

## Review article

# Distribution, historical development and ecophysiological attributes of oak species in the eastern United States

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**Summary** — Approximately 30 *Quercus* (oak) species occur in the eastern United States, of which *Q. alba*, *Q. rubra*, *Q. velutina*, *Q. coccinea*, *Q. stellata* and *Q. prinus* are among the most dominant. *Quercus* distribution greatly increased at the beginning of the Holocene epoch (10 000 years BP), but has exhibited major changes since European settlement in the 18th and 19th centuries. For example, large-scale increases in *Quercus* species have occurred as a result of fire exclusion in the central tallgrass prairie and savanna regions. In the northern conifer and hardwood forests of New England and the Lake States region, *Q. rubra* exhibited a dramatic increase following early logging and fire. *Quercus* species have also increased in the mid-Atlantic region from land-clearing, the charcoal iron industry and the eradication of *Castanea dentata* following European settlement. Studies of the dendroecology and successional dynamics of several old-growth forests indicate that prior to European settlement *Quercus* grew and regenerated in uneven-aged conditions. At times oak growth was very slow (< 1.0 mm/year) for long periods, which is usually characteristic of highly shade-tolerant species. *Quercus* species exhibited continuous recruitment into the canopy during the 17th, 18th and 19th centuries, but stopped recruiting in the early 20th century. Since that time, later successional, mixed-mesophytic species have dominated understory and canopy recruitment, which coincides with the period of fire exclusion throughout much of the eastern biome. Major oak replacement species include *Acer rubrum*, *A. saccharum*, *Prunus serotina* and others. Logging of oak forests that have understories dominated by later successional species often accelerates the oak replacement process. Relative to other hardwood tree species, many oaks exhibit high fire and drought resistance. Adaptations of oaks to fire include thick bark, vigorous sprouting and resistance to rotting after scarring, as well as benefiting from fire-created seedbeds. Their adaptations to drought include deep rooting, xeromorphic leaves, low water potential threshold for stomatal closure, high gas exchange rates, osmotic adjustment and a drought-resistant photosynthetic apparatus. However, oaks typically have low tolerance for current understory conditions, despite the fact that they produce a large seed with the potential to produce an initially large seedling. Oak seedlings in shaded understories generally grow very slowly and have recurring shoot dieback, although they have relatively high net photosynthesis and low respiration rates compared to many of their understory competitors. Oak forest canopies also allow for relatively high light transmission com-

pared with later successional forest types. Thus, without severe competition from non-oak tree species, oaks should have the physiological capability for long-term survival beneath their own canopies in uneven-age (ie, gap-phase) or even-age forest conditions. I argue that fire exclusion this century has facilitated the invasion of most oak understories by later successional species, which are over-topping oak seedlings. If this condition, coupled with severe predation of oak acorns and seedlings, continues into the next century, a major loss of oak dominance should be anticipated.

### **Quercus / fire / drought / physiology / succession**

**Résumé — Les chênes de l'est des États-Unis : répartition, évolution historique et propriétés écophysiologiques.** Environ 30 espèces de chênes (*Quercus*) sont présentes dans l'est des États-Unis. Parmi elles dominent *Q. alba*, *Q. rubra*, *Q. velutina*, *Q. coccinea*, *Q. stellata* et *Q. prinus*. L'extension géographique de ces espèces s'est largement étendue au début de l'Holocène (10 000 BP), mais a subi d'importantes modifications depuis la colonisation européenne des XVIII<sup>e</sup> et XIX<sup>e</sup>s siècles. D'importantes expansions des chênaies se sont ainsi produites en réponse aux incendies dans les régions de « prairie » et de savanes du centre des États-Unis. Dans les forêts mixtes de conifères et de feuillus de la Nouvelle-Angleterre et de la région des Grands Lacs, les peuplements de *Q. rubra* se sont largement étendus à la faveur des premières coupes et des incendies. Les espèces de chênes profitèrent aussi largement des défrichages, de la métallurgie à base de charbon de bois et de l'élimination de *Castanea dentata* qui ont suivi l'installation des colons européens. Des études de dendroécologie et de dynamiques de végétation dans plusieurs forêts protégées, indiquent qu'avant la colonisation européenne les chênes se développaient et se régénéraient en peuplements non équiennes. Par moment, leur croissance restait extrêmement faible (< 1 mm par an) pendant de longues périodes, ce qui constitue une caractéristique d'espèces hautement tolérantes à l'ombrage. Les recrues de chênes se sont développées en continu du XVII<sup>e</sup> au XIX<sup>e</sup> siècle, mais ont brutalement été réduites au début du XX<sup>e</sup>. Depuis lors, des espèces d'installation plus tardive ont largement dominé dans les recrues et les sous-bois, en parallèle avec l'interdiction et la disparition des incendies de forêts. Les espèces de remplacements des chênes les plus importantes comportent *Acer rubrum*, *A. saccharum*, *Prunus serotina* et quelques autres. Les coupes effectuées dans des chênaies dont le sous-bois est dominé par des espèces d'installation plus tardive accélèrent souvent le remplacement des chênes. En comparaison avec d'autres espèces feuillues, les chênes présentent souvent de bonnes résistances à la sécheresse et au feu. Des caractéristiques comme la présence d'une écorce épaisse, une forte capacité de rejet de souche, et une bonne résistance aux pourritures après blessures, ainsi que la propension à utiliser les zones de brûlis pour la germination des glands, constituent de bonnes adaptations aux incendies. La tolérance à la sécheresse s'exprime par un enracinement profond, la présence de feuilles xéromorphes, une fermeture des stomates à des potentiels hydriques déjà faibles, des niveaux d'assimilation nette de CO<sub>2</sub> élevés, l'existence d'ajustement osmotique, et la présence d'un appareil photosynthétique résistant à la dessiccation. Cependant, les chênes présentent une faible tolérance aux conditions de sous-bois, malgré la taille des glands, potentiellement capables de produire des semis de grande taille. Les semis de chênes sous couvert ombré se développent en général très lentement, et présentent des dessèchements récurrents de leurs rameaux, malgré des niveaux de photosynthèse élevés et les faibles intensités de respiration qu'ils présentent par comparaison avec les espèces concurrentes. De plus, les chênaies se caractérisent par une relativement forte perméabilité au rayonnement lumineux en comparaison des couverts d'espèces d'installation plus tardive. De ce fait, les semis de chênes devraient présenter la capacité de survivre suffisamment longtemps sous le couvert de peuplements irréguliers, voire équiennes, s'il n'y avait pas de compétition avec d'autres espèces. Mon opinion est que l'arrêt des feux depuis le début du siècle a favorisé l'invasion de la plupart des sous-bois de chênes par des espèces plus tardives, qui concurrencent sévèrement les semis de chênes. Si ces conditions, ainsi que l'importante prédation de glands et de semis, se maintiennent pendant encore quelques décennies, nous pouvons prévoir la perte de la prééminence des chênes dans de nombreuses forêts.

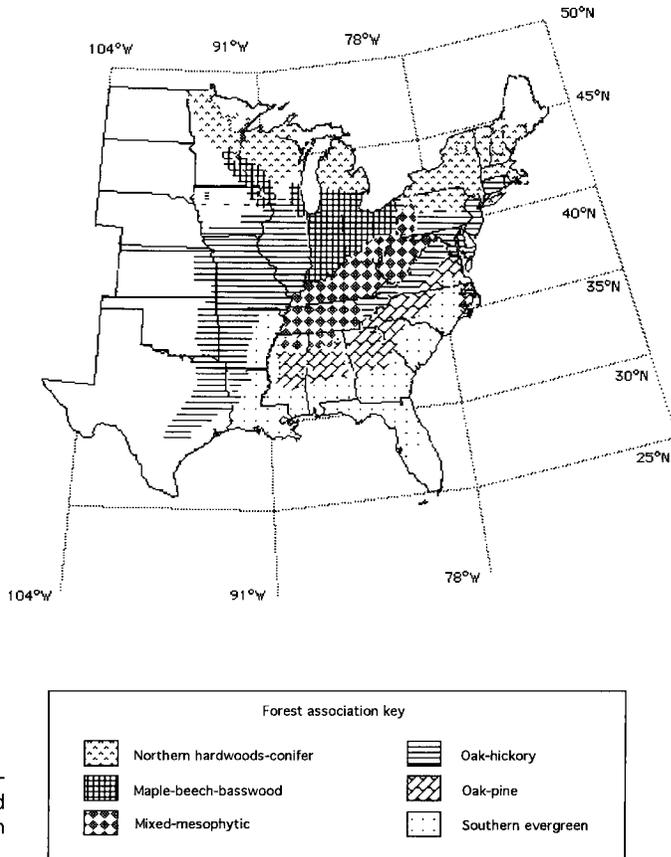
### **Quercus / feux de forêts / sécheresse / physiologie / successions végétales**

**INTRODUCTION**

In the eastern United States, temperate hardwoods dominate forest types east of the 95th meridian between 28°N and 48°N latitudes, covering the region bounded by central Maine to northern Minnesota and north central Florida to eastern Texas (Braun, 1950; Barnes, 1991). This region is considered the eastern deciduous biome, although conifer-dominated forests occur in the northeastern, north central and south-eastern regions. Oak (*Quercus*) species are one of the dominant eastern hardwood groups (Monk et al, 1990; Barnes, 1991; Abrams, 1992). Braun (1950) recognized

nine distinct hardwood-conifer forest regions in eastern North America, but for the purpose of a discussion of oak ecology, this may be simplified to six associations: northern hardwood-conifer, maple-beech-basswood, mixed-mesophytic, oak-hickory, oak-pine and southern evergreen (fig 1; cf Abrams and Orwig, 1994).

While oak species have a long history of domination in eastern North America, their present distribution in various regions exceeds that recorded in the original forests at the time of European settlement (Abrams, 1992). Much of the increase in oak during the late 18th and 19th centuries can be attributed to historical changes in distur-



**Fig 1.** Major forest associations in the eastern United States (adapted from Abrams and Orwig, 1994).

bance regimes in the eastern biome. Moreover, much of the expansion of oak has occurred on xeric or nutrient-poor sites, which indicates the stress tolerance capabilities of many oak species. However, recent evidence indicates that oak forests throughout the region rarely represent a true climax type, and thus appear to be transitional, in the absence of fire, to later successional forest types. These observations have stimulated my students and I, as well as others, to research linkages in the distribution, community dynamics and ecophysiology for oak species of the eastern United States. The purpose of this paper is to review this body of work in relation to the historical changes in oak ecology and the underlying ecophysiological mechanisms.

### CLIMATIC AND EDAPHIC CONDITIONS

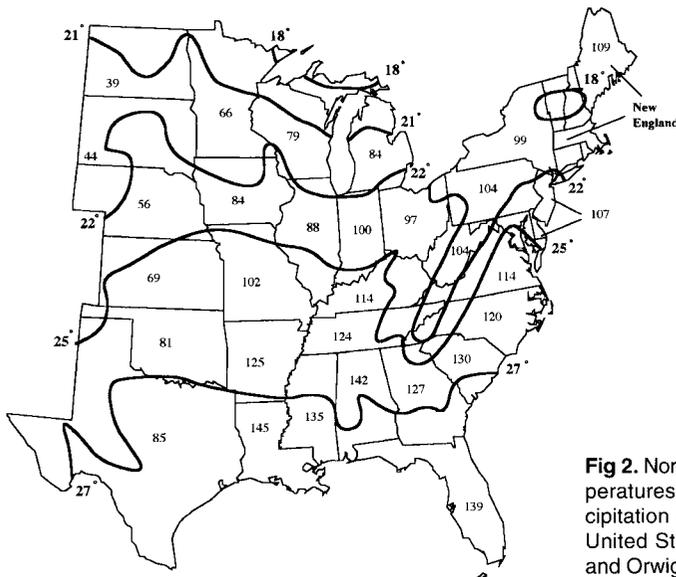
Forests of the eastern biome typically experience temperate climatic conditions (fig 2). Mean summer temperature range from 16 °C in the upper Great Lakes or 18 °C in the northeast to over 27 °C in the south.

Annual precipitation varies significantly with latitude and longitude, increasing from west to east and north to south from a low of 43 cm in North Dakota to a high of 140 cm in Louisiana. Growing season length varies from 90 days in the upper Great Lake States to 300 days in the southeastern Coastal Plain.

Eastern forests contain a variety of soil types associated with different physiographic regions. Forests in the northeast and the Lake States are typically composed of young acidic spodosols and inceptisols formed from glacial deposits under cool, moist conditions. Mid-Atlantic and mid-western forests are composed of deep alfisols, whereas inceptisols are present along the Mississippi River. These soil differences, as well as annual climatic differences, greatly influence species distribution and dominance.

### OAK FOREST ASSOCIATIONS

Approximately 30 *Quercus* species occur in the eastern United States (Elias, 1980).



**Fig 2.** Normal daily mean summer temperatures (°C) and mean annual precipitation (cm) by state in the eastern United States (adapted from Abrams and Orwig, 1994).

However, six species have particularly high dominance in much of the eastern biome; these are *Q alba*, *Q velutina*, *Q rubra*, *Q prinus*, *Q stellata* and *Q coccinea* (table I; cf Monk et al, 1990). This section will review the distribution of important oak and non-oak species for the major forest associations in the eastern United States (cf Elias, 1980; Burns and Honkala, 1990; Barnes, 1991).

### Northern hardwood-conifer

This association stretches from New England to northern Minnesota (fig 1). Several coniferous species including *Tsuga canadensis*, *Pinus strobus*, *P resinosa*, and *P banksiana* occupy this transition zone between the conifer-dominated boreal forests to the north and deciduous forests to the south. In addition to the *Quercus* species listed in table I, deciduous trees including *Acer saccharum*, *A rubrum*, *Fagus grandifolia*, *Tilia americana*, and *Betula*

*alleghaniensis* dominate mature forests throughout the association. Among the *Quercus* in this association, *Q rubra* is the most distinctly mesic in its distribution; *Quercus alba* and *Q velutina* also occur on mesic sites, but are more typical of dry-mesic conditions (cf Archambault et al, 1990). *Quercus ellipsoidalis* is one of the most xeric tree species in the association, and is restricted to the Great Lakes region. *Q macrocarpa* has a bimodal distribution that includes wet-mesic bottomlands as well as xeric upland sites.

### Maple-beech-basswood

This association includes both the beech-sugar maple and sugar maple-basswood regions described by Braun (1950), and is located in portions of the mid-west and Great Lakes region (fig 1). The climate is humid continental with summers being generally warmer than the nearby northern hardwood forests. *A saccharum* is the prominent

**Table I.** Distribution of representative upland *Quercus* species in the major forest associations in the eastern United States.

Northern hardwoods-conifer	Maple-beech- basswood	Mixed- mesophytic	Oak- hickory	Oak- pine	Southern evergreen
<i>Q alba</i>	<i>Q alba</i>	<i>Q alba</i>	<i>Q alba</i>	<i>Q alba</i>	<i>Q alba</i>
<i>Q ellipsoidalis</i>	<i>Q ellipsoidalis</i>	<i>Q coccinea</i>	<i>Q coccinea</i>	<i>Q coccinea</i>	<i>Q chapmanii</i>
<i>Q macrocarpa</i>	<i>Q macrocarpa</i>	<i>Q imbricaria</i>	<i>Q imbricaria</i>	<i>Q falcata</i> <sup>a</sup>	<i>Q falcata</i> <sup>a</sup>
<i>Q rubra</i>	<i>Q muehlenbergii</i>	<i>Q muehlenbergii</i>	<i>Q macrocarpa</i>	<i>Q marilandica</i>	<i>Q incana</i>
<i>Q velutina</i>	<i>Q rubra</i>	<i>Q prinus</i>	<i>Q marilandica</i>	<i>Q muehlenbergii</i>	<i>Q inopina</i>
	<i>Q velutina</i>	<i>Q rubra</i>	<i>Q muehlenbergii</i>	<i>Q prinus</i>	<i>Q laevis</i>
		<i>Q velutina</i>	<i>Q prinus</i>	<i>Q rubra</i>	<i>Q laurifolia</i>
			<i>Q rubra</i>	<i>Q shumardii</i>	<i>Q marilandica</i>
			<i>Q shumardii</i>	<i>Q stellata</i>	<i>Q myrtifolia</i>
			<i>Q stellata</i>	<i>Q velutina</i>	<i>Q shumardii</i>
			<i>Q velutina</i>		<i>Q stellata</i>
					<i>Q velutina</i>
					<i>Q virginiana</i>

<sup>a</sup> *Q falcata* var *falcata*.

species throughout the region, and it shares overstory dominance with *F grandifolia* on the gently rolling till plains of Ohio and Indiana, and with *Tilia americana* in southwestern Wisconsin, northwestern Illinois, northeastern Iowa and southeastern Minnesota. Several *Quercus* species and *Ulmus rubra*, *U americana*, *A rubrum*, *Liriodendron tulipifera* occur as common associates (table I). This association shares many *Quercus* species with the northern hardwoods, but does include *Q muehlenbergii* which occurs on xeric sites in the mid-western region.

### **Mixed-mesophytic**

This association was originally classified separately as mixed and western mesophytic forests (Braun, 1950). The broad classification of this group was required due to the highly varied dominance of many different overstory species, commonly 25 tree species or more per hectare. The association stretches southward from the Appalachians of western Pennsylvania through West Virginia and into the Cumberland Mountains of Kentucky and Tennessee (fig 1). *Aesculus octandra*, *Tilia heterophylla* and *Magnolia acuminata* are characteristic indicator species of this forest type. Additional overstory associates include *F grandifolia*, *L tulipifera*, *A saccharum*, *Prunus serotina*, *T americana* and the seven *Quercus* species listed in table I. Many of the *Quercus* species found in this region are also typical of the northern hardwoods or maple-beech-basswood associations, except *Q coccinea* and *Q imbricaria* which occur on mesic, dry-mesic and xeric sites.

### **Oak-hickory**

The original oak-hickory and the oak-chestnut regions of Braun (1950) are included in this association (fig 1). Former oak-chest-

nut forests are now oak-hickory or mixed-oak forests due to the eradication of overstory chestnut (*Castanea dentata*) by chestnut blight disease during the early part of this century. Western portions of this vegetation type include the Texas Coastal Plain north through the Ouachita and Ozark Plateau provinces and southern Lake States (fig 1). Vegetation growing in close proximity to the tallgrass prairie region may form a forest-prairie transition type consisting of scattered, open-grown oaks with a grassy understory in Missouri, Iowa and eastern Nebraska and Kansas. Eastern portions of these forests presently stretch from the previously glaciated sections of southern New England into western North Carolina and eastern Tennessee (fig 1).

*Quercus alba* and *Q velutina* are two of the most important species throughout the oak-hickory association. The dominant hickory species in the association are *Carya cordiformis*, *C tomentosa*, *C ovata* and *C glabra*. A variety of additional oak species exist in different geographic locations within this type, including the more xeric landscape located west of the mixed-mesophytic association (table I). Prominent southern and western oak species include *Q stellata* and *Q marilandica* on xeric sites and *Q shumardii* on more mesic sites. In the northern and central regions, *Q macrocarpa*, *Q ellipsoidalis* and *Q muehlenbergii* assume greater importance. Oak savannas are common in the western provinces, where xeric conditions and periodic fire have historically precluded the formation of closed forests. The most successful species in these savannas include *Q stellata*, *Q marilandica*, *Q macrocarpa*, *Q velutina* and *Q alba*.

### **Oak-pine**

This region lies between the eastern and western extension of the oak-hickory association, and includes a codominance of

*Pinus* species. The majority of this vegetation type resides within the gently rolling Piedmont Plateau province which encompasses Virginia, the Carolinas and portions of Georgia, as well as the Coastal Plain forests of Alabama and Mississippi (fig 1). Several oak and hickory species (table I) are the dominant canopy associates along with a mixture of transitional, even-aged pine forests containing *Pinus taeda*, *P. echinata*, *P. palustris* and *P. virginiana*. The complement of *Quercus* species in this association is similar to that in the oak-hickory association, except for the importance of *Q. falcata* var *falcata* on dry-mesic to xeric sites from New Jersey to eastern Texas. Interesting variants of this vegetation type are found in the fire-prone pine barrens of New Jersey, Cape Cod and Long Island, which are dominated by *P. rigida*, and occasionally *P. echinata*, in association with shrub-formed *Q. ilicifolia* and *Q. prinoides*.

### **Southern evergreen**

This vegetation association is confined to the southeastern Coastal Plain from Virginia to the Gulf Coastal area of Texas, and includes a high diversity of *Quercus* species (fig 1; table I). *Pinus palustris* is the characteristic species along with the evergreen trees *Q. virginiana* and *Magnolia grandiflora*. Spanish moss (*Tillandsia*) commonly blankets these forests, accentuating their evergreen character. Xeric sites are located on sand hills originating from ancient shorelines in portions of the Carolinas, Georgia, western Florida and southern Alabama and Mississippi. Dominant species on the more xeric sites include *Pinus elliotii*, *P. palustris*, *Q. laevis*, *Q. incana*, *Q. marilandica*, *Q. falcata* var *falcata* and *Q. stellata*. On mesic sites, *Q. laurifolia* and *Q. virginiana* become more prominent. An additional variation of the southeastern evergreen forest include sand pine scrub, dominated by *P. clausa*

and understory scrub oaks *Q. inopina*, *Q. myrtifolia* and *Q. chapmanii* (table I).

### **HISTORICAL DEVELOPMENT OF EASTERN OAK FORESTS**

Evidence indicates that the distribution and dominance of *Quercus* species increased for a period of time following European settlement in much of the eastern deciduous biome. This section will highlight several case studies that illustrate the major changes and developmental pathways of *Quercus* that has occurred as a direct or indirect result of anthropogenic influences over the last two centuries.

#### ***Oak ecology in tallgrass prairie***

Prior to European settlement, tallgrass prairie and oak savannas dominated vast areas of the Central Plains, southern Lake States and mid-western regions of the United States (Kuchler, 1964; Nuzzo, 1986). Much of this region is now part of oak-hickory forest association. Tallgrass prairie and oak savannas in this drought-prone region were maintained by frequent fire at 1- to 10-year intervals that were initiated by Indian (Native American) activity or lightning strikes (Cottam, 1949; Day, 1953; Pyne, 1983; Axelrod, 1985; Abrams, 1992).

Eastern Kansas represents the western limit of the eastern deciduous forest, and oak species often grow along streams and ravines forming relatively thin bands of "gallery" forests. A study of the forests in a Kansas (Konza) tallgrass prairie was completed to characterize the composition, structure, development and successional dynamics of this oak-dominated forest type (Abrams, 1986). The range of sites on Konza Prairie included mesic riparian benches to xeric limestone ridges. Tree

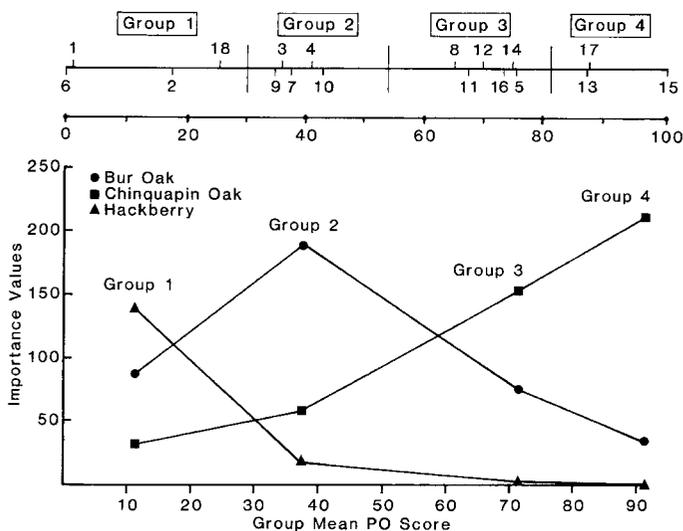
species importance varied with site moisture relations with *Celtis occidentalis* - *Q macrocarpa* (Group 1), *Q macrocarpa* (Group 2), *Q muehlenbergii* - *Q macrocarpa* (Group 3) and *Q muehlenbergii* (Group 4) dominating forests along a continuum from mesic to xeric, respectively (fig 3). In each of the 18 gallery forests studied, oak species represented the oldest and largest individuals, whereas the understory trees and regeneration layers were dominated primarily by *C occidentalis*, *Ulmus rubra* and *U americana*, and *Cercis canadensis*. An analysis of the historical records, including the original land survey in 1858 and aerial photographs taken in 1939 and 1978, indicated that the extent of the gallery forests has greatly expanded from about 5 ha at the time of settlement to over 200 ha at present.

This study exemplifies a major developmental pathway of oak forests in the western oak-hickory association. High fire frequency and intensity during the period of Indian habitation maintained tallgrass prairie species and retarded oak distribution, relegating oak species to savannas and pro-

tected woodlands (fig 4). Following European settlement, the influence of fire decreased due to road construction, expansion of towns, cattle grazing, fire suppression activities and the elimination of Indian fire activity (Pyne, 1983; Abrams, 1986). With less fire, oak species expanded into the tallgrass prairie vegetation, with *Q macrocarpa* and *Q muehlenbergii* dominating mesic and xeric sites, respectively, in this example. Thus, a significant proportion of the oak-hickory forest in the former tallgrass prairie region is a recent phenomenon in response to fire exclusion following European settlement (Gleason, 1913; Kucera, 1960).

### Oak ecology in northern hardwood-conifer forests

Presettlement forests of the upper Lake States and northeast were dominated by *Tsuga canadensis*, *Pinus strobus*, *A saccharum*, *F grandifolia* and *Betula allegheniensis*, with generally a very small percentage of *Quercus* (eg, *Q alba*, *Q rubra* and *Q velutina*) (McIntosh, 1962; Siccama,



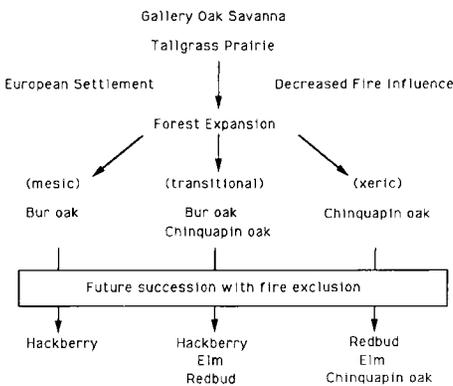
**Fig 3.** Polar ordination (PO) analysis and the mean importance values for the dominant tree species in 18 gallery forest stands on Konza Prairie in eastern Kansas. The four stand types are labeled Groups 1–4 (after Abrams, 1986).

1971; Finley, 1976; Whitney, 1986). In contrast, *Quercus* species now represent a significant proportion of northern hardwood-conifer forests, and *Q. rubra* in particular has developed prominence (Whitney and Davis, 1986; Crow, 1988). We studied the presettlement forest records and current forest composition and structure of 46 *Q. rubra* forests along an edaphic gradient in north-central Wisconsin to gain an understanding of their historical development and current and future ecological status (Nowacki et al, 1990).

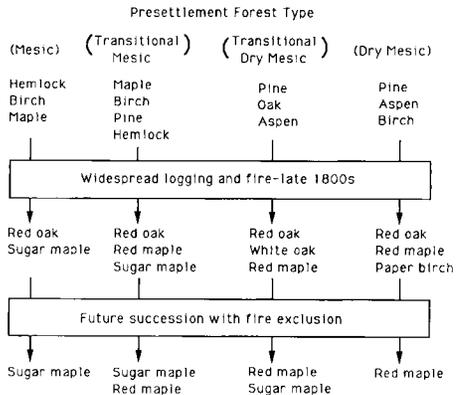
Prior to European settlement, forests on mesic and transitional mesic sites in the study area were dominated by *Tsuga canadensis*, *Betula*, *Acer* and *Pinus* (fig 5). Transitional dry-mesic sites formerly comprised *Pinus*, *Quercus* (*Q. velutina*, *Q. macrocarpa* and *Q. alba*) and *Populus*, while dry-mesic sites were dominated by *Pinus*, *Populus* and *Betula*. In contrast, many forests of the region are presently dominated by *Q. rubra*, with relative importance values of 37–51% (Nowacki et al, 1990). Other important overstory trees included *Acer rubrum* on transitional and dry-mesic sites, *A. saccharum* on mesic and transi-

tional mesic sites, *Q. alba* on transitional dry-mesic sites and *Betula papyrifera* on dry-mesic sites (fig 5). Understory trees and reproduction layers were dominated primarily by *A. saccharum* on mesic sites, *A. saccharum* and *A. rubrum* on transitional sites and *A. rubrum* on dry-mesic sites.

The results of this study indicate another major developmental pathway for *Quercus* in eastern North America, namely *Q. rubra* expansion in northern hardwood-conifer forests. *Quercus rubra* on mesic and transitional mesic sites developed following disturbance to the original conifer-northern hardwood forests (fig 5). Forests on transitional dry-mesic and dry-mesic sites developed from former oak-pine and pine forests, respectively. A postsettlement increase in *Q. rubra* has been documented in other forests in the northeastern and Lake States regions (cf Elliot, 1953; Whitney, 1986, 1987; Whitney and Davis, 1986; Crow, 1988; Abrams, 1992), and appears to be a direct result of widespread cutting and subsequent fire in the middle to late 1800s and early 1900s. Evidence indicates that *Q. rubra* in the overstory was present in relatively low numbers in presettlement forest, but may



**Fig 4.** Historical development of oak forests in eastern Kansas and future succession with fire exclusion (after Abrams, 1986).



**Fig 5.** Historical development of northern red oak forests in north-central Wisconsin and future succession with fire exclusion (after Nowacki et al, 1990).

have been pervasive in the understory of the former pine forests. This coupled with the widespread dispersal of acorns by birds and small mammals facilitated the expansion of this species following large-scale disturbances of the original northern hardwood-conifer forests (Crow, 1988).

### **Postsettlement variations in eastern mixed-oak forests**

Presettlement forests of southern New England and the mid-Atlantic region were dominated by *Quercus* in combination with other species (table II). The leading tree species were *Q. alba*, *Q. velutina*, *Q. rubra*, *Q. prinus*, *Carya* spp., *Castanea dentata* and *Pinus* spp (including *P. strobus* and *P. rigida*). Evidence from eye witness accounts and charcoal studies indicate that precolonial fires from Indian activity and lightning strikes were pervasive in the region and probably played an important role in the long-term stability of

these forest types (Day, 1953; Watts, 1980; Lorimer, 1985; Patterson and Sassaman, 1988; Abrams, 1992).

As in other regions of eastern North America, disturbances associated with European settlement had a dramatic impact on the original oak-hickory and oak-pine forests. Widespread logging and increased fire associated with land clearing, the charcoal iron industry, tanbark and chemical wood cuts and lumbering of high quality hardwood and conifers (eg, *P. strobus* and *Tsuga canadensis*) occurred during the initial settlement period (Pearse, 1876; Abrams and Nowacki, 1992; Russell et al, 1993; Mikan et al, 1994). In one example from central Pennsylvania, there were nine active iron furnaces and ten forges in Centre County in 1826, which were responsible for the clearing of vast forest acreage each year for charcoal production (Abrams and Nowacki, 1992). By the mid-1800s iron production slowed in the region due, in part, to the unavailability of wood. This type of disturbance regime was respon-

**Table II.** Presettlement forest types in the oak-hickory and oak-pine associations of the eastern United States.

<i>Presettlement composition</i>	<i>State</i>	<i>References</i>
<i>Q. alba</i> - <i>Q. velutina</i> - <i>Pinus</i>	MA	Whitney and Davis, 1986
<i>Q. alba</i> - <i>Q. velutina</i> - <i>Carya</i>	NY	Glitzenstein et al, 1990
<i>Q. rubra</i> - <i>Castanea dentata</i>	NJ	Ehrenfeld, 1982
<i>Q. alba</i> - <i>Q. velutina</i> - <i>C. dentata</i> - <i>Carya</i>	NJ	Ehrenfeld, 1982
<i>Q. alba</i> - <i>Q. velutina</i> - <i>Carya</i>	NJ	Russell, 1981
<i>Q. alba</i> - <i>Q. velutina</i> - <i>Carya</i>	PA	Abrams and Downs, 1990
<i>Q. velutina</i> - <i>Q. alba</i> - <i>C. dentata</i> - <i>Carya</i>	PA	Mikan et al, 1994
<i>Q. prinus</i> - <i>Q. alba</i> - <i>Pinus rigida</i> - <i>C. dentata</i>	PA	Nowacki and Abrams, 1992
<i>Q. alba</i> - <i>P. strobus</i> - <i>Carya</i>	PA	Nowacki and Abrams, 1992
<i>Q. alba</i> - <i>Q. rubra</i>	VA	Spurr, 1951
<i>Q. alba</i> - <i>Q. rubra</i> - <i>Q. prinus</i> - <i>Carya</i> - <i>Pinus</i>	VA	Spurr, 1951
<i>Q. alba</i> - <i>Q. rubra</i>	VA	Orwig and Abrams, 1994
<i>C. dentata</i> - <i>Q. rubra</i>	VA	Braun, 1950
<i>Q. rubra</i> - <i>Q. prinus</i> - <i>C. dentata</i>	VA	Braun, 1950; Stephenson, 1986
<i>Q. alba</i> - <i>C. dentata</i> - <i>Carya</i> - <i>Pinus</i>	WV	Abrams et al, 1995
<i>C. dentata</i> - <i>Q. prinus</i> - <i>Q. rubra</i> - <i>Carya</i>	TN, NC	Woods and Shanks, 1959

sible for significant changes in species assemblages. In central Pennsylvania, the original *Q alba* – *P strobus* – *Carya* forests that were clear-cut and burned in the 1800s became dominated almost exclusively by *Q alba* and *Q velutina* (Abrams and Nowacki, 1992). Cutting for charcoal in New Jersey resulted in the increased dominance of *Quercus* and *Betula*, and decreased dominance of *Tsuga* and *Fagus* (Russell, 1980). The importance of *Quercus rubra* increased from 7% in presettlement *P strobus* forests in Massachusetts to nearly 20% in present-day forests in response to land-clearing and logging (Whitney and Davis, 1986). The decrease in *T canadensis* and *P strobus* in these examples can be related, at least in part, to their inability to reproduce vegetatively.

Another major anthropogenic influence to eastern *Quercus* forests has been the introduction of the chestnut blight fungus (*Endothia parasitica*) during the early 1900s. This fungus has been responsible for the elimination of overstory *C dentata* throughout the eastern biome. The changes to former chestnut-dominated forests has been the subject of several studies, most of which indicate that *Quercus* species were one of the major beneficiaries of this disturbance. For example, former oak-chestnut forests in North Carolina became dominated by *Q rubra*, *Q prinus*, *Q alba* and *Carya* spp (Keever, 1953) (tables II and III). In southwestern Virginia, *Q rubra* represented 69% importance in forests where *C dentata* formerly comprised up to 85% of the canopy (Stephenson, 1986). In the ridges of central Pennsylvania, *Q prinus*, *Q rubra* and *Acer rubrum* increased where *Castanea* and *Pinus* were previously important (Nowacki and Abrams, 1992). Thus, postsettlement disturbances to eastern forests via land-clearing, the charcoal iron industry, lumbering and the chestnut blight have led to increases in *Quercus* above levels estimated in the original forest.

## DENDROECOLOGY AND COMMUNITY DYNAMICS OF EASTERN OAK FORESTS

Coupling of composition, age-diameter and tree ring data provides a powerful tool for analyzing long-term species recruitment patterns, records of suppression and release, stand dynamics in relation to disturbance or climatic factors, and successional change. This information is greatly lacking in eastern oak forests, but has been the subject of several studies over the last few years. This section will describe the dendroecology and succession dynamics of several old-growth and second-growth oak dominated forests in the eastern United States.

### *Dynamics of an old-growth white oak-white pine forest*

*Q alba* and *P strobus* dominated the original forests on mesic valley floor sites within the eastern Ridge and Valley Province, which extends from southeastern New York to southern Tennessee (Braun, 1950). The composition, diameter and age structure, and radial growth chronologies were studied in one of the few remaining undisturbed remnants of this forest type located in southern West Virginia (Abrams et al, 1995). The forest is presently dominated by *P strobus* (34%), *Q alba*, *Q rubra* and *Q velutina* (26% total) and *Acer rubrum* (24%), and is uneven-aged with *Q alba* (max age = 295 years) and *P strobus* (max age = 231 years) representing the oldest and largest trees (fig 6). *Q alba* exhibited continuous recruitment into the tree size classes from 1700–1900, whereas peak recruitment of *P strobus* occurred between 1830 and 1900. Interestingly, the increase in *P strobus* was followed by a wave of *Q rubra* and *Q velutina* recruitment, suggesting possible facilitation of these red oaks by *P strobus* (cf Crow, 1988; Abrams, 1992). After 1900,

**Table III.** Overstory and understory composition reported for *Quercus* forests in the major vegetation associations of the eastern United States.

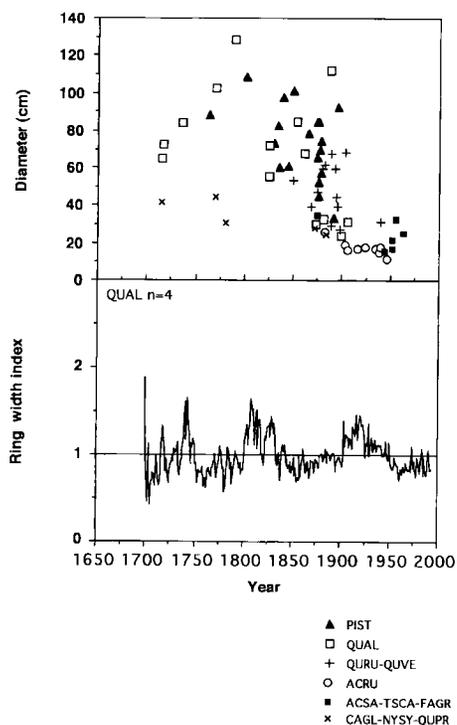
Overstory	Understory	State	Reference
Oak-hickory			
<i>Q macrocarpa, Celtis occidentalis</i>	<i>C occidentalis, Ulmus</i>	KS	Abrams 1986
<i>Q muehlenbergii</i>	<i>Ulmus, Cercis canadensis, Q muehlenbergii</i>	KS	Abrams, 1986
<i>Q velutina, Q alba</i>	<i>Prunus serotina, Acer negundo, Ulmus</i>	WI	McCune and Cottam, 1985
<i>Q marilandica, Q stellata</i>	<i>Q marilandica, Q stellata</i>	OK	Rice and Penfound, 1959
<i>Q alba, Carya ovata</i>	<i>A saccharum</i>	IL	Adams and Anderson, 1980
<i>Q alba</i>	<i>A saccharum</i>	MO	Pallardy et al, 1988
<i>Q alba, Q velutina</i>	<i>A rubrum, A saccharum, Betula lenta</i>	NJ	Little, 1974
<i>Q alba, Fagus grandifolia</i>	<i>A rubrum, A saccharum, P serotina</i>	PA	Abrams and Downs, 1990
<i>Q alba, Q velutina</i>	<i>A rubrum, P serotina</i>	PA	Abrams and Nowacki, 1992
<i>Q prinus, Q rubra</i>	<i>A rubrum, Q prinus, B lenta</i>	PA	Nowacki and Abrams, 1992
<i>Q prinus</i>	<i>A rubrum, B lenta, B alleghaniensis</i>	PA	Mikan et al, 1994
Oak-pine			
<i>Q alba, Liriodendron tulipifera</i>	<i>Nyssa sylvatica, Cornus florida</i>	VA	Orwig and Abrams, 1994
<i>Q alba, Q coccinea</i>	<i>N sylvatica, A rubrum, C florida</i>	VA	Orwig and Abrams, 1994
<i>Q alba, Q prinus, Q coccinea</i>	<i>N sylvatica, Carya, C florida</i>	VA	Farrell and Ware, 1991
<i>Q rubra</i>	<i>A saccharum, A rubrum</i>	VA	Stephenson, 1986
<i>Q alba</i>	<i>A rubrum</i>	NC	Christensen, 1977
<i>Q rubra, Q prinus, Q alba</i>	<i>Q rubra, A rubrum, Carya</i>	NC	Keever, 1953
Maple-beech-basswood			
<i>Q alba, Q velutina</i>	<i>P serotina, A rubrum</i>	MI	Dodge and Harman, 1985
<i>Q macrocarpa, Q alba</i>	<i>A saccharum, Fagus grandifolia</i>	OH	Cho and Boerner, 1991
<i>Q alba, Q rubra, Q velutina</i>	<i>A saccharum, F grandifolia, A rubrum</i>	OH	McCarthy et al, 1987
<i>Q alba, Q velutina, Q rubra</i>	<i>A saccharum, F grandifolia</i>	IN	Schmelz and Lindsey, 1970
<i>Q rubra, Q alba, Q macrocarpa</i>	<i>A saccharum, Aesculus glabra</i>	IN	Parker et al, 1985
Northern hardwood-conifer			
<i>Q velutina, Q rubra, Pinus strobus</i>	<i>A rubrum</i>	MA	Lorimer, 1984
<i>Q prinus, Q rubra</i>	<i>A rubrum, A saccharum</i>	NY	McIntosh, 1972
<i>Q velutina, Q alba</i>	<i>A rubrum</i>	MI	Host et al, 1987
<i>Q rubra, Q alba</i>	<i>A saccharum, A rubrum</i>	WI	Nowacki et al, 1990
<i>Q ellipsoidalis</i>	<i>P serotina, A rubrum</i>	WI	Reich et al, 1990
Mixed-mesophytic			
<i>Q alba, P strobus</i>	<i>A rubrum, F grandifolia, Tsuga canadensis</i>	WV	Abrams et al, 1994
<i>Q alba, Q coccinea, Q prinus</i>	<i>A rubrum, A saccharum, F grandifolia</i>	KY	Muller and McComb, 1986
<i>Q alba, Q velutina</i>	<i>A rubrum, N sylvatica</i>	KY	Campbell, 1987
<i>Q prinus, Q alba</i>	<i>Q prinus, Q alba</i>	TN	Schmalzer, 1988
Southern evergreen			
<i>P palustris, P elliotii, Q laevis</i>	<i>Q laevis, Q geminata, Carya floridana</i>	FL	Myers, 1985
<i>F grandifolia, Q laurifolia, Magnolia</i>	<i>Liquidamber styraciflua, N sylvatica, Fagus</i>	GA	Quarterman and Keever, 1962

*Pinus* and *Quercus* recruitment stopped, while that of *A. rubrum*, *A. saccharum*, *F. grandifolia* and *T. canadensis* greatly increased.

Radial growth analysis of the four oldest *Q. alba* indicated a series of releases between 1710 and 1740, 1800 and 1830 and 1900 and 1930, with low or decreasing growth in the interim and most recent periods (fig 6). In the early 1800s, releases in radial growth were associated with high *P. strobus* recruitment, while releases in the

early 1900s coincided with episodic *A. rubrum* recruitment. Individual radial growth chronologies for trees of various species and age classes indicated a series of major and moderate releases every 20–30 years throughout the forest (data not shown). The asynchronous nature of these releases suggest a series of small-scale disturbances with localized impacts.

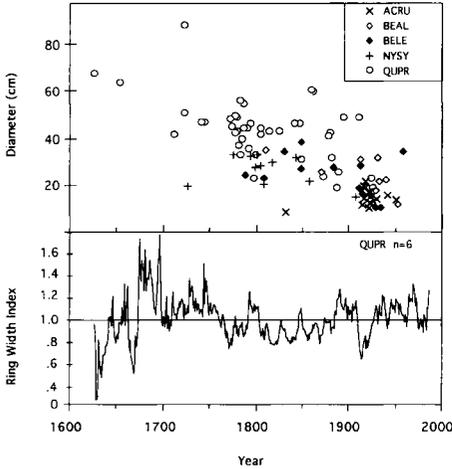
We found evidence of fire scars, soil charcoal and windthrow throughout the forest, and believe that these disturbance factors significantly influenced the ecology of this old-growth forest. *Quercus* and *Pinus* perpetuated themselves during the 1600s, 1700s and 1800s, but not in the 1900s, despite evidence of blowdown during this century. These data are consistent with the fire exclusion hypothesis, which led to a shift in tree recruitment from *Quercus* and *Pinus* to *Acer*, *Fagus* and *Tsuga*. Without intensive management in the future, including prescribed fire, we predict this forest will no longer support a significant *Quercus* and *Pinus* component.



**Fig 6.** Mean ring width index for the four oldest white oak and age-diameter data for all cored trees in an old-growth white pine-mixed oak forest in southern West Virginia (adapted from Abrams et al, 1995). PIST: *Pinus strobus*; QVAL: *Quercus alba*; QURU: *Q. rubra*; QUVE: *Q. velutina*; ACRU: *Acer rubrum*; ACSA: *A. saccharum*; TSCA: *Tsuga canadensis*; FAGR: *Fagus grandifolia*; CAGL: *Carya glabra*; NYSSY: *Nyssa sylvatica*; QUPR: *Q. prinus*.

### **Dendroecology of old-growth *Quercus prinus***

We identified an old-growth *Q. prinus* forest on a dry talus slope with canopy trees up to 367 years old at the Hopewell Furnace National Historic Site in southeastern Pennsylvania (Mikan et al, 1994). The dendroecology and successional dynamics of this xeric oak forest were the subject of study. In 1992, *Q. prinus* represented 32% importance, while *A. rubra*, *Betula alleghaniensis*, *B. lenta* and *Nyssa sylvatica* had a combined 56% importance. *Q. prinus* represented 90% of the canopy-dominant trees, but less than 15% of the intermediate and overtopped trees. Continuous recruitment of *Q. prinus* occurred between 1625 and 1920 (fig 7). Peak recruitment periods for *Q. prinus* occurred during the late 1700s and early



**Fig 7.** Mean ring width index for the six oldest chestnut oak and age-diameter data for all cored trees in an old-growth chestnut oak forest in southeastern Pennsylvania (adapted from Mikan et al, 1994). ACRU: *Acer rubrum*; BEAL: *Betula alleghaniensis*; BELE: *B. lenta*; NYSY: *Nyssa sylvatica*; QUPR: *Quercus prinus*.

1800s, which coincided with a release in radial growth (indicative of disturbance) during this period. After 1920, tree recruitment was predominately by the mixed-mesophytic species, although several *Nyssa* and *Betula* trees dated back to the 18th century. A 1915 release was associated with abundant *Acer* and *Betula* recruitment.

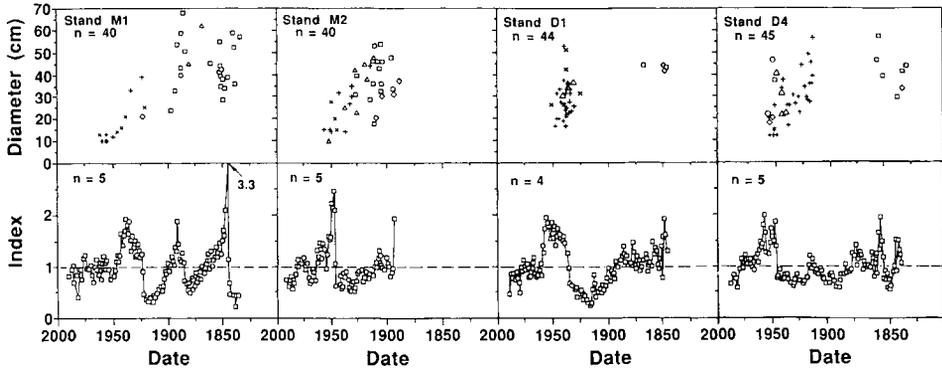
Ironically, this forest is located near a major 18th and 19th century charcoal iron settlement, where adjacent forests were logged on a 20–30 year rotation. The extreme talus slope undoubtedly protected this forest from cutting during that period. Frequent cutting and occasional burning of most forests in the region promoted oak coppicing and checked the advance of later successional species until the late 1800s when charcoal iron production ceased at Hopewell Furnace. Consistent with this idea, *Q. velutina* (33%), *Q. alba* (17%), *Castanea* (15%), *Carya* (15%) and *Q. prinus* (7%) dom-

inated forests prior to European settlement. Fire suppression activities and less forest cutting during the 20th century promoted *Acer* and *Betula* dominance in area forests. Despite the extreme edaphic condition, we predict that *Q. prinus* will eventually be replaced by more shade-tolerant *Acer*, *Nyssa* and *Betula* species. Thus, if true oak climaxes exist in the eastern oak region, they must occur on drier or more nutrient-poor sites than even this study site.

### **Accelerated maple-cherry succession following oak logging**

Recent studies indicate that disturbances can accelerate succession to later stages, which contradicts the typical notion that disturbance sets back succession to an earlier stage (cf Abrams and Scott, 1989). This situation may arise following canopy destruction in forests with pioneer or mid-successional overstory species and late successional understorey species. Many eastern oak forests may currently be prime candidates for accelerated replacement of oak following logging. Dendroecological techniques were used to examine forests logged between 1936 and 1946 versus relatively undisturbed mixed-oak forests in central Pennsylvania (Abrams and Nowacki, 1992).

Presettlement valley floor forests in central Pennsylvania were dominated by *Q. alba* (39%), *P. strobus* (26%), *Carya* (14%) and *Q. velutina* (11%), with very little *Acer* or *Prunus* (< 2%). Mature forests presently comprise *Q. alba* (23%), *P. strobus* (12%), *Q. velutina* (12%), *Carya* (8%) and *Acer* and *Prunus* (25% total). Age-diameter and tree ring data for two mature and two disturbed forests indicate that mature stand 1 originated after logging in 1844 (fig 8). Another disturbance in 1884 promoted the next wave of *Quercus* establishment and accelerated radial growth. A final disturbance in 1921 stimulated a limited amount of *Acer*, *Prunus* and



**Fig 8.** Mean ring width index for the four or five oldest oaks and age-diameter data for all cored trees in two mature and two extensively logged (between 1936 and 1946) mixed-oak forests in central Pennsylvania (adapted from Abrams and Nowacki, 1992). +: *Acer*;  $\diamond$ : *Carya*;  $\Delta$ : *Pinus*; x: *Prunus*; | : *Quercus*; O: others.

*Carya* recruitment. Mature stand 2 originated after logging in 1890. Tree recruitment after 1930 was predominantly from *A rubrum* and *P serotina*, which included a disturbance in 1942. The *Quercus* established in disturbed stand 1 after 1848 were extensively cut in 1936, promoting the episodic canopy recruitment of *A rubrum*. In disturbed stand 4, the oldest *Quercus* became established after 1830, but *A saccharum* recruited extensively after disturbances in 1912 and 1945.

Extensive cutting of the original *Quercus-Pinus* forests following European settlement promoted increased oak dominance during the 19th century. Fire was pervasive during this period, but it decreased by 99% during the 20th century. In 1908, the first year fire records were available, 404 700 ha burned throughout Pennsylvania, compared to < 3 400 ha per year between 1980 and 1989 (Abrams and Nowacki, 1992). Decreased logging and fire during this century promoted *Acer* and *Prunus* invasion into the *Quercus* understories. While logging and other disturbances promoted oak during the 19th century, logging in the 20th century caused an accelerated replacement of these species by releasing understory

*Acer* and *Prunus*. We believe this form of accelerated succession may occur routinely in other eastern oak and pine forests containing an understory dominated by later successional species (see Discussion in Abrams and Scott, 1989 and Nowacki et al, 1990 for other oak-related examples).

### SUCCESSIONAL STATUS OF OAK FOREST

Despite the importance of oaks throughout the eastern forest biome, there is little indication based on current understory composition and stand structure and dynamics that they represent a true climax species. Table III lists the principal overstory and understory composition in various oak forest types, and indicates that *Acer rubrum* and *A saccharum* are the two most important understory species. Most researchers conclude that given the current conditions and disturbance regimes, these two *Acer* species represent the major replacement species of oak throughout much of the biome (cf fig 5; Abrams 1992). However, west of the *Acer* range, *Celtis occidentalis* and *Cercis canadensis* appear to be important oak

replacement species, as described in the tallgrass prairie section (fig 4; Abrams, 1986). In the Lake States and mid-Atlantic regions, *Prunus serotina* has potential in this regard (Reich et al, 1990; Abrams and Nowacki, 1992). In the mid-Atlantic region, south of *A saccharum*'s range, *Nyssa sylvatica* may be a future overstory dominant in current oak forests (Ross et al, 1982; Farrell and Ware, 1991; Orwig and Abrams, 1994). *Fagus grandifolia* is only occasionally noted as an important understory or potential overstory replacement species in oak forests, and these are generally limited to the maple-beech-basswood, mixed-mesophytic and southern evergreen associations (table IV). However, a presettlement-origin *Q alba* forest in southwestern Pennsylvania is presently dominated by *F grandifolia*, *A rubrum* and *Liriodendron tulipifera* (Abrams and Downs, 1990), indicating that *F grandifolia* may play an important successional role in eastern oak forests as they move from second-growth to old-growth condition.

Although in the minority, a few recent studies predict long-term stability of this species group on very extreme sites. Examples of this include, xeric *Q marilandica* and *Q stellata* forests derived from former oak savannas in Oklahoma, *Q marilandica* - *Q velutina* in xeric, upland glades in Illinois, and mixed-oak forests on nutrient-poor barrens sites in New Jersey (Little, 1974; Adams and Anderson, 1980; Dooley and Collins, 1984). While these forests may in fact represent edaphic climaxes, they may alternatively be exhibiting slow rates of successional replacement and thus not have long-term stability in the absence of fire. Clearly, the rates of succession on mesic oak sites greatly exceeds that on xeric or nutrient-poor sites (cf Abrams, 1992). However, oak forests located to the south and west of the peak distribution of *A saccharum*, *A rubrum*, *F grandifolia* and *P serotina* may be experiencing less successional pressure than oak forests in the northeastern and north-central United States and may

**Table IV.** Adaptations to fire, drought and understory conditions in upland oak species of eastern North America.

<i>Fire</i>	<i>Drought</i>	<i>Understory</i>
Thick bark	Deep rooting	Moderate shade tolerance
Rotting resistance after scarring	High predawn $\Psi$	Large seed and cotyledons
Deep rooting	Thick leaves	Large initial seedling
Vigorous sprouting	High leaf mass per area	Relatively high <i>A</i>
Improved fire-created seedbed	High stomatal density	Relatively low <i>R</i>
Increased germination	High leaf nitrogen	Low light compensation point
Increased seedling survival	High <i>A</i>	Medium <i>K</i> values
Lowered seed and seedling predation	High leaf conductance	Slow seedling growth
	Low $\Psi$ threshold for stomatal closure	High C-based phenolics
	High osmotic adjustment	Shoot dieback
	Low $RWC_0$	Intense seed and seedling predation
	Low nonstomatal inhibition	Often over-topped by competing species
	Leaves not drought deciduous	Responsive to canopy gaps

$\Psi$ : leaf water potential;  $RWC_0$ : relative water content at zero turgor; *A*: net photosynthesis; *R*: respiration; *K*: light saturation constant.

have stable oak populations even in the absence of fire.

### ECOPHYSIOLOGICAL ATTRIBUTES OF EASTERN OAK SPECIES

The studies reviewed in the previous sections indicate that eastern oak species have expanded in the tallgrass prairie region, are prevalent on xeric sites throughout the biome, have increased in importance following early disturbances, have been influenced historically by periodic understory burning, but may be transitional to later successional species in the absence of fire. Thus, oak species presumably possess a suite of ecophysiological adaptations for drought stress and disturbance, but not for competing in a closed forest understory dominated by later successional species. This section will summarize the major ecophysiological features of oak in relation to fire, drought and understory conditions (table IV).

#### *Fire adaptations*

In an early opinion survey of the fire resistance of 22 northeastern tree species, oaks (*Q prinus*, *Q velutina*, *Q alba* and *Q coccinosa*) were rated in four of the top six positions (Starker, 1934). It was further determined that these oak species had a much greater bark thickness/trunk diameter ratio than several mixed-mesophytic species, such as *A rubrum*, *P serotina* and *F grandifolia* (Spalt and Reifsnyder, 1962; Harmon, 1984). Among oak species, a ranking of increasing bark thickness and fire resistance was reported as follows: *Q macrocarpa* > *Q velutina* > *Q alba* > *Q rubra* (Lorimer, 1985; Hengst and Dawson, 1994). Fire may also be beneficial to oaks, relative to other hardwood species, because they have relatively high resistance to rotting after scar-

ring, deep rooting and vigorous sprouting ability, and increased germination and survival on fire-created seedbeds with reduced litter layers (table IV). Mean fire intervals of 4 to 20 years have been reported for several oak forests in the eastern and central United States (Buell et al, 1954; Henderson and Long, 1984; Abrams, 1985; Guyette and Cutter, 1991).

#### *Drought adaptations*

The adaptations and responses to drought in North American oak species have been the subject of a review article (Abrams, 1990); this section will highlight the major conclusions of that review and some of the more recent articles on this subject (table IV). Oaks are among the most deeply rooted tree species in the eastern United States, which allows oaks to maintain relatively high predawn shoot water potential ( $\Psi$ ) from superior overnight rehydration. For example, during a severe drought in central Pennsylvania, predawn  $\Psi$  for naturally occurring saplings of *Fraxinus americana* was  $-0.95$  MPa, compared with  $-0.10$  to  $-0.36$  MPa in *Q rubra*, *Q prinus* and *Q ilicifolia* (Kubiske and Abrams, 1991). In a Missouri shade-house study, *Q stellata* and *Q alba* exhibited a greater capacity for deep root growth and supplying water to leaves than did *A saccharum* (Pallardy and Rhoads, 1993).

Oaks leaves often have greater thickness, mass per area and stomatal density and may have higher nitrogen content than leaves of non-oak species (Abrams and Kubiske, 1990; Reich et al, 1990, 1991). These factors may contribute to the relatively high net photosynthesis ( $A$ ) and leaf conductance of water vapor ( $g_{wv}$ ) often exhibited by oak species (Abrams, 1990; Reich et al, 1991; Kloeppel et al, 1993; Abrams et al, 1994). In Missouri, *Q stellata* and *Q alba* had higher  $A$  and  $g_{wv}$  than *A saccharum* and *Juglans nigra* in both well-

watered and droughted seedlings (Ni and Pallardy, 1991). In a study of 19 hardwood tree species in central Pennsylvania, *Q velutina* had among the highest dry year  $A$ , while *Q macrocarpa* had among the highest wet year  $A$  and  $g_{wv}$  (Kubiske and Abrams, 1994). A study of four Pennsylva-

nia barrens tree species also indicated that *Q velutina* had relatively high  $A$  and  $g_{wv}$  (Kloppel et al, 1993). Most species with high gas exchange rates need to develop the necessary tissue water relations to support this level of activity. Consistent with this idea, oak species often have lower diurnal

**Table V.** Species, maximum net photosynthesis ( $A_{max}$ ), dark respiration ( $R$ ), light saturation constant ( $K$ ) and light compensation point (LCP) for various oak and non-oak species in shaded understory or greenhouse condition in eastern North America. All units are in  $\mu\text{mol m}^{-2}\text{s}^{-1}$ .

Species	$A_{max}$	$R$	$K$	LCP	Reference
<i>Sassafras albidum</i>	7.6	0.3	561	22	Kloppel et al, 1993
<i>Quercus velutina</i>	6.3	0.5	361	29	"
<i>Q prinus</i>	4.8	0.9	152	33	"
<i>Acer rubrum</i>	3.6	0.5	139	22	"
<i>Fagus grandifolia</i>	4.3	0.9	301	11	Loach, 1967
<i>A saccharum</i>	—	0.9	—	—	"
<i>A rubrum</i>	2.6	0.4	168	12	"
<i>Q rubra</i>	4.5	0.5	250	11	"
<i>Q velutina</i>	—	0.8	—	—	"
<i>Liriodendron tulipifera</i>	6.6	1.5	301	26	"
<i>Populus tremuloides</i>	8.8	3.5	880	43	"
<i>F grandifolia</i>	5.2	0.3	575	8	Teskey and Shrestha, 1985
<i>Q alba</i>	6.6	0.7	650	6	"
<i>L tulipifera</i>	7.7	1.2	720	15	"
<i>Q rubra</i>	7.0	0.8	700	21	"
<i>Liquidamber styraciflua</i>	5.1	0.8	525	8	"
<i>Tilia americana</i>	4.8	0.1	135	—	Jurik et al, 1988
<i>Q rubra</i>	4.7	0.1	115	—	"
<i>F grandifolia</i>	4.4	0.1	115	—	"
<i>A rubrum</i>	4.4	0.2	120	—	"
<i>A saccharum</i>	3.9	0.1	115	—	"
<i>Prunus serotina</i>	3.7	0.1	115	—	"
<i>Populus grandidentata</i>	9.0	1.5	316	45	Abrams and Mostoller, unpubl data
<i>Carya tomentosa</i>	4.1	0.9	158	37	"
<i>P serotina</i>	6.2	0.9	273	37	"
<i>A rubrum</i>	5.2	0.9	182	41	"
<i>Cornus florida</i>	3.8	0.7	271	40	"
<i>Fraxinus americana</i>	6.0	1.2	209	40	"
<i>P pennsylvanica</i>	5.0	0.4	126	15	Bazzaz and Carlson, 1982
<i>F americana</i>	9.7	0.1	200	1	"
<i>Platanus occidentalis</i>	7.0	0.2	175	5	"
<i>Q imbricaria</i>	4.7	0.3	497	28	"
<i>Q rubra</i>	7.4	0.2	200	5	"
<i>Aesculus glabra</i>	3.3	0.3	200	22	"
<i>T americana</i>	3.3	0.2	130	20	"
<i>A saccharum</i>	3.4	0.4	83	13	"

leaf water potential  $\Psi$ , osmotic potentials ( $\Psi\pi$ ) and relative water content at zero turgor ( $RWC_0$ ) and have a lower  $\Psi$  threshold for stomatal closure than non-oak species (Abrams, 1990).

Recent studies indicate that xeric oak species often exhibit less nonstomatal inhibition of photosynthesis during drought than mesic oak or non-oak species or genotypes. *Q stellata* and *Q alba* seedlings had less nonstomatal inhibition of  $A$  during water stress and/or superior drought recovery than *A saccharum* and *J nigra* (Ni and Pallardy, 1992). Xeric *Q rubra* genotypes in central Pennsylvania exhibited higher  $A_{max}$  and  $A/\Psi$  relationships, more xerophytic leaves and less nonstomatal inhibition of  $A$  at the early and middle stages of drought than did mesic *Q rubra* genotypes (Kubiske and Abrams, 1992). In a study evaluating nonstomatal limitations in field plants in central Pennsylvania, tree saplings on a xeric site (including *Q velutina*) had lower stomatal and nonstomatal limitations of  $A$  than did species on a mesic site during a drought year (Kubiske and Abrams, 1993).

### **Adaptations to forest understory conditions**

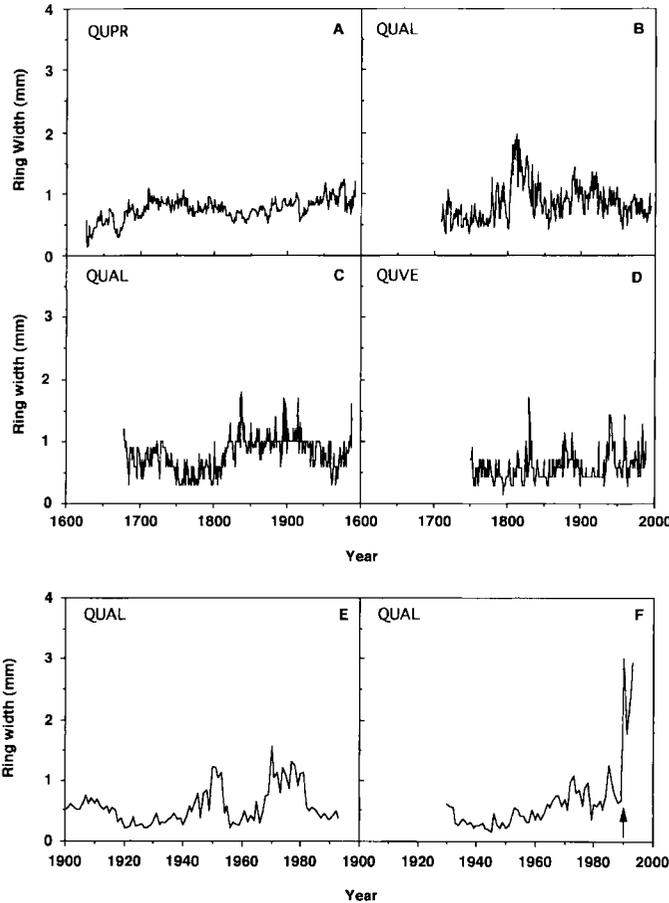
Eastern oak species are generally considered to have rather low tolerance of understory conditions (Burns and Honkala, 1990; Abrams, 1992). When considering the understory dynamics of oak species, temporal variation becomes very important (table IV). The oak acorn is very large relative to the seed of most other eastern tree species, and oak seedlings should have higher initial growth from large cotyledons (Grime and Jeffrey, 1965; Kolb and Steiner, 1990). However, in forest understories oak seedlings typically exhibit very slow growth after the first year (Brinkman and Liming, 1961; Carvell and Tryon, 1961; Lorimer, 1989; Cho and Boerner, 1991). In a survey

of 296 *Q rubra* seedlings in Pennsylvania forest understories, seedling ages were typically  $< 10$  years, with heights consistently  $< 0.2$  m (Steiner et al, 1993). Sapling density for oak species is generally very low relative to many non-oak tree species, indicating that there is a severe "bottleneck" in oak growth between the seedling and sapling stages (Abrams and Downs, 1990; Nowacki et al, 1990; Nowacki and Abrams, 1992; Orwig and Abrams, 1994). Data from greenhouse studies often contradict field studies and report that 1- or 2-year-old seedlings of various oak species can actually outgrow seedlings of other tree species, including *A rubrum*, under a wide range of light levels (Loach, 1970; Gottschalk, 1985). However, short-term greenhouse studies may have little relevance to field situations (cf Crow, 1988). Thus, identifying the physiological mechanism for slow growth in understory oak seedlings has been difficult. One would expect oak species in low light to have lower  $A$  and higher light compensation point or dark respiration rates than many of their competitors, but that has generally not been reported in either greenhouse or field studies (table V). Maximum  $A$  rates of oak in shaded conditions is often higher than in non-oak species, while oak respiration rates are low to moderate. Oaks have a fairly low light compensation point and a low to moderate light saturation constant to approach their  $A_{max}$  levels.

If oak species exhibit above average physiological responses to shaded understory conditions, then why do they also exhibit low seedling height growth? The answer to this question may be related to unique carbon partitioning and growth habits in oaks, seedling predation and the impact of competing vegetation. Oak seedlings often produce large root systems, experience recurring partial or complete shoot dieback and have high levels of carbon-based phenolic compounds (used in plant defense) relative to other tree species

(McQuilkin, 1983; Crow, 1988; Kleiner et al, 1989; Kolb and Steiner, 1990; Abrams, 1992). Allocating carbon in this manner may limit height growth in the understory. In contrast, oaks are capable of establishing large numbers of seedlings and may have rapid height growth in high light environments (Brinkman and Liming, 1961; Carvell and Tryon, 1961; Hibbs, 1982; Steiner et al, 1993). For example, after 3 years of growth in ambient CO<sub>2</sub>, *Q rubra* had the highest plant mass in the high light, low nitrogen treatment, but the lowest mass in low light with high or low N compared to five other hardwood species, including *A rubrum* (Baz-

z et al, 1993). Oaks may also have a high photosynthesis/respiration (A/R) ratio in canopy gaps, but low A/R in the shade relative to later successional tree species (Bazzaz, 1979). Intense competition from weedy species, such as hay-scented fern (*Dennstaedtia punctilobula*), and seedling browsing by deer (despite high phenolic levels) are fairly recent severe deterrents to oak seedling longevity and height growth, which were not major factors in presettlement forests (Horsley and Marquis, 1983; Crow, 1988; Steiner et al, 1993). It has been reported that the saliva of deer can reduce the absorption and toxic effects of tannins (a

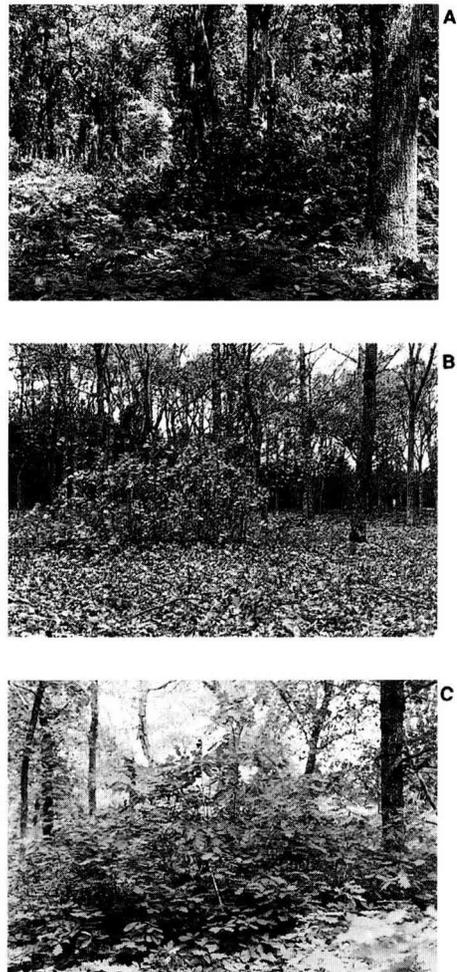


**Fig 9.** Dendrochronology of four old-growth oak (A–D) in primary forests and two understory oak (E, F) in second-growth forests in the mid-Atlantic region. QUPR in panel A is a *Q prinus* in southeastern Pennsylvania; QUAL in panel B is *Q alba* in southern West Virginia; QUAL and QUVE in panels C and D, respectively, are *Q alba* and *Q velutina* in southwestern Pennsylvania; QUAL in panels E and F is *Q alba* in north-central Virginia (adapted from Abrams and Downs, 1990; Mikan et al, 1994; Abrams et al, 1995). The arrow indicates the creation of a known canopy gap following windthrow (panel F).

phenolic), which allows them to eat and digest oak foliage (McArthur et al, 1991). There also exists the possibility that oak species may have decreasing shade tolerance with age (Carvell and Tryon, 1961), which would further limit seedling growth during long periods of shade-induced suppression, and promote over-topping by more shade-tolerant tree species.

However, slow growth of oak in closed forests is not a recent phenomenon. Our studies of oak dendroecology in old-growth forests identified oak trees that exhibited radial growth of  $< 1.0$  mm/year for protracted periods (fig 9). Two understory *Q alba* in second-growth mixed-oak forests in Virginia were up to 95 years old and still capable of responding to past or recent canopy gaps with increased radial growth (fig 9e, f). This coupled with the fact that oak had continuous recruitment into the tree size classes during the 1700s and 1800s indicate that slow growth was not a major limitation to oak ecology in presettlement forests (figs 6 and 7). Indeed, a somewhat analogous situation to this has been reported for *Q rubra* plantations in France, where, due to a lack of competing vegetation and deer browsing, oak regeneration in the understory averaged 271 300 stems/ha (fig 10; Steiner et al, 1993). Most of the French stands had many saplings  $> 2$  m in height, and *Q rubra* was particularly responsive to canopy gaps in terms of increased reproduction density and height growth (fig 10). Several US studies have also noted the gap-phase potential of *Q rubra* in mature hardwood forests (cf Crow, 1988; Abrams and Downs, 1990). A comparison of light characteristics for six deciduous and conifer stand types in southern New England indicated that the percent transmission of photosynthetically active radiation was quite high for *Q rubra* canopies (Canham et al, 1994). However, these authors also predicted that the sapling mortality rate for *Q rubra* was among the highest under canopies dominated by late suc-

cessional species. These studies suggest that without significant competition from other species, oak forests may allow for adequate light transmission, and that oak species may possess adequate understory tolerance to perpetuate themselves beneath



**Fig 10.** Understory conditions in a 97-year-old *Q rubra* plantation near Bordeaux, France. (A) *Q rubra* reproduction totaling approximately 400 000 stems/ha; (B) *Q rubra* reproduction response to a canopy gap in autumn condition; (C) *Q rubra* reproduction response to a canopy gap in summer condition. Photos taken by K Steiner.

their own canopies in even-age or uneven-age (gap-phase) conditions.

However, with the widespread invasion of oak understories by later successional species and the explosion in the deer populations in the eastern United States, oak seedlings are readily being over-topped and have very low recruitment beyond the seedling stage. Thus, a probable scenario is that recurring fire in presettlement oak forests maintained low numbers of fire sensitive, non-oak tree species, while allowing for oak canopy recruitment in small and large-scale gap situations. Following European settlement, many oak coppice forests were formed following widespread logging, allowing oaks to flourish in even-aged conditions. Presently, a lack of fire facilitating understory and subcanopy domination by later successional species and intense deer browsing are acting in concert to prevent adequate oak canopy recruitment.

## CONCLUSION

The rise in oak dominance in the eastern United States at the beginning of the Holocene epoch (10 000 years BP) was associated with warmer and drier conditions and the increased occurrence of fire (Watts, 1980; Davis, 1985; Webb, 1988). It is well documented that American Indians actively used fire for a multitude of purposes, and they were probably responsible for increasing the incidence of forest and prairie fires above that caused by lightning strikes (Day, 1953; Pyne, 1985; Patterson and Sassaman, 1988). While fires were too frequent in the tallgrass prairie region and too infrequent in the northern hardwood forests for oaks to prosper, the intermediate frequency and intensity of fire in presettlement oak-hickory, oak-chestnut and oak-pine forests were apparently necessary for their long-term stability (Abrams, 1992).

Initially following European settlement, oak populations throughout much of the eastern biome increased due to fire exclusion in tallgrass prairie and southern pine forests, widespread logging and burning of northern hardwood-conifer forests, and logging, burning and the chestnut blight in the eastern mixed-oak forest types. Moreover, oak species have typically shown a strong affinity for drought-prone sites, which are fairly common in the eastern United States from extreme edaphic, physiographic and/or climatic factors. Despite their low to moderate shade-tolerance rating, at least several eastern oak species maintained themselves in pre-European settlement forests in uneven-aged conditions, often growing very slowly for long intervals. Recurring fire in presettlement oak understories most likely prevented significant invasion by later successional species. This coupled with adequate light transmission through oak canopies probably facilitated oak establishment and recruitment in presettlement forests. Consistent with these ideas, oak species exhibit a suite of adaptations for fire and drought resistance. Moreover, oak species generally have fairly high photosynthesis and low respiration in actual or simulated understory conditions relative to many of their competitors. However, recent evidence indicates that oak seedlings typically grow very slowly and experience recurring shoot dieback in shaded understories. Thus, oaks appear to have a relatively high physiological tolerance but a low ecological tolerance to understory conditions in present-day forests.

Widespread invasion of most oak understories by later successional tree species and a lack of oak recruitment coincide with the start of fire exclusion in the early 1900s. It has been argued that continued fire exclusion will lead to a vast reduction in oak dominance in the eastern forest (Lorimer, 1985; Abrams, 1992). However, white-tailed deer populations have also risen dramatically in many eastern regions during the 1900s.

Considering that many oak species are highly preferred browse species, large deer populations are exacerbating the oak regeneration problem. It is important to note, however, that *Acer rubrum* and *A. saccharum*, two major oak replacement species, are also preferred browse for deer (Marquis, 1981; Fargione et al, 1991; Hughes and Fahey, 1991). Thus, the increase in *Acer* and other later successional trees in many oak forests is probably more a function of fire exclusion than differential deer browsing.

What does the future hold in store for the eastern oak forests? Will elevated CO<sub>2</sub> and potential global warming improve the situation for oak? Some models predict increased oak importance in the northern forests due to increased global warming and possibly fire occurrence (Overpeck et al, 1991), while others predict larger increases in maple-hardwood forests (Huston, 1991). It seems certain that severe competitive exclusion of oak by later successional tree species will occur much more rapidly than any benefit oak may realize from global warming. Thus, without intensive management to reduce competition from non-oak species and the predation of seeds and seedlings, such as through the increased use of fire and controlling deer populations, a major loss of oak dominance can be anticipated for the near future.

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