camus, 1934–1952), ecological (Duchaufour, 1948), silvicultural (Perrin, 1963) and genetic (Kremer and Petit, 1993) characteristics, to name just a few.

The aim of this article is to give a general overview of oaks in France, and to clarify their distribution and importance, both ecological and economic, by integrating various types of information dispersed in different publications, whether forestry, ecological or even ecophysiological.

THE DIFFERENT SPECIES, NATURAL RANGE, CLIMATE AND SOIL

Figure 1 shows the geographic distribution of the six main species of oak which exist in France and they cover large or small areas (table I). The distribution of these species depends on the wide variety of ecological

Table I. Oak forest areas, growing stock and total volume production in France (Artificial stands for *Quercus rubra* and *Quercus cerris*).

Species	*Surface (ha)*	*Growing stock (m^3)*	*Total volume production (m^3/ha)*
Quercus robur	2 386 563	245 933 662	7 595 090
Quercus petraea	1 811 743	224 980 768	6 544 233
Quercus pubescens	855 466	46 058 583	1 743 218
Quercus ilex	342 595	11 690 168	546 713
Quercus suber	64 634	3 588 242	110 267
Quercus pyrenaica	35 152	4 288 102	158 355
Quercus cerris	380	48 549	1 616
Quercus rubra	16 855	1 685 799	101 430
Total	5 513 388	538 273 873	16 800 922

From French National Forestry Survey data, 1994.

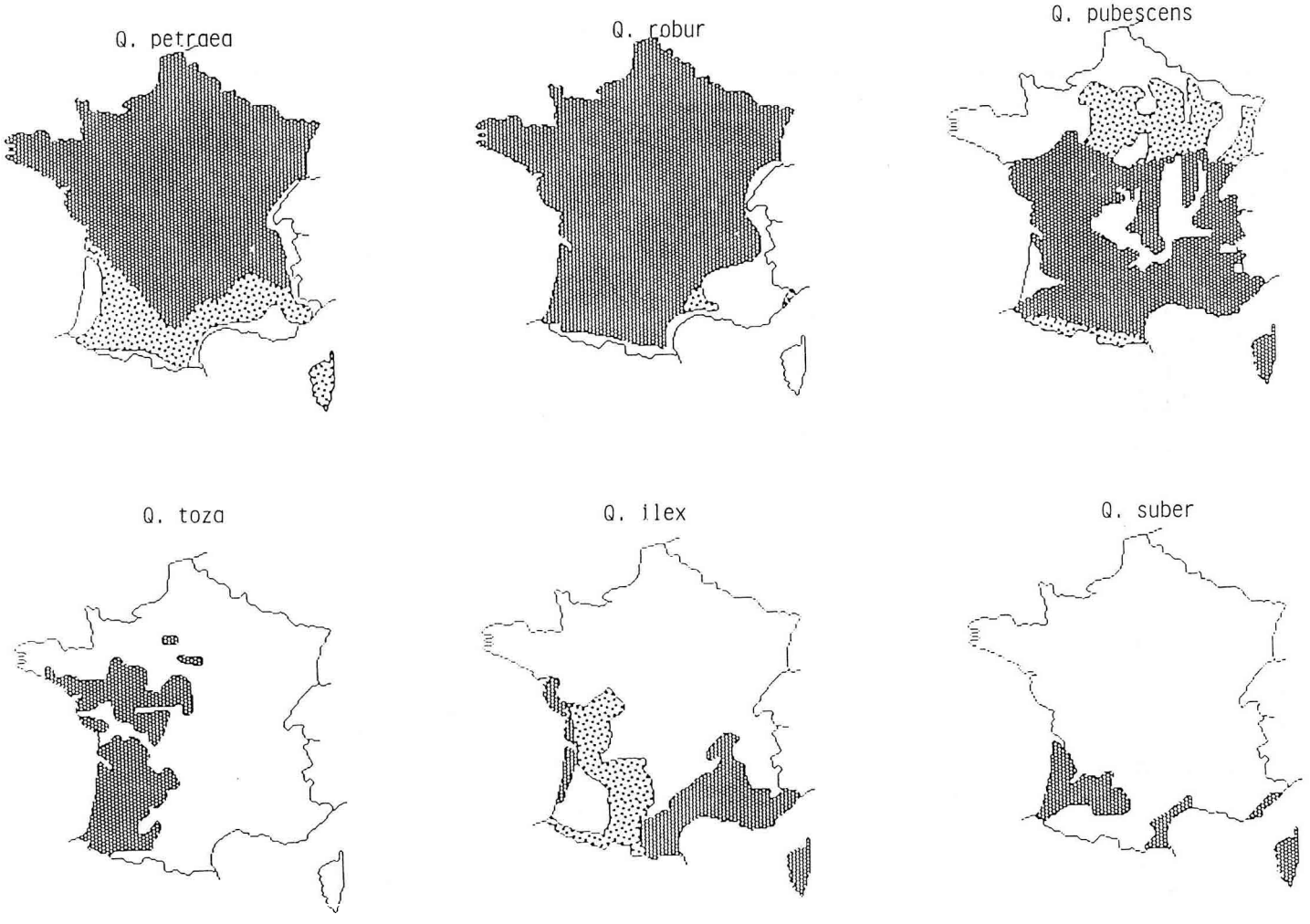


Fig 1. Areas of distribution of indigenous oak species in France. Grey-tinted area: very frequent species; dotted area: sparse species; white area: species absent. (From Rameau et al, 1989).

conditions found in France and especially on the climatic diversity: oceanic, continental and Mediterranean climates with their mountain variants.

Pedunculate oak (*Q robur* L) is the most widespread, covering 2 386 500 ha. It is found throughout France except in mountainous regions and Corsica. Sessile oak (*Q petraea* (Matt) Liebl) also covers a large area (1 812 000 ha) and is found nearly everywhere in the country except for the southwest and the Mediterranean region. These two species occur in pure or mixed stands. Pubescens oak (*Q pubescens* Willd) is the third most predominant species (855 500 ha) and is found mainly in the south of France, but also exists on calcareous soils and south-facing slopes, in a region further north. In the southwest, on acid soils, it is replaced by the Pyrenean oak (*Q pyrenaica* (Willd) (*Q toza* Bast); in fact the latter is an essentially Iberian species and only occupies 35 000 ha in France.

In the Mediterranean region, apart from pubescens oak, one finds holm oak (*Q ilex* L) (342 000 ha) on calcareous and even acid soils, and cork oak (*Q suber* L) but only on deep acid soils. The latter species is also found in the southwest near the Atlantic Ocean, and occupies a total area of 64 000 ha in France. The kermes oak (*Q coccifera* L) is another species of oak typical of the Mediterranean region, but is a moderately-sized bush which grows on shallow calcareous soils degraded by erosion and fire. The Turkey oak (*Q cerris* L) should also be mentioned as it is very rare in France, and is only found in the Jura and the Var.

In addition to the indigenous species, there are several other exotic species which have been introduced into France in parks or plantations. The most widespread in forests is the American red oak (*Q rubra* L) which covers an area of 17 000 ha in different regions of the southwest, central-west and east of France.

On a countrywide scale the distribution of oak species can be interpreted using two simple climatic parameters, mean annual temperature and annual precipitation (fig 2 and table II). On a regional and local scale, site characteristics (depth and physico-chemical properties of the soil, aspect and altitude) become preponderant and explain the presence of species. Except for *Q suber*

Table II. Annual average of optimum temperature, frost resistance mean annual rainfall and pluviometry regime for the different oak species.

Species	*Temperature (°C)*		*Mean annual rainfall* [a] *(mm)*	*Pluviometric regime* [a]
	Average annual (optimum) [a]	*Frost resistance* [b] *		
Quercus robur	13	−30	700–1 000	Oceanic
Quercus petraea	11	−30	600–800	Oceanic
Quercus pubescens	13	−20	600–900	Oceanic and Mediterranean
Quercus ilex	14	−15	500–800	Mediterranean
Quercus suber	14,5	−10	600–900	Mediterranean
Quercus coccifera	14	−5	500–800	Mediterranean
Quercus pyrenaica	13		600–1 400	Oceanic

From [a] Perrin, 1964 and [b] Aussenac and Pardé, 1985. * Temperature at first appearance of injury.

and *Q pyrenaica* which are completely calcifuge, the other species grow indiscriminately on all soil types; however, *Q pubescens* and *Q ilex* are found essentially on calcareous soils in the northern part of their range.

ECOLOGICAL AND ECOPHYSIOLOGICAL FEATURES

Today, the general ecology of oaks is understood relatively well, but unfortunately the same is not true for ecophysiological processes which are incompletely and unevenly understood depending on the species concerned, despite a large research project carried out during the last 15 years; in this domain, their characterization is still difficult.

COLD RESISTANCE

Table II shows the cold resistance thresholds (first appearance of damage in the most sensitive organs). Of all the indigenous species in French forests, *Q petraea* and *Q robur* are the most resistant (–30 °C) and reach the highest altitudes in the mountains: up to 1 300 m in southerly aspects in the Pyrenees and the Alps (table III). In spring, they are sensitive to late frosts, especially the sessile oak, as they have early bud burst. As a result, the frequency of late frosts conditions the frequency of the acorn crop and thus the ease of natural regeneration, which is difficult in certain regions, especially in the east of France. *Q coccifera* is the least resistant species (–5 °C) and is localized at low altitudes on the calcareous soils of the Mediterranean garrigue. *Q pubescens* is fairly resistant (–20 °C) but it exhibits very clear thermophilous behavior characterized by the fact that although indifferent to the nature of the soil in the Mediterranean region, it is localized on the 'warm' calcareous soils in the north of France. The same is true of *Q ilex*, which is less resistant (–14 °C); Larcher (1969) and Larcher and Mair (1969) have shown in particular that the trunks of standard trees were more resistant than trunks from coppiced boles. *Q suber* is even more thermophilous and only resists the cold to –10 °C. Winter temperatures rarely kill oaks in their natural range, but can cause serious wounds (frost

Table III. Limit of altitude (m) of oak forests in France.

Species	*Region*					
	Vosges	*Alps and Pyrenees*	*Pyrenees*	*Provence*	*Roussillon*	*Aquitaine*
Quercus robur	700	1.300				
Quercus petraea	700		1.300			
Quercus pubescens				800–1 000		
Quercus ilex				700	1.400	
Quercus suber					500	
Quercus coccifera				300	300	
Quercus pyrenaica						300

From the Vegetation Map of France, scale of 1/200.000°, CNRS ed.

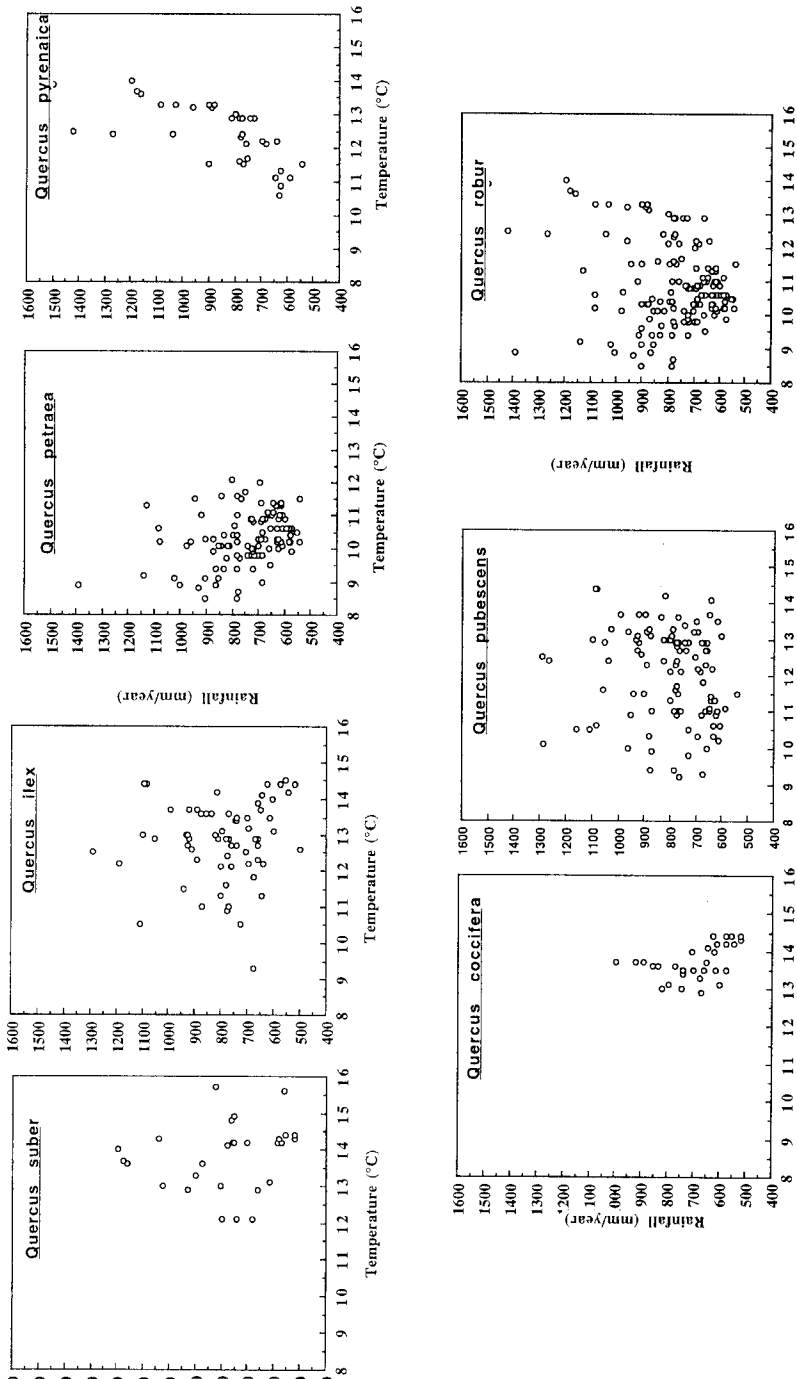


Fig 2. Relationship between mean total rainfall and mean annual temperature (each point represents a station) in different sites for indigenous oak species in France (from Meteo-France data and the Vegetation Map of France at the scale of 1/200.000°, CNRS Éd).

cracks/heart shake) especially on the trunks, which are as important to health as they are technologically. Cinotti (1989, 1990) showed that this phenomenon depended on genetic and ecological factors for *Q robur* and *Q petraea*.

DROUGHT SENSITIVITY

The distribution of oaks is also dependent on their capacity to resist drought or excess of water in the soil or even the two phenomena successively. The Mediterranean oaks, *Q pubescens*, *Q pyrenaica*, *Q cerris*, *Q ilex* and *Q coccifera*, are the most resistant to drought. *Q suber* is very different from the other Mediterranean species as it only grows on moist soils deep enough for or penetrable by its tap root system, and requires a relatively high atmospheric humidity. Drought resistance of oaks depends on various physiological mechanisms such as stomatic control of transpiration, osmoregulation, resistance to embolism of the wood vessels, morphological and anatomic properties of the leaf system and a strong rooting system which can penetrate deeply into skeletal soils. Abrams (1988) came to the same conclusions for American oaks. Such adaptations are often described as 'strategies' and demonstrate avoidance on tolerance phenomena to drought, which could be partially characterized by tree water potential and gas exchanges. They have been studied in oaks by various authors (eg, Aussenac and Valette, 1982; Scuiller, 1990; Acherar et al, 1991; Acherar and Rambal, 1992; Bréda et al, 1993; Dreyer et al, 1993; Epron et al, 1993; Vivin et al, 1993) (table IV). Mediterranean oaks are very resistant to drought; complete closure of stomata plays a part in the predawn water potentials at −3.5 to 4.0 MPa, whereas in *Q robur* and *Q petraea*, transpiration control occurs earlier during a drought and stomata close when predawn water potentials are about −1.8 to 2.0 MPa (Aussenac and Valette, 1982; Leterme, 1983; Rambal, 1984; Vignes, 1988; Epron and Dreyer, 1990; Oliviera et al, 1992). *Q robur* is more sensitive to cavitation and embolism of the sap transport vessels than other indigenous oaks (Cochard et al, 1992; Bréda et al, 1993; Dreyer et al, 1993); this seems to be the cause of its greater sensitivity to drought and the decline observed in the center of France after the severe droughts of 1996 and 1991 (Becker and Levy, 1983; Durand et al, 1983; Becker, 1984).

EDAPHIC DEMANDS

With the exception of *Q suber*, *Q pyrenaica* and *Q rubra* which are calcifuges and thus oligotrophic, the other oak species can thrive on a wide variety of soils. This is the case for *Q robur* in particular, but it does however show optimum growth in rich soils. The mineral contents of leaves give some idea of the nutrient contents and thus the nutrient deficiencies affecting the different species depending on the sites considered. Bonneau and Delmas (1985) and Bonneau (1986) published standards which are very useful for the mineral nutrition of oaks (*Q robur* and *Q petraea*, table V). Oaks are sensitive to excess water in the soil especially during the growing season. Pedunculate oak, which develops a rooting system adapted to excess water (Belgrand, 1983; Belgrand and Levy, 1986), is the most tolerant and manages to colonize marne and impermeable alluvial soils (Becker and Levy, 1990).

At the site scale, it is possible to schematize the edaphic range of oaks, using a hydrotrophic diagram, and thus to differentiate them clearly, as proposed by Rameau et al (1989) for the six main species (fig 3). In particular, the very different optima for *Q robur* and *Q petraea* can be observed.

PLACE OF OAKS IN THE VEGETATION DYNAMICS SERIES

In France, the climax (climatic) vegetation at low altitude is often oak forest. At present all oak forests are not true climax, but rather, transitional vegetation types; this phenomenon is related to the heliophilic nature of oaks, and thus their capacity to take their place, with different behavioral characteristics, in a succession leading to a true climax. Today they are considered to be postpioneer species (Rameau, 1987, 1989), intermediate between real pioneers, such as pines and birches, and the shade-tolerant species, such as beech and fir.

Because of their economic interest, oaks have often been favored by foresters to the detriment of other species. Thus, for example, in the northeastern plains of France, many oak or oak–hornbeam forests have replaced beech–oak forests after centuries of management as coppice with standards. However, one finds true climatic pedunculate oak forests in the Adour valley (southwest) and the Saône Valley (Bourgogne), and sessile oak forests on poor acid soils in central France.

SILVICULTURE AND PRODUCTIVITY OF OAK STANDS

In France, due to their capacity to produce large volumes (tables I and VI) of high quality wood with a wide range of applications, only *Q robur* and *Q petraea* are subjected to advanced silvicultural practice (Bary-Langer and Nebout, 1993). The different sensitivities of the two species to drought, revealed by decline and ecophysiological work, shows that it is important for forest managers to be able to identify correctly between the two oaks, which are botanically very similar (Dupouey, 1989), and to cultivate each under suitable ecological conditions (Becker and Levy, 1990). Of course this is essential during reforestation, but also for the management of existing stands, for which it is necessary to judge their aptness to site conditions.

For a species like oak, productivity is a function of age relative to site conditions, particularly mineral and hydric nutrition. This phenomenon can be expressed in terms of the Site Index employed in the United States. In France, the Production Tables use the theoretical concept of 'fertility class' (Decourt, 1964; Decourt and Vannière, 1984).

Table IV. Ecophysiological characteristics of French oak species.

Species	*Maximum stomatal conductance (mmol m^{-2} s^{-1})*	*Water potential at turgor less (MPa)*	*Maximum photosynthesis (μmol m^{-2} s^{-1})*
Quercus robur	980	–3.0	17
Quercus petraea	950	–3.0	17
Quercus pubescens		–3.5	8
Quercus ilex	500	–4.1	12
Quercus suber	450		15
Quercus coccifera	325	–4.1	12

From Vivin et al, 1993; Epron et al, 1993; Dreyer et al, 1993.

The present tendency is to place the idea of production into a site context, but the variety of types of forest management make the use of a single method difficult (Buffet and Girault, 1989). Besides a simple adaptation to site conditions, the type of stand has to be taken into account; for example, in the east of France, Courtoisier (1976) demonstrated that the quality of *Q petraea* wood was better when it came from stands mixed with beech than from pure oak stands.

Sessile oak is well adapted to growth in high forest stands as used in most French oak forests. *Q robur* grows well in coppice with standards, as it has larger crowns which require more light. For this species, forest management should take site conditions into account, with large clearings at very fertile sites and more careful management in mixed stands or on poor soils. Natural regeneration of sessile and pedunculate oak stands in high forest is a critical phase which depends on the ecological conditions over a relatively long period: floral induction, fruiting, germination and growth of young seedlings require the use of complicated cultural techniques which consider the ecophysiological characteristics of the two species.

The other oaks, which are managed essentially as coppice or coppice with standards, are less affected by the role of fruiting and the importance of seedlings, even though these phenomena are essential to maintain long-term viability of the stands.

CONCLUSION

With their genetic diversity oaks are present, or are potentially present, throughout France, except in the mountains above an altitude of 1 000 m, where they are replaced by beech and conifers. This remarkable phenomenon can be explained first by the inter- and intraspecific genetic variability giving rise to stands which are well adapted to the ecological conditions (climate and soil) and by the fact that they form stable and durable (climax) vegetation communities as well as transitional forest stands. Finally, in a country with an old civilization like France, it must also be remembered that oak distribution cannot be interpreted without taking man's actions into account, which have favored them to the detriment of other species. Today oaks provide high-quality timber and firewood, and also have a major role in

Table V. Standards of mineral nutrition for adult indigenous oak.

Species	*Level*	*N (%)*	*P (%)*	*K (%)*	*Ca (%)*	*Mg (%)*	*Reference*
Quercus sp	Critical	1.5					Bonneau, 1973
Quercus robur	Critical		0.13				Czerney,Fielder, 1969
Quercus robur	Correct		0.17				Czerney, 1969
Quercus robur	Correct	2.9	0.25	1.2	0.22	0.19	Ovington, 1956
Quercus robur	Correct					0.354	Stone, 19698
Quercus sp	Optimum	2.0	0.15	0.8	0.5	0.20	Bonneau, 1986
		2.5	0.20	1.3	0.8		

Table VI. Sylviculture of oaks in France: main features (treatment, rotation, stand regeneration, mean productivity and main uses).

Species	*Treatment*	*Rotation (years)*	*Regeneration*	*Production m^2/ha/year*	*Utilization*
Q robur	HF, SC conv	120–150	Nat assisted or plantation	4–8	Timber
Q petraea	HF, SC conv	120–150	Nat assisted or plantation	4–8	Timber
Q pubescens	Coppice	25	Cut back	2–3	Fuel
Q toza	Coppice	25	Cut back	1–2	Fuel
Q ilex	Coppice	25–30	Cut back	1–2	Fuel

HF: high forest; SC: standard with coppice; conv: conversion in high forest.

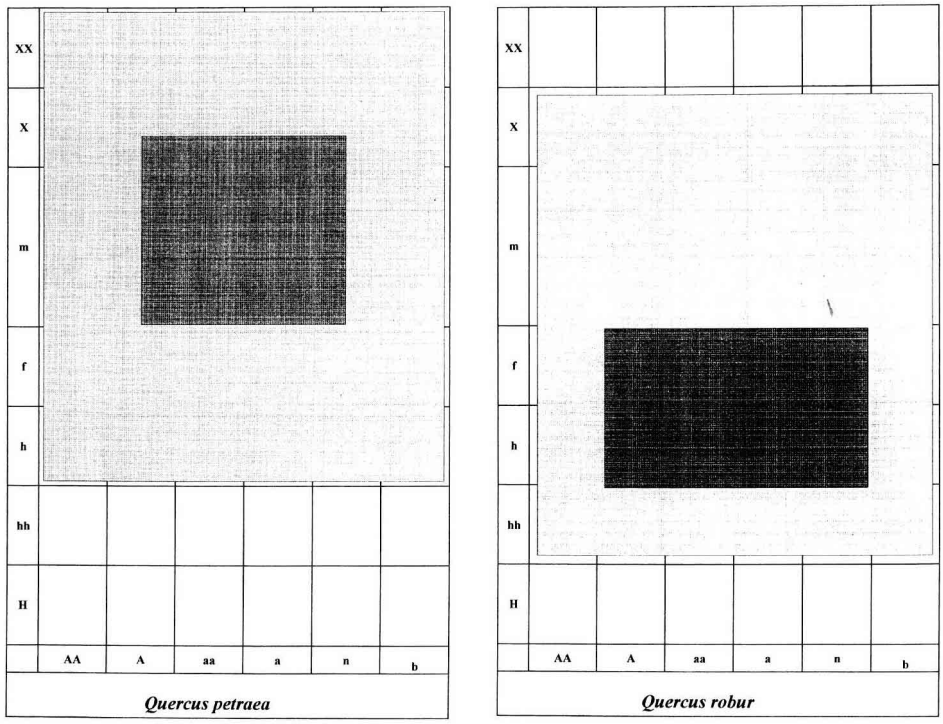
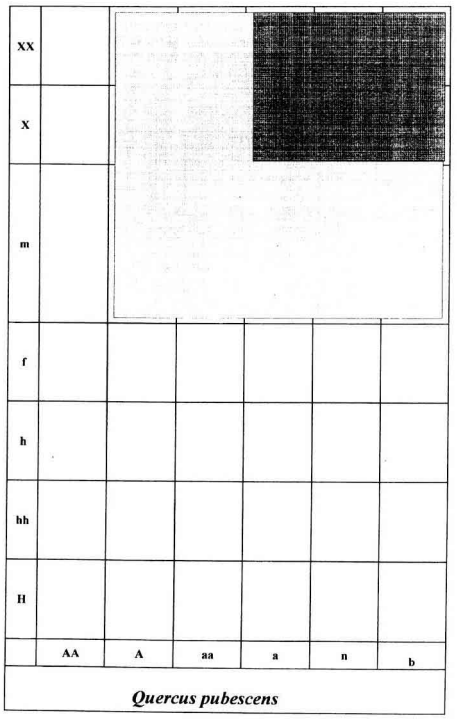
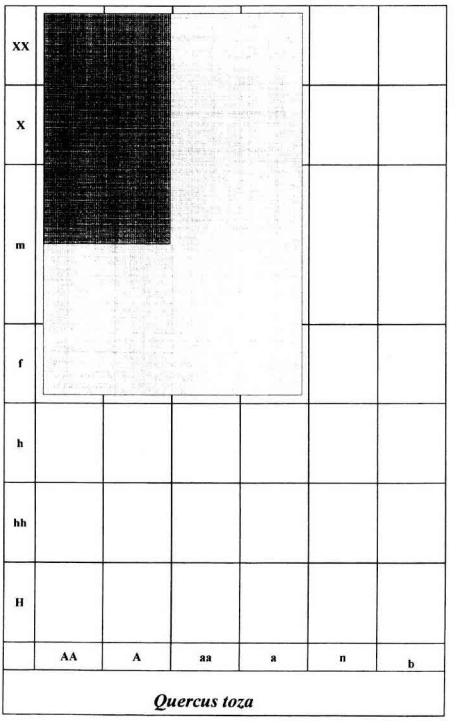


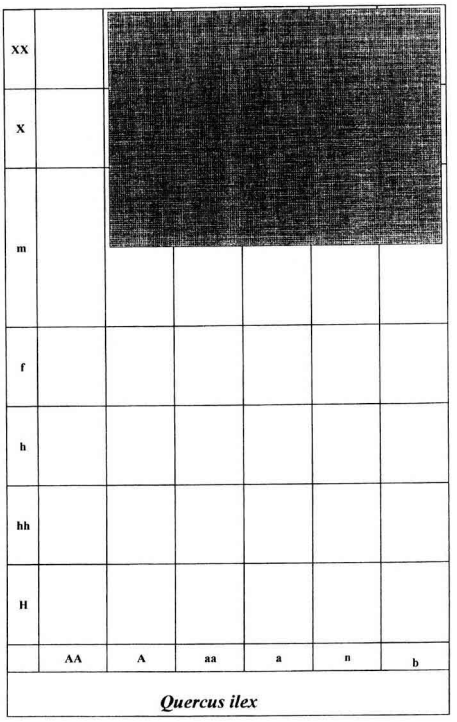
Fig 3. Soil ecological diagrams: position of indigenous oak species in relation to the acidity (AA: very acidic; A: acidic; aa: fairly acidic; a: slightly acidic; n: neutral; b: calcareous) and the humidity of soil (**xx**: very dry; x: dry; m: mesophitic; **f**: fresh; h: rather humid; hh: humid; H: waterlogged). Dark grey tinted area: optimum for the species; grey tinted area: species sparse; light grey tinted area: species very sparse (redrawn from Rameau et al, 1989).



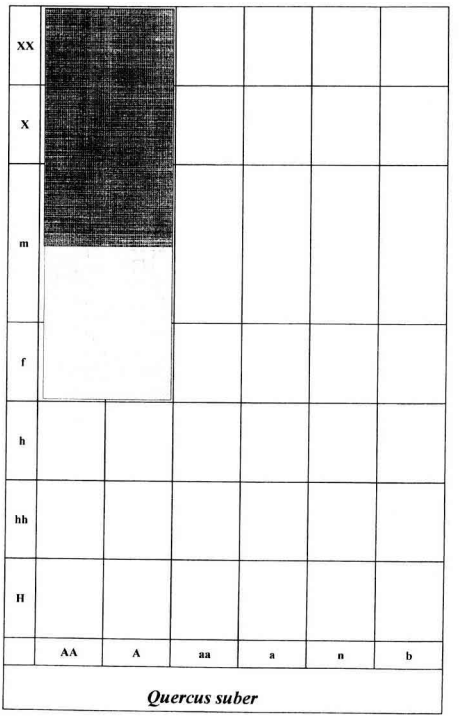
Quercus pubescens



Quercus toza



Quercus ilex



Quercus suber

wildlife conservation and biodiversity in France.

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