Age and diameter structure of a managed uneven-aged oak forest

Edward F. Loewenstein, Paul S. Johnson, and Harold E. Garrett

Abstract: We studied the age and diameter structure on one section (259 ha) of a 63 000-ha privately owned forest in the Ozark Highlands of Missouri. The forest has been managed using a partial cutting strategy since 1954. Because a majority of the trees predate current management practices, the existing stand structure is a function of not only the current silvicultural system and the dynamics of this ecosystem but also the initial stand conditions. To determine age structure and evaluate the relationship of diameter and age, a random sample of 600 oaks ≥4 cm DBH were collected from ten 0.4-ha plots. Based on the test of a binomial proportion, the oak populations on 7 of the 10 plots were deemed uneven aged, two were deemed two aged, and one was even aged. DBH accounted for 40 (red oaks) to 62% (white oaks) of the variation in tree age. Although the overall diameter frequency distribution of oaks formed a reverse-J shape, the age-frequency distribution approximated a normal (bell-shaped) distribution. We show how this apparent inconsistency between diameter and age distributions can be an artifact of a minimum sampling diameter. Such a truncation of the sampled population reduces the observed frequency of trees in the younger age-classes, which in turn results in a bell-shaped rather than a reverse-J-shaped age-frequency distribution. Thus, the lack of a reverse-J-shaped age distribution should not be interpreted as a failure to sustain regeneration in an uneven-aged stand.

Résumé : Les auteurs ont étudié la structure d'âge et de diamètre d'une section de 259 ha d'une forêt privée de 63 000 ha, dans les monts Ozarks du Missouri. La forêt était aménagée en utilisant la stratégie des coupes partielles, depuis 1954. Puisqu'en majorité les arbres étaient antérieurs aux pratiques présentes d'aménagement, la structure actuelle du peuplement est fonction non seulement du système sylvicole en cours et du dynamisme de cet écosystème, mais aussi des conditions initiales du peuplement. Afin de déterminer la structure d'âge et d'évaluer la relation entre l'âge et le diamètre, un échantillon de 600 chênes ≥4 cm au DHP a été choisi au hasard dans 10 placettes de 0,4 ha. En se basant sur le test de la proportion binomiale, les populations de chêne dans sept des 10 placettes ont été jugées inéquiennes, deux ont été jugées à deux classes d'âge et une était équienne. Le DHP comptait pour 40% (chênes rouges) et 62% (chênes blancs) de la variation dans l'âge des arbres. Bien que dans l'ensemble la distribution de la fréquence des diamètres des chênes formait une courbe en J renversé, la distribution de la fréquence d'âge se rapprochait d'une distribution normale (en cloche). Les auteurs montrent comment cette inconsistance entre les distributions du diamètre et de l'âge peut représenter un artéfac résultant d'un diamètre minimum d'échantillonnage. Un tel échantillonnage tronqué de la population réduit la fréquence observée des arbres dans les classes d'âge plus jeunes ce qui entraîne, en retour, une distribution de la fréquence d'âge en forme de cloche plutôt qu'en forme de J renversé. Par conséquent, l'absence d'une distribution d'âge en forme de J renversé ne doit pas être interprétée comme une incapacité à maintenir la régénération dans un peuplement inéquienne.

[Traduit par la Rédaction]

Introduction

The oak–hickory forests of the central and eastern United States have generally not been regarded as suited to uneven-aged silviculture (Roach and Gingrich 1968; Sander and Clark 1971). Although much silvicultural research has been conducted in oak–hickory forests, regenerating oaks remains a serious problem in specific ecosystems regardless of the silvicultural system employed. Because uneven-aged stands must support at least three age-classes for effective management (Smith 1986), regularly episodic regeneration events, and subsequent recruitment into the overstory, are necessary to sustain oak dominance under a selection system. However, the requisite recruitment of oaks under the partial shade of uneven-aged stands is problematic given the oak's relative intolerance of shade.

Parker and Merritt (1995) broadly categorize forest stands in the oak–hickory type as either subclimax or successionally stable. Subclimax stands have the highest site indices (≥22 m, base age 50 years) and are the most difficult to regenerate to oak. Succession on these sites tends toward more shade-tolerant and (or) mesophytic species (Parker and Merritt 1995; Johnson 1993; Sander and Graney 1993). Successionally stable oak–hickory stands can occur on poor- to medium-quality sites that tend to be droughty. Few non-oak species can persist on these sites as canopy dominants (Weitzman and Trimble 1957; Roach and Gingrich 1968; Sander and Clark 1971; Parker and Merritt 1995). Beneath

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the canopies of these stands, populations of oak saplings and seedling sprouts become established and persist for several decades (Merz and Boyce 1956; Ward 1966; Tryon and Powell 1984). Such stands have been referred to as "autoaccumulators" of oak reproduction (Johnson 1993).

In even-aged silviculture, successful oak regeneration usually requires oak reproduction to be present in advance of the overstory removal (Sander 1966; Clark 1970; McQuilkin 1975; Loftis 1983). Moreover, the size of this advance reproduction affects it competitive ability following overstory removal (Sander 1971; Loftis 1990; Dey et al. 1996). Although oak reproduction of sufficient size and numbers to regenerate a stand are often present in autoaccumulating ecosystems, this is rarely the case in subclimax stands, because oak regeneration potential is inversely related to site quality (Weitzman and Trimble 1957; Carvell and Tryon 1961; Sander and Graney 1993). On high-quality sites where oaks are successionally displaced by mesic and shade-tolerant species, reducing stand density to encourage oak reproduction often has the unwanted consequence of stimulating the growth of less desirable shade-tolerant species (Johnson 1977). This dynamic is evident in studies of selection silviculture in oak–hickory forests, which typically have resulted in silviculturally undesirable compositional shifts toward more shade-tolerant species (Trimble 1970, 1973; Schlesinger 1976; Della-Bianca and Beck 1985). In light of these studies, it is not surprising that conventional silvicultural wisdom asserts that oaks must be managed by even-aged methods. Moreover, upland oak forests are generally unable to maintain the reverse-J-shaped diameter structure presumed necessary for sustaining an uneven-aged state (Gingrich 1967). Thus, past research and existing silvicultural guidelines indicate that neither the desirable species composition nor the requisite stand structure is sustainable in oak–hickory forests under an uneven-aged system. However, much of this research has been conducted in oak forests on highly productive sites where oaks are subclimax.

The Ozark Highlands of Missouri represents a xeric to dry mesic oak-dominated ecosystem that is relatively stable successionally. Historically, these forests have been subject to repeated disturbance of varying intensity resulting from drought, wind (Rebertus and Burns 1997), fire (Cutter and Guyette 1994), and more recently logging. The system is resistant to change in terms of species composition and relative canopy position; even following a stand-replacing disturbance the oak species typically recapture dominance on the site within 20 years (Dey et al. 1996). Although shade-tolerant species such as flowering dogwood (*Cornus florida* L.), blackgum (*Nyssa sylvatica* Marsh.), and maples (*Acer* spp.) are present, these species are at a competitive disadvantage to the more xerophytic species and are largely relegated to the subcanopy (Dey et al. 1996). Advance oak reproduction also is more likely to be adequate here than in more mesic ecosystems (Parker and Merritt 1995). Finally, white oak (*Quercus alba* L.) is a major component of the ecosystem. This relatively shade-tolerant oak can survive beneath a forest canopy for up to 90 years (Rogers 1990). Given sufficient growing space, continual recruitment of white oaks into the overstory sufficient to sustain a reverse-J-shaped diameter structure would appear biologically plausible (but see McGee 1981; McGee and Bivens 1984). Collectively, the prevailing ecological conditions and regeneration dynamics in the Ozark Highlands suggest that uneven-aged silviculture may be an alternative to total reliance on even-aged systems.

An opportunity to evaluate the response of a successionally stable oak forest to an uneven-aged silvicultural system occurred when the owner of a large, private forest located in the Ozark Highlands of southern Missouri made available a continuous forest inventory (CFI) data base for analysis. The Pioneer Forest covers over 63 000 ha and has been under a program of partial cutting for more than 40 years.

The requirements for a viable and sustainable uneven-aged silvicultural system for oak stands include (*i*) the creation and maintenance of stands comprised of multiple age-classes (If this condition is not met, it can be concluded that past cutting practices have not resulted in an uneven-aged state.); (*ii*) if the uneven-aged condition is present, its sustainability requires the maintenance of a desirable species composition through time; (*iii*) the regeneration of desirable species must occur periodically and reproduction must continually or episodically be recruited into the overstory and through successive size classes in sufficient numbers to replace trees lost to natural mortality and those removed by silvicultural treatment; and (*iv*) these structural and compositional attributes must occur at or below the spatial scale of a stand. Meeting these requirements collectively determine the silvicultural sustainability of the uneven-aged state.

Study objectives

Partial cutting does not guarantee the creation of an uneven-aged stand. Because of the longevity of many tree species, it is possible to maintain an even-aged assemblage, even with periodic cutting for >100 years (Clark and Watt 1971). Therefore, as a first step in the assessment of potential for uneven-aged silviculture in stands dominated by oaks, this study was designed to test stand age structure. The following null hypothesis was tested: the age structure of the oak component at a scale of 0.4 ha does not differ from the Society of American Foresters (SAF) definition of an even-aged stand (the oldest and youngest trees differ by no more than 20% of an even-aged rotation) (Helms 1998).

In addition, although silvicultural systems are broadly classified according to the age structure, treatments in an uneven-aged system are typically accomplished by managing the diameter structure of a stand (Larsen et al. 1999). However, the relationship between age and diameter is suspect. For this reason, diameter structure was also examined to determine whether it is of value in evaluating the age structure of a stand. The null hypothesis of no relationship between tree age and diameter was tested.

This study, located in the Missouri Ozarks, is part of a continuing assessment of single-tree selection in a successionally stable oak–hickory forest (Loewenstein 1996). Associated research has shown that, after 40 years, (*i*) there has been no detectable shift in composition toward more shade-tolerant species (Loewenstein et al. 1995), (*ii*) the forest-wide diameter distribution has remained stable through time and the negative exponential function adequately describes the diameter distribution for all major species groups

Table 1. Mean (±SE) and relative basal area and density of tree species in the study area.

Species	Basal area/ha (m^2)	Relative basal area (%)	Trees/ha	Relative trees/ha (%)
Acer spp.	0.58±0.26	3.4	117.6±38.8	10.3
Carya spp.	1.53±0.37	9.1	135.4±28.5	11.9
Cornus florida	0.43±0.11	2.5	140.4±32.4	12.4
Nyssa sylvatica	0.53±0.26	3.1	77.1±19.5	6.8
Pinus echinata	1.10±0.43	6.5	24.7±8.6	2.2
Quercus alba	6.44±1.06	38.2	457.6±129.1	40.3
Quercus coccinea	3.71±1.26	22.0	64.2±15.9	5.7
Quercus rubra	1.09±0.65	6.5	27.7±15.5	2.4
Quercus velutina	0.68±0.30	4.1	23.7±10.1	2.1
Other[a]	0.77±0.30	4.6	67.2±24.4	5.9
Total	16.85±1.31	100.0	1135.7±105.8	100.0

[a]Other species include *Carpinus caroliniana* Walt., *Cercis canadensis* L., *Fraxinus americana* L., *Fraxinus pennsylvanica* Marsh., *Halesia carolina* L., *Juglans cinera* L., *Juglans nigra* L., *Ostrya virginiana* (Mill.) K. Koch, *Platanus occidentalis* L., *Sassafrass albidum* (Nutt.) Nees, *Ulmus americana* L., *Ulmus rubra* Muehl., and *Viburnum rufidulum* Raf.

(Loewenstein 1996; Wang 1997), and (*iii*) the forest-wide diameter distribution reoccurs with high probability at a spatial scale of 0.24 ha (Loewenstein 1996). Collectively, these studies provide a basis for developing silvicultural options for the region.

Methods

The study area

The study area is a 259-ha stand (one management unit), located at 91°15′W, 37°15′N within the Pioneer Forest. Operational units on the forest are 259 ha (1.62 × 1.62 km), but topography rather than section lines are used to delimit stand boundaries. This section, like the rest of the forest, is generally steep with broad flat ridges. Soils tend to be rocky and droughty but range from deep gravel and rock outcrops to depths of more than 1.2 m. Soils are derived mainly from dolomitic limestone. Site index (base age 50 years) ranges from 16.8 to 27.4 m for black oak (*Quercus velutina* Lam.) (Larsen 1980), 17.8 to 28.4 m for scarlet oak (*Quercus coccinea* Muenchh.), and 15.5 to 26.1 m for white oak (McQuilkin 1974). Although the stand is oak dominated, shortleaf pine (*Pinus echinata* Mill.) is scattered throughout the forest and can occur in pure stands on upper south-facing slopes. Lower north-facing slopes and deep valleys are typically mixtures of oak with more mesophytic species. At the time of purchase (1954) the forest was understocked, averaging only 195 trees/ha and 8.3 $m^2 \cdot ha^{-1}$ of basal area[2] for all trees ≥12.5 cm DBH. By 1992, on average basal area had increased by 68%, and tree density, by 89% (Loewenstein 1996).

The study area was selected at random from all stands on the forest that had at least three major cutting events while under the current ownership. This stand is typical of the forest as a whole in terms of species composition, tree density, and basal area. Based on the 1992 CFI inventory, forest wide, the oaks comprise >70% of the basal area and about one half of the total number of trees (Loewenstein et al. 1995; Loewenstein 1996). In the study area, these figures are 71.1 and 49.9%, respectively (Table 1). The forest average basal area of all trees ≥12.5 cm DBH is 15.72 $m^2 \cdot ha^{-1}$ (Loewenstein 1996) compared with 16.85 $m^2 \cdot ha^{-1}$ on the study area (Table 1).

Historical records indicate that the study area was originally logged ca. 1915. From then until 1954, there are no records. Since 1954, there have been three thinnings for pine posts: 0.12 $m^3 \cdot ha^{-1}$ was harvested in 1954, 0.82 $m^3 \cdot ha^{-1}$ in 1962, and 0.29 $m^3 \cdot ha^{-1}$ in 1976.[3] In 1956, as allowed by the original purchase agreement, 0.41 $m^3 \cdot ha^{-1}$ of white oak bolts were removed by the previous owners. This operation, a species-specific diameter-limit harvest, greatly reduced white oak stocking. In 1978, 4.02 $m^3 \cdot ha^{-1}$ were cut, of which nearly 75% was comprised of the red oak group (primarily black and scarlet oak, hereafter referred to as red oaks). Salvage of windthrown red oaks in 1985 and 1987 comprised 0.53 and 0.10 $m^3 \cdot ha^{-1}$, respectively. The most recent treatment in 1990, removed 12.68 $m^3 \cdot ha^{-1}$, most of which was comprised of red oaks (10.78 $m^3 \cdot ha^{-1}$).

Prior to 1978, the stand treatments are best described as thinning or partial cutting. However, beginning with the 1978 cut, treatments more closely resemble a single-tree selection system. The forest is operated on a cutting cycle of approximately 20 years. However, treatments occur when stands reach 21.8–23.0 $m^2 \cdot ha^{-1}$ of basal area. At each entry, stand density is reduced to approximately 14.9 $m^2 \cdot ha^{-1}$. The silvicultural objective when marking a stand is to create or maintain a three-tiered forest canopy comprised of an overstory, a midstory, and a sapling or reproduction layer. This loosely defined "target" structure is created or maintained primarily by treating the overstory trees. Only merchantable trees (hardwoods ≥25 cm and pine ≥22.5 cm DBH) are removed from the stand. Lack of markets and the length of time required to grow small-diameter stems to merchantable size makes the cost of precommercial thinning prohibitive. Only where a market exists are smaller stems removed. Cull trees that suppress potential crop trees are felled. Each tree in the merchantable size classes is examined for possible removal. Trees deemed likely to die before the next entry are cut. Additionally, whenever crop trees are obviously competing, one is removed. Vigor, potential value (e.g., branching patterns that limit merchantable height gain), slope position, aspect, and species are used to identify trees for removal. Within the limits of optimal spacing, the best trees are left and the worst are cut.

The preceding description may not seem to fit the classical

[2] Based on diameters (DBH) measured 1.37 m above the ground.
[3] Harvested volumes were recorded in board feet (Doyle rule). The conversion to cubic metres per hectare was a rough approximation and was calculated at 225 board feet per cubic metre.

definition of single-tree selection because it does not include tending across all size classes (Helms 1998). However, Troup (1952) recognized that there are some unique circumstances affecting the application of this silvicultural system in a dry region dominated by shade-intolerant tree species. Such stands tend to be much more open and bear little resemblance to a selection forest composed primarily of shade-tolerant trees. As an example, the target residual basal area in this Ozark Highlands forest is 14.9 $m^2 \cdot ha^{-1}$, compared with Arbogast's (1957) recommendation of 21 $m^2 \cdot ha^{-1}$ for northern (shade-tolerant) hardwoods. With shade-intolerant species, a lower-density approach is required to ensure survival and maintain vigor in the subordinate size classes. Because of their sensitivity to stand density, it is possible to affect the vigor and number of trees in subordinate size classes by treating primarily the larger trees. At the beginning of a cutting cycle, the relative density of the overstory is reduced enough to ensure that deficiencies do not develop in the smallest size classes. Toward the end of the cutting cycle, stand density attains a level sufficient to keep surplus numbers of small diameter trees in check. In effect, tending has occurred across all size classes although a treatment has only been applied to the largest trees (see Larsen et al. 1999).

Study design

Within the 259-ha study area, tree ages and diameters were subsampled on 10 randomly selected 0.4-ha plots during the summer and fall of 1992. Diameters of all trees ≥4 cm at breast height (DBH at 1.37 m) were measured on five randomly located 0.02-ha plots within each 0.4-ha plot. Tree ages were sampled using a 3 × 3 m grid superimposed on each 0.4-ha plot to form 400 grid-line intersections. Sixty of those intersections were selected randomly, and the age of the nearest oak ≥4 cm DBH or recently cut stump was determined. Species and DBH were recorded for each tree. For trees <15 cm DBH, ages of sample trees were determined from disks removed 0.3 m above the groundline. For trees ≥15 cm DBH, ages were determined from increment cores also extracted 0.3 m above groundline. Disks also were removed from stumps, and stump diameters and heights were recorded to facilitate estimating DBH from stump diameter and height using regression equations independently developed for that purpose. Because tree age could not be accurately determined on 22 of the 600 trees, the usable sample size was reduced to 578 trees.

The frequent occurrence of an even-aged state at this scale (0.4 ha) would indicate that a stand does not conform to the general definition of an uneven-aged state, i.e., a population of trees comprised of at least three age-classes that are closely intermingled on the same area (Helms 1998). Because oaks dominate most stands in the Ozark Highlands and are usually of greatest silvicultural interest, only oaks were considered in the analyses of age distributions and age–diameter relations. More importantly, restricting this study to the oak species group reduces problems associated with discussing the age–diameter relations of species that have highly variable growth rates. Finally, oaks down to 4 cm DBH were included in the analysis of tree age distributions, because small trees are an essential component of uneven-aged stands. Their presence in requisite numbers is an indicator of the long-term sustainability of the forest managed under this silvicultural system.

Data analysis

Linear regression analysis was used to evaluate the relation between tree age and diameter. We used the test of a binomial proportion with correction for continuity (Snedecor and Cochran 1989) to determine whether the oaks on each 0.4-ha plot were even aged, two aged, or uneven aged. The test was applied using SAF's definition of the even-aged state, i.e., the ages of the oldest and youngest trees in a stand differ by no more than 20% of the rotation length (Helms 1998). To facilitate statistical testing, we chose 90 years as a reasonable rotation for average sites in the Ozark Highlands. By SAF definition, this rotation length therefore limits a tree population to an 18-year maximum age range if the population is to qualify as even aged. To qualify as two aged, a population must span no more than 36 years (i.e., two 18-year age ranges that are not necessarily adjacent to one another). By default, an uneven-aged population is one that does not meet the criteria for either even-aged or two-aged populations. The age interval used to characterize the age state of each plot was identified by the 18- or 36-year period containing the largest possible number of sample trees. We termed this segment of an observed age range the "modal age interval."

The binomial proportion test was run twice for each sample plot. The null hypothesis for the first test was that the age distribution of trees on a plot does not differ from an even-aged population; the alternative hypothesis was that the population is not even aged. The second test was conducted only when the null hypothesis for the first test was rejected. Accordingly, the null hypothesis for the second test was that the age distribution of trees does not differ from a two-aged population; the alternative hypothesis was that the population is uneven aged. The test statistic, Z_{calc}, is given by

$$[1] \qquad Z_{calc} = (|r - np| - (1/2n))/\sqrt{npq}$$

where r is the number of trees that fall within the modal age interval, n is the number of observations, p is the expected proportion of trees in the modal age interval, and q is the expected proportion of trees outside the modal age interval (i.e., $1 - p$). The null hypothesis was rejected when Z_{calc} exceeded the table value of Z (for a one-tailed test and $\alpha = 0.01$) for sample size n. In all tests, p was set to 0.99 to avoid forcing the denominator of the test statistic to 0, which occurs when p equals 1.

Our test procedure provides a conservative analysis of age structure. First, we set $\alpha = 0.01$ to control the type I error rate. With a sample size of 60 trees, this had the practical effect of allowing for two trees outside the modal age interval without resulting in rejection of the null hypothesis. Setting $\alpha = 0.05$ or 0.10 allows only one tree outside the modal age interval for the same sample size and value of p. In addition, although not stated, it seems likely that the SAF took into account the tails of the age distribution when defining an even-aged stand as tree age differing by no more than 20% of the rotation length (Helms 1998). In contrast, Schnur's (1937) study of "normally" stocked even-aged oak stands included stands with tree ages that spanned no more than 8 years. Consequently, on a productive site where the rotation length might be as short as 60 years, the permissible age range would only be 13% of the rotation; where the rotation is 90 years, the total age range would be less than 9% of the rotation length.

Results and discussion

Stand density, composition, and diameter structure

Based on the five 0.02-ha plots within each of the ten 0.4-ha plots, the basal area on the study area averaged 16.9 $m^2 \cdot ha^{-1}$ and trees ≥4 cm DBH numbered, on average, 1136/ha. Stocking percentage based on Gingrich's (1967) equation averaged 78%. The four major oak species comprised 71% of the total stand basal area and 55% of the trees. The oaks accounted for most of the large-diameter trees. The hickories (*Carya* spp.) were the most prominent non-oak species group with 9.1% of stand basal area followed by shortleaf pine with 6.5%. The remaining species accounted for 13% of stand basal area (Table 1). Collectively, the trees formed a reverse-J-shaped diameter distribution

Fig. 1. Observed diameter-frequency distribution of trees in the study area by species group (based on fifty 0.02-ha plots).

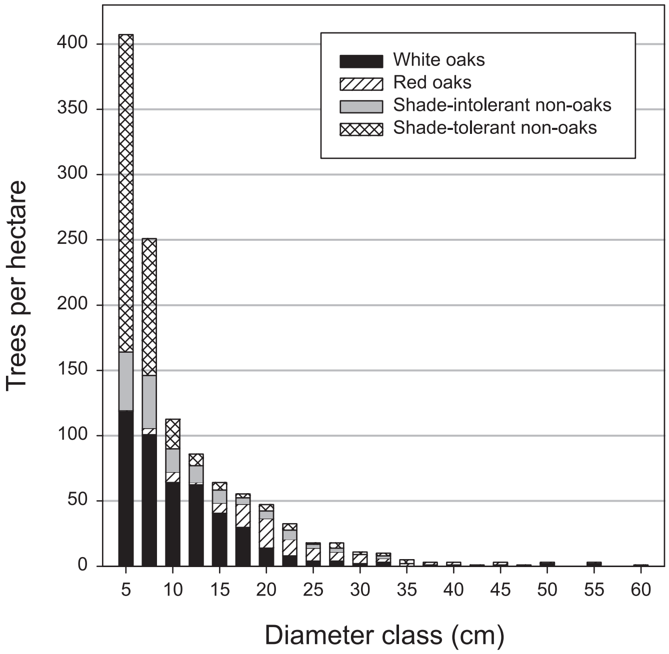
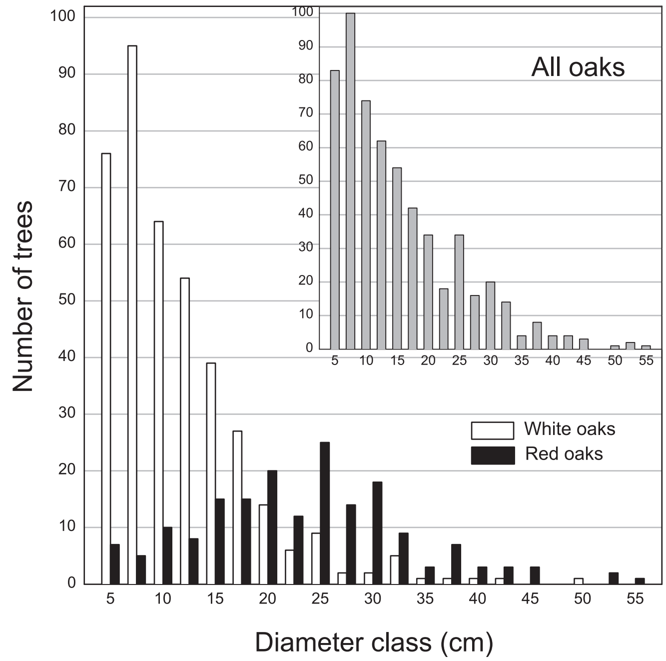


Fig. 2. Observed diameter-frequency distribution of oaks by species group (based on 578 oaks sampled on line-intersection grids).



considered characteristic of many uneven-aged stands, as did the oak component itself (Fig. 1). Below the 10-cm DBH class, non-oaks were more abundant than oaks, although oaks still accounted for 39% of the trees in those size classes and were present in numbers more than double what is required to maintain any of the currently recommended guiding curves (Larsen et al. 1999). The most abundant species in the smallest DBH classes was flowering dogwood, a subcanopy species. The proportion of non-oaks declined with increasing DBH; 85% of the non-oaks occurred in DBH classes ≤10 cm. Oaks were the most abundant species in all diameter classes ≥10 cm DBH.

Like the oaks on the areal plots, the composite diameter distribution of oaks that were aged approximated a reverse-J-shaped distribution (Fig. 2). This diameter structure was largely driven by the white oak component (*lepidobalanus*); the diameter distribution of the red oaks (*erythrobalanus*) was bell shaped.

The observed reverse-J-shaped diameter distribution allows for natural mortality, selection of crop trees, and replacement (through ingrowth) of trees removed by harvest (Schlesinger 1976). The accumulation of oak reproduction, which is common in the understory of Ozark Highland stands, is potentially available for recruitment into the overstory. It is this dynamic that supports the maintenance of a reverse-J-shaped diameter distribution and, therefore, a silviculturally sustainable uneven-aged state if it is maintained through time.

Nevertheless, it is possible for an even-aged, mixed-species stand to form a reverse-J-shaped diameter distribution because of different growth rates and shade tolerances among species (Smith 1986). Differences in growth rates can account for one half to three fourths of the observed dispersion of diameters in upland hardwood stands (Gingrich 1967). Where slow-growing, shade-tolerant species occur in mixed species stands, they may largely account for the trees occupying the lower canopy strata and thus the smaller DBH classes. Therefore, shade-tolerant species may predominate in the left side of a reverse-J-shaped diameter distribution, whereas shade-intolerant overstory trees often occur as a bell-shaped diameter distribution characteristic of maturing even-aged population. Such a distribution is transient. A composite diameter distribution thus may appear to be uneven aged when in fact the diameters are simply segregated by species (Stout 1991). For this reason, the analysis of age structure or diameter structure must consider species composition and the successional dynamic of each species within an observed distribution. We chose to limit our investigation to the oak component.

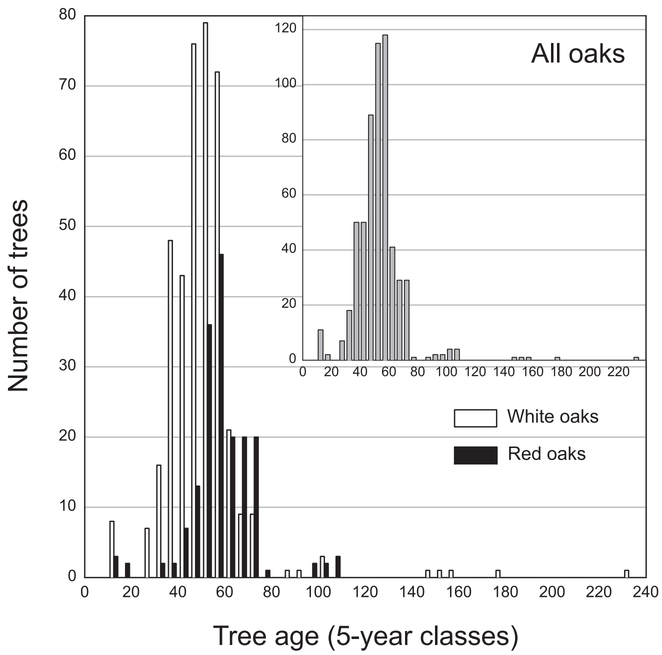
Stand tables for even-aged upland oak forests provide further empirical evidence of the existence of the uneven-aged state in the sample stand. “Normal” stand tables generalized over much of the oak range in the eastern United States (Schnur 1937) suggest that the largest expected range of diameters of red oaks in 100-year-old stands on oak site index 24.4 m is 35 cm (20–55 cm). In contrast, the observed DBH range for red oaks in the sample stand was 5–55 cm (Fig. 2). This range of diameters is greater than expected if the red oak component was even aged. Moreover, the shape of the red oak diameter distribution is not consistent with that expected in an even-aged state. The observed proportion of trees in the 5-cm DBH class (3.9% of all trees) would be expected to occur in a 40-year-old even-aged stand on oak site index 12.2 m, a 30-year-old stand on site index 15.2–18.3 m, or a 20-year-old stand on site index 21.3–24.4 m (Schnur 1937). In each case, the largest expected red oak DBH is 22.5 cm. The inconsistency between the sample stand and these attributes of the normal stand tables suggests the presence of more than one age-class in the sample stand.

Table 2. Age characteristics of oak populations and their defined age states by plot.

Plot	*N*	Age (years) Mean±SD	Range	Outside modal 18-year interval	Outside modal 36-year interval	Age-state classification[a]
1	55	61.1±14.8	45–109	8	3	UEA
2	60	51.0±10.9	27–103	13	3	UEA
3	61	49.2±4.9	29–59	1	0	EA
4	59	56.0±14.2	42–157	3	1	TA
5	60	46.7±34.4	12–233	24	9	UEA
6	58	42.9±10.5	13–73	13	4	UEA
7	57	61.0±13.2	31–105	17	5	UEA
8	60	42.2±10.8	25–72	15	2	TA
9	52	56.3±13.6	33–104	9	5	UEA
10	56	63.4±18.0	29–179	9	3	UEA

[a]Based on the outcome of the binomial proportion tests (eq. 1). UEA, uneven aged; EA, even aged; TA, two aged.

Fig. 3. Observed age-frequency distribution of oaks by species group (based on 578 oaks sampled on line-intersection grids).



The diameter distribution of the white oaks also did not conform to that expected of an even-aged stand. This is true even when the single 50-cm DBH tree is deleted from the data set. The observed range of diameters spanned 5 to 42.5 cm; the mode occurred in the 7.5-cm DBH class. According to Schnur's (1937) stand tables, 42.5 cm white oaks are not expected to occur until a stand attains an age of 100 years on oak site index 24.4 m. At that age, the expected range of diameters is 35 cm (7.5–42.5 cm) and the distributional peak occurs in the 22.5-cm DBH class. The occurrence of the mode in the 7.5-cm diameter class is not expected in even-aged stands older than 20 years on site index 21.3–24.4 m, 30 years on site index 15.2–18.3 m, or 40 years on site index 12.2 m. The empirical diameter distribution evidence thus suggests that the white oaks in the study span an age range of at least 60 years, which is inconsistent with that expected of an even-aged stand.

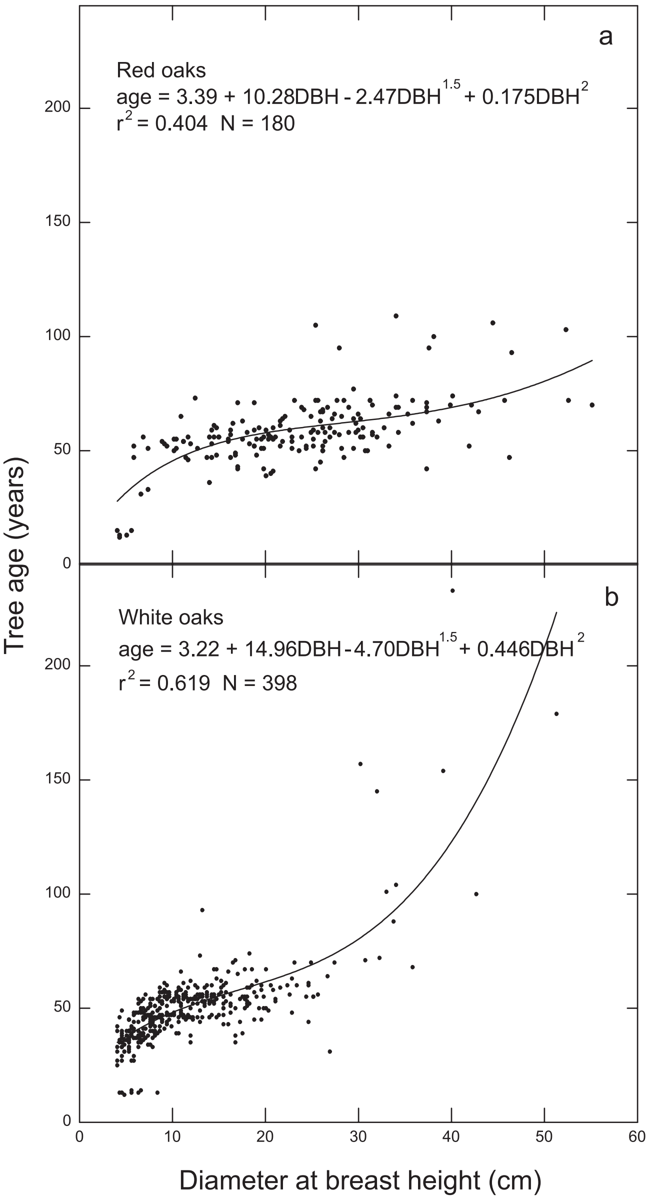
Age structure

Unlike the diameter distribution, the composite age distribution did not form a reverse-J-shaped frequency distribution (Fig. 3). The distribution of tree ages approximated a normal distribution with most observations occurring within the range of 35–75 years. Only white oaks were present in the oldest age-classes. The oldest white oak was more than 200 years old, whereas the oldest red oak was 107 (Fig. 3). The white oaks also dominated the younger age-classes. Only 5% of red oaks were less than 40 years old compared with 31% of white oaks. The frequency distributions differed little between the two species groups in the 45- to 60-year range (57% of white oaks and 53% of red oaks, respectively). However, red oaks were three times more numerous than white oaks in the 60- to 75-year range (33 vs. 10%, respectively).

Based on the application of the binomial test to the age distributions in each of the 10 study plots, only one plot was classified as even aged. Tree ages in that plot ranged from 39 to 59 years, and only one tree lay outside the 18-year modal age interval that defined the limits for the even-aged state (39–56 years) (Table 2). Two plots were classified as two age (four and eight). The trees on plot four ranged from 42 to 157 years old, and only one tree lay outside the 36-year modal interval that defined the limits for the two-aged state. Recall that the two 18-year intervals defining the 36-year modal interval need not be adjacent to one another. Trees on plot eight ranged from 25 to 72 years of age, and two of those lay outside the two-aged modal interval. Of the seven plots classified as uneven aged, numbers of trees occurring outside the two-aged modal intervals ranged from three to nine (Table 2).

The results of statistical testing thus indicate that, at a scale of 0.4 ha, the study area is currently uneven aged on 70% of its area. However, the binomial proportion test as it was applied is conservative in rejecting departures from "even agedness." Had Schnur's (1937) criterion for defining an even-aged stand been applied, all 10 plots would have qualified as uneven aged. Based on SAF (Helms 1998) criterion, only one plot was classified as even aged. Even on that plot, the 20-year age range of trees was 2.25 times larger than Schnur's (1937) limits for defining the even-aged state. It is also likely that the three plots not classified as uneven

Fig. 4. Relationship of age to DBH for red oaks (*a*) and white oaks (*b*) in the study area.



aged will move toward the uneven-aged state through time. Plot 8, which is predominantly oak, may be the first of these to become uneven aged, because the ages of trees there now nearly fill the two-aged modal interval. The ingrowth of one tree into the 5-cm diameter class would change the age state of the plot to uneven aged provided that the maximum tree age did not decrease. In plots 3 and 4, the ages of oaks are largely concentrated within the 40- to 60-year range. These plots are currently at 76 and 68% stocking, respectively, based on Gingrich's (1967) stocking equation. These stocking levels suggest that during the last one or two cutting cycles, conditions have been favorable for the development of large oak reproduction (Larsen et al. 1997). Such stems will likely be recruited into the overstory. The ingrowth of only two such oaks into the overstory (trees ≥4 cm DBH) would change the age states of either plot: plot 3 would become two aged and plot 4 would become uneven aged. Assuming the 10 study plots are representative of the study area, the stand currently conforms to the uneven-aged state at a scale of 0.4 ha on 70% of its area.

Relationship between age and diameter

We used linear regression analysis to evaluate the relation between tree age and DBH of the oaks on the study area. DBH explained 41% of the variation in tree age based on the model:

$$[2] \qquad \text{Age} = 34.44 + 1.18(\text{DBH})$$

where age is in years and DBH is in centimetres (n = 578, $p < 0.0001$). However, a systematic pattern (heterogeneity) in the residuals indicated that the relationship was not linear (Neter et al. 1989). First- or second-order polynomial regression models neither corrected this problem nor reduced the residual error.

To test for possible differences between the two oak species groups and to improve the fit of the model to the data, "species" was included as a predictor using dummy coding (Pedhazur 1982). Although a quartic model fit the data best (R^2 = 0.62) and reduced the pattern in residual error, the model produced decreasing predicted ages beyond 48 cm DBH. Because this is biologically impossible, the quartic term was dropped from the model. Among the polynomial models tested, the following provided the "best" fit, which was linear for the red oaks and cubic for the white oaks:

$$[3] \qquad \text{Age} = 36.329 + 0.919(\text{DBH}) + 0.000\,83\,(\text{DBH}^3)S$$

where S is equal to 1 for white oaks and 0 for red oaks (p < 0.0001, R^2 = 0.56, and DBH, DBH^3, and S were significant (p < 0.001)). Although this model did not completely eliminate the pattern in residual error, it was less pronounced than in the simple linear model (eq. 2).

Among other biologically logical models evaluated, models fit separately to the two species groups that produced sigmoidal curves provided the best overall fit to the data. The red oak model is given by

$$[4] \qquad \text{Age} = 3.39 + 10.28(\text{DBH}) - 2.47(\text{DBH}^{1.5}) + 0.175(\text{DBH}^2)$$

(n = 180, p < 0.0001, R^2 = 0.404). Although the model intercept did not differ significantly from 0 (p = 0.7330), the remaining coefficients were significant (p = 0.0004, 0.0021, and 0.0039 for DBH, $\text{DBH}^{1.5}$, and DBH^2, respectively) (Fig. 4*a*).

The white oak model is given by

$$[5] \qquad \text{Age} = 3.22 + 14.96(\text{DBH}) - 4.70(\text{DBH}^{1.5}) + 0.446(\text{DBH}^2)$$

(n = 398, p < 0.0001, R^2 = 0.619). The intercept did not differ significantly from 0 (p = 0.5817) and the other coefficients were significant (p < 0.0001) (Fig. 4*b*).

All of the models fit to the data show a statistically significant, positive relationship between age and diameter. Regardless of functional shape, each model explained between 40 and 60% of the observed variation. The sigmoidal function, however, most closely mimics the shape of the data, leaving no discernible pattern in the residuals. Unfortunately, the age–diameter models substantiate that accurate prediction of tree age from diameter is impossible because of the wide range of diameters within age-classes. The total diameter range within a 10-year age-class spanned 27 and 43 cm for white oaks and red oaks, respectively.

The theoretical basis for managing uneven-aged stands via diameter structure

Although silvicultural systems are classified according to whether they lead to even-aged or uneven-aged stand conditions, stands are usually managed for a specified diameter distribution rather than an age structure. The age distributions of tree populations are relatively difficult and time consuming to accurately characterize, whereas diameter distributions are easily obtainable. Given that diameter is not a good indicator of tree age, it should not be surprising that diameter distributions bear little resemblance to their respective age distributions. In fact, given that forest inventories are usually specified above some minimum diameter (e.g., all trees ≥4 cm DBH), a reverse-J-shaped diameter distribution should be expected to produce a normal age distribution for the range of diameters considered.

This relationship between age structure and diameter structure can be illustrated by considering an idealized uneven-aged stand with a perfectly “balanced” age structure originating from the establishment of a cohort of 1000 trees every ten years. Let us further assume that 25% of the population is lost to mortality every 10 years.[3] Thus, if there are 1000 trees at age ten, 750 (or 0.75 × 1000) trees will survive to age twenty, 563 (or 0.75 × 750) will survive to age 30, etc. Moreover, this mortality is assumed to be proportionate across the range of diameters within an age-class (i.e., the shape of the diameter distribution does not change). Our example also assumes that at age 10, trees average 1.3 m in height and 0 cm DBH, diameters remain normally distributed, and mean DBH growth is constant at 4.167 cm per decade. Consistent with even-aged stand dynamics, the range of diameters within an age-class is assumed to increase over time. This rate was held constant, with the variance increasing by 0.833 every 10 years. The resulting age series of diameter distributions is illustrated in Fig. 5*a* (only 4 of the 10 cohorts’ distributions are illustrated).

A random sample of trees ≥12.5 cm DBH drawn from the hypothetical uneven-aged population of trees (Fig. 5*a*) will produce a negative exponential diameter distribution (Fig. 5*b*). In contrast, the age distribution of the same sample approximates a normal distribution (Fig. 5*c*). By itself, the resulting age distribution might lead to the conclusion that there has been a failure in the recruitment of reproduction into the stand. After all, there are insufficient 20- and 30-year-old trees to form the left tail of the negative exponential distribution, and almost no 10-year-old trees in the random sample. Nevertheless, in reality we know that our hypothetical stand is uneven aged. In fact, both age and diameter distributions are perfectly balanced. The mismatch between the two distributions is the combined result of the left truncation of diameter range (caused by the minimum sampling diameter) and the lack of a high correlation between age and DBH. Closer inspection of Fig. 5*a* reveals that, among the 1000 trees comprising the 10-year-old cohort (averaging 0 cm DBH), only six (0.6%) are larger than the 12.5 cm threshold DBH. Thus, trees from the 10-year-old cohort have only a very small chance of being included in a random sample of trees. It is not until age 40 that half of the trees in a 10-year age-class (211 of 422 live 40-year-old trees) have grown into the sampling range. For about 30 years, ingrowth into the minimum DBH class approximately balances mortality. So derived, the age-frequency distribution peaks in the 50-year age-class (Fig. 5*c*). Beyond the 50-year age-class, mortality exceeds ingrowth and the frequency of occurrence of trees continually declines. Nevertheless, ingrowth can potentially occur in all age-classes including the 100-year-old class, which includes 3% of its population below the minimum observed diameter.

Is it possible to rectify the discordance between diameter and age distributions by modifying the sampling scheme? Only by sampling the entire diameter distribution down to the smallest basal diameter can bias in the age-frequency distribution be completely eliminated. Even reducing the minimum sampling diameter to 0 cm DBH does not eliminate the problem because half the trees in the 10-year-old age-class have not attained 1.3 m in height. The truncation and skewedness of the age distribution simply shifts further to the left as the minimum observed diameter decreases.

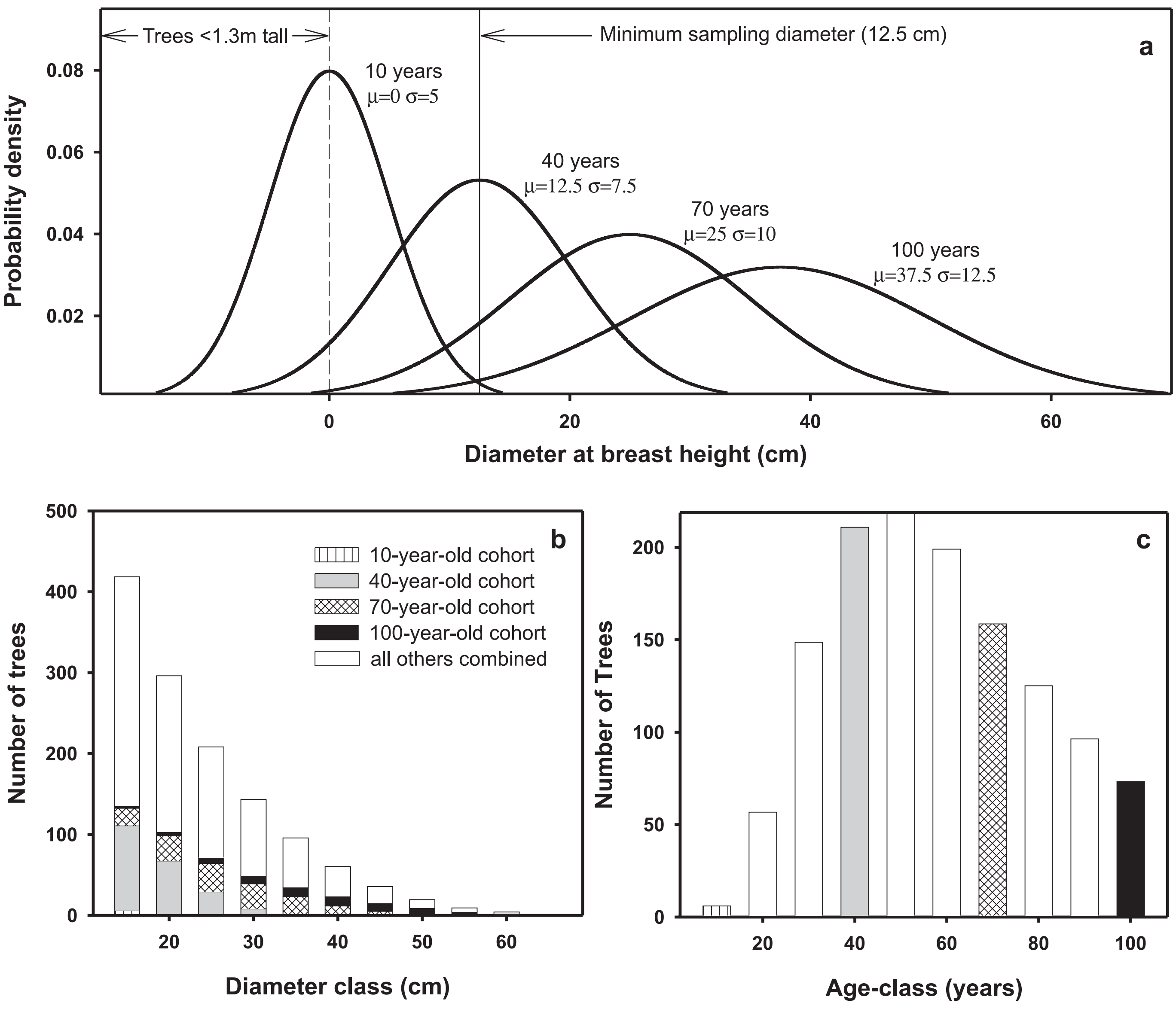
Even if we overlook the impracticality of determining age-frequency distributions as a basis for assessing the sustainability of an uneven-aged silvicultural system, using this measure is potentially misleading. The standard practice of managing and monitoring stand structure by diameter-frequency distributions is sound in practice and in theory. Although the total range of diameters within an age-class may exceed 40 cm, the mean diameter of the age-class does increase with time. Thus, if new cohorts are not periodically recruited into the overstory, the left side of the diameter distribution will decline and eventually disappear. Nonetheless, the time required for its disappearance from graphical view depends on the observed minimum diameter. If the observed minimum diameter is relatively large, insufficient ingrowth of trees into the overstory may not be apparent for decades. Thus, assessment of an uneven-aged silvicultural system should include periodic regeneration inventories.

Future trends in forest structure

The fact that ages of the sampled oaks in the study area ranged from 12 to 233 years suggests that a significant proportion of them were already established when the current cutting strategy was initiated. In fact, only 13% of the trees sampled (≥4 cm DBH) have been established since 1954. At the same time, from 1957 until 1992, forest average basal area and tree density have increased by 68 and 89%, respectively, for all trees ≥12.5 cm DBH (Loewenstein 1996). These figures suggest that large numbers of small-diameter trees were already present in 1954 and that continual recruitment into the overstory has occurred. However, the amount of growing space available for establishment and development of trees has been steadily declining as the forest has recovered from its initial understocked condition. Although silvicultural treatments have increased in intensity as stocking

[3] This is equivalent to an annual survival rate of 0.9717.

Fig. 5. Effects of a minimum sampling diameter on observed tree age and diameter distributions based on a hypothetical "balanced" uneven-aged population. (*a*) The hypothetical dispersion of diameters for 10-year age-classes scaled to a probability density function, by diameter classes with specified means (μ) and variances (σ); to avoid graphical confusion, only four age-classes are shown. Numbers of trees in the 10-year-old age-class was set to 1000 and was successively reduced in each older age-class by 25%; this is equivalent to an annual survival rate of 0.9717. (*b*) The diameter frequency distribution of trees ≥12.5 cm DBH, by 5-cm DBH classes; shaded bars correspond to the four age-classes illustrated in Fig. 5*a* and unshaded bars correspond to the six age-classes not shown. (*c*) The age-frequency distribution of trees ≥12.5 cm DBH by 10-year age-classes.



levels have risen, harvest volume plus natural mortality does not yet equal growth (Loewenstein 1996). To maintain an uneven-aged condition, the stocking level must provide sufficient growing space for the establishment and growth of new trees to replace those lost to harvest, natural mortality, and ingrowth into larger diameter classes. Because stocking levels on the forest continue to increase, the future probability for establishing new cohorts and the survival and growth rates of the most subordinate age classes are unknown at this time.

Despite the silvicultural uncertainties associated with stand history, important ecological differences between the two oak species groups are apparent in their patterns of establishment (Fig. 3) and their age–diameter relations (Fig. 4). Whereas 17% of white oaks sampled were established under the current silvicultural system, only 5% of the red oaks were established during the same period. Because of the red oaks' shade-intolerance, we might reasonably deduce there will be further future reductions in their population. Currently, the red oaks diameter distribution appears normally distributed, a characteristic often attributed to even-aged stands. The left tail of the distribution nevertheless does not completely disappear (Fig. 2). A similar diameter distribution pattern was observed in old-growth oaks stand in Missouri where red oaks were a minor but persistent component even in high-density stands (Shifley et al. 1995).

In contrast, white oak as a species has been increasing in prominence over time. Forest wide, white oak has increased in numbers per hectare and basal area at rates exceeding all other species combined (Loewenstein et al. 1995). Moreover, white oak is the most abundant species in the reproduction size classes (Loewenstein 1996). The paucity of large-diameter white oaks on the study area may largely be related to the highgrading of 1956. That harvest removed most of the merchantable, high-quality white oaks, leaving only cull and small-diameter trees. Trees of high quality are also usually the youngest and most vigorous trees in a given diameter class. Thus, trees removed in the 1956 harvest were probably concentrated in the lower right-hand quadrant of the age–diameter scatter diagram (Fig. 4). Those trees largely comprise the sawtimber size classes and age-classes from 50 to 100 years. Had those trees not been harvested, they would have grown 7.5 to 15 cm in DBH over the next 36 years (to 1992) and thereby increased the proportion of white oaks in the larger diameter classes. Given that the ratio of establishment of white oaks to red oaks is 7.5:1 under the current silvicultural system, it seems likely that white oak/red oak ratio will continue to increase beyond the current 2:1 ratio.

Current stand attributes are consistent with the general definitions of an uneven-aged stand and an uneven-aged forest and evidence a rate of ingrowth of oaks into the overstory sufficient to maintain an uneven-aged state. Although future changes in age structure and species composition appear inevitable, the reverse-J-shaped diameter distribution occurs on the study area and across the forest as a whole (Loewenstein 1996; Wang 1997). This distribution also occurs at a small spatial scale at high probability (Loewenstein 1996). At least at current and recent stand densities, the reverse-J-shaped diameter distribution may be intrinsic to this ecosystem. Relative diameter structure on the forest has remained stable from 1957 through 1992, even though basal area has increased by almost 90%. This stability cannot be attributed solely to cutting practices, because even though the minimum diameter harvested on the forest is 25 cm, the relative frequency distribution has remained stable across the range of diameters down to the 12.5-cm DBH class (Loewenstein 1996). Further, the reverse-J distribution has been found to occur in unmanaged, oak-dominated, old-growth forests in Missiouri (Shifley et al. 1995). Additional research is needed to determine whether this distribution is indeed an intrinsic characteristic of the system and if so, how this information might be utilized in developing silvicultural prescriptions.

Summary and conclusions

The overall diameter distribution of the oaks in the study area conformed to that of an uneven-aged stand with a reverse-J shape. Whereas the white oaks formed a reverse-J-shaped diameter distribution, the red oaks approximated a normal distribution. However, the red oaks spanned a DBH range that would be uncharacteristically wide for an even-aged stand.

Statistical analysis of the age structure confirmed the empirical evidence from the diameter structure. At a scale of 0.4 ha, the oak populations in 7 of the 10 sample plots were deemed uneven aged, whereas the other three were not. However, the latter appeared to be transitional to the uneven-aged state. Thus, the generally accepted tenet that suggests oaks cannot be maintained in an uneven-aged state at a “small” spatial scale would not appear to apply to the study area and, by extension, to similar oak-dominated ecosystems.

Ages and diameters of oaks were not highly correlated in this partially cut stand. DBH explained 40–62% of the variation in age, depending on species group. There was also little similarity between the shape of the DBH frequency distribution and the age-frequency distribution. Unlike the reverse-J-shaped diameter distribution, the age-frequency distribution was nearly normal (bell shaped). This apparent inconsistency between diameter and age distributions may largely be an artifact of the minimum observed (measured) DBH. This conclusion is consistent with the dispersion of diameters within age classes reported in even-aged stand tables. Just as a reverse-J-shaped diameter distribution, by itself, does not confirm the existence of the uneven-aged state (species composition must be taken into account), the occurrence of a bell-shaped age distribution does not preclude its existence. It is therefore appropriate that, when managing a stand using uneven-aged silvicultural systems, diameter structure should be the primary factor considered when determining treatment.

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