Sustaining Recruitment of Oak Reproduction in Uneven-aged Stands in the Ozark Highlands

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IMPORTANCE OF OVERSTORY DENSITY TO THE DEVELOPMENT OF OAK REPRODUCTION

There is evidence that the single-tree selection method can be successfully applied to oak stands in the Ozark Highlands of Missouri (Loewenstein 1996, Wang 1997). However, the success of the method depends on sustaining adequate growth (recruitment) of oak reproduction into the overstory. A major limitation in obtaining the requisite recruitment is high overstory density. Oak reproduction is relatively intolerant of shade and therefore requires a low to moderate overstory density to provide the light necessary for its establishment and growth beneath the forest canopy. Silviculturists have generally concluded that the single-tree selection method is unsuitable for oaks because the method maintains a relatively uniform overhead shade (Roach 1962, 1974; Gingrich 1967; Sander and Clark 1971; Trimble 1973; Sander et al. 1983; Marquis and Johnson 1989; Sander and Graney 1993). However, we propose that the method's suitability depends on the dynamics of the ecosystem it is applied to. The characteristics of the oak regeneration process, which differ greatly among the oak-dominated forests of the Eastern States, are therefore a key factor in the method's successful application (Johnson 1993a, 1993b).

This paper describes some relations between overstory density and oak reproduction. Based on these relations, we present criteria for selecting a residual stand structure and density appropriate to the single-tree selection method in the Ozark Highlands that is consistent with the regeneration ecology of oaks and thus sustaining a forest dominated by oaks.

PRINCIPLES OF OAK REGENERATION APPLIED TO UNEVEN-AGED FORESTS

Uneven-aged silviculture involves creating and maintaining uneven-aged stands. Trees of at least three age classes (e.g., 20-year classes) must be present for a stand to be categorized as uneven-aged (Smith 1986). In an idealized uneven-aged stand, trees of every age class would be present. Such a distribution reflects the continual or frequently periodic growth of trees, including reproduction, into successively older age classes. However, only part of the trees in any age class survive to become members of the next older class. Maintaining an uneven-aged distribution of trees is thus an essential feature of sustaining an uneven-aged stand. However, because of the impracticality of determining the age of every tree, an uneven-aged stand is silviculturally maintained by controlling its diameter distribution.

Such control is usually obtained through the creation and maintenance of a diameter frequency distribution that forms a reverse J-shape (fig. 1). Such distributions often develop naturally in old-growth forests (Meyer et al. 1952). However, reverse J-shaped distributions also may characterize even-aged stands when they are young or where species differ greatly in growth rate or shade tolerance. It is important to have information on the current diameter distribution at the outset of a stand's management. Ideally, the forest manager should have information on both age and diameter distributions, and on the variation in those distributions among species. However, in most cases, it is impractical to determine age distributions. It is not unusual for shade-tolerant species forming an uneven-aged
population with a reverse J-shaped diameter distribution to co-occur with an even-aged population of shade-intolerant species forming a bell-shaped distribution (Stout 1991). Even-aged oak forests commonly form bell-shaped diameter distributions by the time they reach a mean diameter of 8 inches d.b.h. (Schnur 1937, Gingrich 1967). The paucity of small-diameter trees in such distributions reflects the inability of oak reproduction to become established, survive in a subordinate crown position, and grow into the overstory. Such relations are implicit in Schnur’s (1937) stand tables for “normal” even-aged oak stands (i.e., stands at average maximum density) in the Eastern United States.

![Graph of a reverse J-shaped diameter distribution](image)

**Figure 1.—**A reverse J-shaped diameter distribution.

As even-aged stands grow older, and in the absence of stand-replacing disturbance, natural canopy gaps develop whenever large trees die singly or in small groups. The vacated growing space is subsequently captured by preestablished tree reproduction, which can respond to the increased light and availability of other resources. If this gap-formation process continues, even-aged stands can eventually evolve into uneven-aged stands comprised of complex mosaics of very small even-aged groups of trees. Depending on ecosystem-specific successional processes, which differ among the many different kinds of forests, the species currently dominating the main canopy may or may not be replaced by new species. In many oak forests, the relatively shade-intolerant oaks are successively replaced by more shade-tolerant species (Nowacki et al. 1990, Abrams and Nowacki 1992, Nowacki and Abrams 1992).

Although the theory underlying the silvicultural application of reverse-J diameter distributions has been widely presented in silvicultural textbooks and other sources (e.g., Roach 1974, Smith 1986, Nyland 1996), there has been relatively little discussion of how such distributions are related to forest regeneration. We propose that selecting an appropriate reverse-J distribution depends on: (1) silvicultural objectives, and (2) the natural dynamics of the forest where it is to be applied. Silvicultural objectives that do not consider natural forest dynamics are unlikely to be realized. To ensure success, the selected diameter distribution therefore must be compatible with the natural dynamic of the stand being managed. Compatibility, in turn, depends largely on the characteristics of the regeneration process and the likelihood of sustaining adequate recruitment of reproduction into the overstory.

The upland forests of southern Missouri lie within the Ozark Highlands Section of the Eastern Broadleaf Forest (continental) Province as defined by McNab and Avers (1994). These forests are typically dominated by some combination of white oak (Quercus alba L.), black oak (Q. velutina Lam.), scarlet oak (Q. coccinea Muenchh.), northern red oak (Q. rubra L.), and post oak (Q. stellata Wangenh.). The oaks tend to persist as canopy dominants over successive generations. Unlike oak forests in many other regions of the Eastern United States, Ozark Highland oak forests are generally not successional to non-oaks. The persistence of oaks in the Ozarks is largely related to this regeneration dynamic and to the frequency of stand disturbance. The oak reproduction beneath mature stands typically accumulates over several decades (Liming and Johnston 1944, Johnson 1993a). This accumulation produces populations of oak seedling sprouts. Some of these have large root systems and the potential for rapid shoot growth when natural or human-caused disturbances sufficiently reduce overstory density (Johnson 1979, Dey et al. 1996) (fig. 2). The resultant regeneration process is typical of the relatively dry sites that characterize the Ozark Highlands, where the site index for black and scarlet oaks ranges from about 40 to 80 ft at
Total oak reproduction densities typically range from 1,000 to 3,000 seedlings and seedling sprouts per acre. However, most of these seedlings and seedling sprouts are typically less than 1 ft tall (Sander 1979). Only a small proportion attain large size (e.g., >4.5 ft tall) (Larsen et al. 1997). In uneven-aged silviculture, the presence of large oak reproduction nevertheless is necessary for sustaining recruitment into the overstory. Because white oak is more tolerant of shade than the other oaks, it is often better represented in the large reproduction size classes and small overstory d.b.h. classes than the other oaks. White oak's presence in these size classes is essential to the success of the single-tree selection method in the Ozarks (Loewenstein 1996, Wang 1997).

Figure 2.—Oak reproduction growing beneath an uneven-aged forest canopy. In the Ozark Highlands, the shoots of oak seedlings typically die back one or more times to form “seedling sprouts.” Some of these eventually develop large roots and thereby the capacity for rapid shoot growth and the ability to capture canopy gaps created when overstory trees are harvested.

The predominant non-oaks in xeric Missouri Ozark forests include hickories (Carya spp.), sassafras (Sassafras albidum [Nutt.] Nees), flowering dogwood (Cornus florida L.), blackgum (Nyssa sylvatica Marsh.), red maple (Acer rubrum L.), and shortleaf pine (Pinus echinata Mill.). These species are usually relegated to subordinate crown classes in mature stands. Exceptions are the hickories and shortleaf pine, which commonly attain dominance but usually make up only a small proportion of the main canopy of a mature forest. Although the broadleaf non-oaks persist in xeric Missouri Ozark forests, their dominance in canopy gaps is usually limited to the first 10 to 15 years of recovery. However, by the end of the second decade, oaks usually have reemerged as the dominant species. The oak's capacity to persist as a dominant member of uneven-aged forests is evidenced by the successful application of the single-tree selection method in a large privately owned forest in the Ozark Highlands. After the method had been applied for 40 years, oaks accounted for 70 percent of total basal area of trees ≥5 inches d.b.h., and there was no evidence that their importance as a canopy dominant was declining (Loewenstein et al. 1995, Loewenstein 1996).

In uneven-aged silviculture, the objective of creating and maintaining a reverse J-shaped d.b.h. distribution is to facilitate a predictable rate of movement (recruitment) of trees from one diameter class to the next. This property of the distribution is key to the systematic management, regulation, and sustainability of an uneven-aged forest. Specifying a d.b.h. distribution for this purpose is often limited to trees above some arbitrary minimum d.b.h. such as 5 or 6 inches. However, if the distribution is to be sustained, it must in reality extend downward into the smaller size classes including reproduction (i.e., trees ≤1.5 inches d.b.h.).

A common assumption in uneven-aged silviculture is that the requisite recruitment of trees follows a more or less constant rate among d.b.h. classes. Such a rate, in turn, is represented by a constant ratio of trees between adjacent d.b.h. classes. Silviculturists usually express this as the constant ratio of trees in one d.b.h. class to that in the next larger class. The use of this ratio, or quotient (generally referred to simply as q), originated in 19th century French forestry (de Liocourt 1898). In silvicultural application in North American hardwood forests, commonly recommended values of q range from 1.1 to 1.4 based on 1-inch d.b.h. classes (1.2-2.0 for 2-inch classes) (Trimble 1970; Leak 1978, 1987; Leak et al. 1987; Smith 1980; Smith and Lamson 1982; Law and Lorimer 1989). The related progression of diameters mathematically follows the negative exponential function whereby numbers of trees decrease logarithmically with increasing d.b.h. However, other types of diameter distributions generally
characterized by declining numbers of trees with increasing d.b.h. also have been described and applied to uneven-aged silviculture (Leak 1996).

The importance of reproduction in sustaining an uneven-aged forest can be illustrated by various negative exponential diameter (d.b.h.) distributions (fig. 3). If we consider the 2-inch d.b.h. class as the lower limit of trees making the “overstory,” then the 1-inch class would represent the largest reproduction class. The assumption that a proportion of the reproduction in this largest class must be periodically recruited into the overstory provides a conceptual basis for establishing a criterion for the minimum number of “large” stems of reproduction needed to satisfy the recruitment requirements associated with a specified diameter distribution.

In general, the probability of observing a given density and size of reproduction decreases as stand density increases. For a given stand density, probabilities for all species combined are much larger than for the oaks alone. For example, the probability of observing total reproduction densities of ≥250 and ≥500 per acre ranges from about 0.9 to nearly 1 under stands at ≤80 ft² of basal area per acre (fig. 4A). In contrast, the probability of observing oak reproduction densities of ≥50 or ≥100 per acre ranges from about 0.25 to 0.82 for stands ≤80 ft² (fig. 4B). Probabilities for oaks also decline faster with increasing stand density than do probabilities for all species combined. These relations emphasize the sensitivity of oak reproduction to overstory density in comparison to the total population of tree reproduction. It should be noted that although we would expect oak reproduction density to be affected by site quality (Dey et al. 1996), including this variable did not significantly increase predictability and thus it was not included in the model. Therefore, the probabilities presented represent the average of the observed range of sites.

The high probabilities for all species point out the ubiquitous nature of tree reproduction in Ozark forests. They also reflect the potential for tree reproduction to capture growing space vacated by the death or removal of the parent stand at any given time or place. Preestablished tree reproduction present at the time of
canopy disturbance largely determines the future composition of canopy gaps created by the single-tree selection method. However, for either level of reproduction density (i.e., ≥50 or ≥100 per acre for oaks, ≥250 or ≥500 per acre for all species), probabilities decline rapidly for any given overstory density as the reproduction height criterion increases. Thus, there is relatively little reproduction ≥4.5 or ≥6.5 ft tall. Yet, it is the larger reproduction that has the greatest chance of growing into the overstory. The larger reproduction, modified by its species-dependent persistence as a canopy dominant, largely predetermines future stand composition and structure.

Nevertheless, even small reproduction has some probability of growing into the overstory (Dey et al. 1996). This is especially true of the oaks, some of which recurrently die back and resprout to produce populations of seedling sprouts with highly variable root:shoot relations and thus highly variable growth potentials (Johnson 1979) (fig. 2). For example, a 6-inch-tall oak seedling sprout with a basal diameter of one-half inch (and a correlated large root system) is likely to grow much faster in a canopy gap than a 6-inch tall oak seedling that has recently germinated (Sander 1971). Consequently, the probability of recruiting reproduction into the overstory is highly variable within a reproduction height class. Conceptualizing reproduction as an extension of the overstory diameter distribution (fig. 3) and estimating reproduction probabilities from overstory density (fig. 4) nonetheless provide a basis for understanding how regeneration dynamics are linked to overstory density and structure in uneven-aged oak stands in the Ozark Highlands.

**SELECTING AN APPROPRIATE OVERSTORY DENSITY AND STAND STRUCTURE**

Despite the highly variable growth potential of oak reproduction of a given size, it is apparent from figure 4 that lower stand densities are associated with larger probabilities of occurrence of high oak reproduction densities and large reproduction size. However, there is a practical lower stand density limit for managing oak forests. This limit is determined by two factors: (1) the utilization of growing space by trees, and (2) tree bole quality. We propose managing oak stands at densities that fully utilize growing space most of the time and that are sufficient to prevent bole degrade from epicormic branching associated with low stand densities (Dale and Sonderman 1984). Based on Gingrich's (1967) stocking equation, full use of growing space occurs at approximately ≥55 percent stocking.1 This equates to

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1 Gingrich (1967) tested his stocking equation across a wide range of stand structures and concluded that stocking is independent of diameter distribution.
about ≥56 ft² of basal area per acre (for trees ≥2 in. d.b.h.) when d.b.h. distributions are reverse J-shaped.²

Accordingly, we recommend a total residual stand density that ensures adequate use of growing space, maintenance of tree bole quality, and within those constraints the highest possible probability of obtaining adequate oak reproduction. Although 56 ft² of basal area approximates minimum stocking for full use of growing space, we recommend reducing total stand stocking to 50 ft² to increase the likelihood of sustaining adequate oak regeneration. We also recommend maintaining stand structures within the q range of 1.2 to 1.3 based on 1-inch d.b.h. classes (1.4 to 1.7 for 2-inch classes). These recommendations thus focus on the maintenance of a stand structure and density that is consistent with sustaining adequate oak reproduction. Conversion of normally stocked even-aged stands or irregular uneven-aged stands to the specified structure and stocking levels may require several cutting cycles depending on current stand stocking and diameter structure.

We chose the selected stand density and range of q values for three reasons: (1) a large privately owned oak forest in the Ozark Highlands has been successfully managed at a q value of approximately 1.3 (for 1-inch d.b.h. classes) for 40 years (Loewenstein 1996, Wang 1997); (2) total stand densities below 50 ft² basal area result in unused growing space during much of the cutting cycle and encourage epicormic branching and associated reduction in tree bole quality (Dale and Sonderman 1984); and (3) decreasing total residual stocking from 56 to 50 ft² substantially increases the probability of obtaining more and larger reproduction (fig. 4B). Stands reduced to 50 ft² of basal area every 20 years can be expected to grow at a rate of approximately 1.3 ft² per acre per year on average sites (Gingrich 1967). Therefore, by the end of a 20-year cutting cycle, total basal area can be expected to reach approximately 76 ft² per acre. Stands will consequently average about 63 ft² of basal area during a cutting cycle. At that average density, we can expect oak densities of ≥50 stems of reproduction per acre at least 2.5 ft tall about 50 percent of the time (fig. 4B).

Diameter distributions used to control timber harvesting ("guiding curves") can be applied directly or indirectly in marking stands to a specified structure and density at the end of each cutting cycle. Although harvesting across the entire range of diameters provides maximum control of stand structure, there is little evidence that this is necessary (Wang 1997). A minimum cutting diameter of 10 inches d.b.h. can maintain the desired structure even though there may be substantial fluctuation in q below the cutting threshold. To maintain maximum control of stand structure and composition, we recommend a minimum cutting diameter that is as small as operationally feasible. Practical guidelines for their field application are presented by Law and Lorimer (1989).

If sustaining oaks is the primary management objective, we recommend that guiding curves be applied to the species that usually dominate the forest canopy (predominantly oaks and hickories) (fig. 5). However, other species also may occupy significant growing space, especially in the smaller diameter classes. These trees should be considered in determining total stand stocking. However, because they rarely attain canopy dominance, they need not be considered in defining the guiding curve. We know from experience that, in uneven-aged oak forests in the Ozark Highlands, oaks average 70 percent of the basal area and other merchantable species make up another 20 percent of the basal area (Loewenstein 1996). Accordingly, we propose a guiding curve that defines only the residual stocking of the species that dominate the forest canopy.

Based on the negative exponential function, we present coefficients for guiding curves for the potential canopy dominants for q values of 1.2, 1.25, and 1.3, (1-inch classes) and a residual

² The numeric relation between stand basal area and stocking percent is close to 1:1 when stand structure conforms to a negative exponential diameter distribution that includes trees ≥2 in. d.b.h., and stands are at low to moderately high stocking. For example, for a q of 1.3, the basal area range of 35 to 75 ft² per acre corresponds to 34 to 73 percent stocking. Basal area, therefore, only slightly overestimates the percent of growing space used by trees under the uneven-aged stand structures typical of Ozark oak forests. The relation becomes less exact as minimum diameter increases.
SUMMARY AND CONCLUSIONS

This knowledge and the resultant silvicultural recommendations are based primarily on the analysis of 40 years of records from a large managed uneven-aged forest in the Ozark Highlands. This represents the largest and most complete database currently available for evaluating the application of the single-tree selection method in that region. Success in applying the single-tree selection method to the oak forests of the Ozark Highlands depends on several factors including:

- **Sustaining adequate recruitment of oak reproduction into the overstory.** Adequate recruitment of oak reproduction depends on maintaining a population of large oak seedling sprouts beneath the canopy of the parent stand. Such reproduction has the growth potential to capture canopy gaps created by the single-tree selection method.

- **Maintaining ecologically appropriate stand densities.** Because high stand densities severely limit the survival and development of the relatively shade-intolerant oak reproduction, stands should be managed at densities compatible with the survival and development of oak reproduction of adequate number and size.

- **Maintaining silviculturally adequate overstory densities.** There also is a lower practical limit in overstory density that is determined by the minimum density for full or nearly full utilization of growing space by trees and the related maintenance of tree bole quality. Based on those considerations, together with oak regeneration requirements, we recommend reducing total stand density to approximately 50 ft² of basal area per acre (for trees ≥2 inches d.b.h.) every 20 years or less.

- **Controlling stand density and structure with an appropriate guiding curve.** We recommend controlling stand density and structure using a guiding curve based only on the oaks and other potential canopy dominants. Assuming that this merchantable component accounts for approximately 90 percent of total residual (after harvest) stocking, we recommend a guiding curve based on a residual basal area of 45 ft²/acre.
Table 1.—Coefficients for the negative exponential function for recommended guiding curves for the merchantable species

<table>
<thead>
<tr>
<th>q for guiding curve (1-inch d.b.h. classes)</th>
<th>Coefficients for the guiding curve</th>
<th>Number of 20-inch d.b.h. trees per acre represented by guiding curve</th>
<th>Number of 1-inch trees per acre required by the guiding curve</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>a</td>
<td>b</td>
<td></td>
</tr>
<tr>
<td>1.20</td>
<td>34.799</td>
<td>-0.1823</td>
<td>0.91</td>
</tr>
<tr>
<td>1.25</td>
<td>55.205</td>
<td>-0.2231</td>
<td>0.64</td>
</tr>
<tr>
<td>1.30</td>
<td>83.060</td>
<td>-0.2624</td>
<td>0.44</td>
</tr>
</tbody>
</table>

1 Coefficients or numbers of 20-inch trees can be used to derive numbers of trees per 1-inch d.b.h. class for three values of q, and for a residual basal area of 45 ft² per acre for trees 2 to 20 inches d.b.h.

2 Based on the negative exponential function, which is given by:

\[ N_i = ae^{bD_i} \]  

where \( N_i \) is the number of trees in \( i^{th} \) d.b.h. class, \( a \) and \( b \) are coefficients of the negative exponential function (\( b \) is the natural logarithm of \( q \), and is always negative), \( e \) is the base of natural logarithms, and \( D_i \) is the midpoint diameter of the \( i^{th} \) d.b.h. class in inches. Coefficients are given for 1-inch d.b.h. classes. Values of \( q \) corresponding to other d.b.h. classes are the values given in the table for 1-inch classes raised to the power given by the class width (e.g., second, third, and fourth powers for 2-, 3-, and 4-inch d.b.h. classes, respectively). A method for calculating \( a \) for any given \( q \) and stand density (expressed as either basal area per acre or stocking percent based on Ginterich’s stocking equation) is presented by Moser (1976). Alternatively, guiding curves can be calculated from equation 2, below, which does not require specifying \( a \).

3 The number of trees in other 1-inch d.b.h. classes can be calculated by sequentially multiplying \( q \) times the number of trees in successively smaller d.b.h. classes. For example, the number of 19-inch trees equals \( q \) times the number of 20-inch trees, the number of 18-inch trees equals \( q \) times the number of 19-inch trees, etc. For any given value of \( q \), residual stand basal area, and range of diameters, the number of trees in a given maximum d.b.h. class \( (N_{\text{max}}) \), i.e., the largest d.b.h. retained in the residual stand based on the guiding curve, can be calculated by:

\[ N_{\text{max}} = \frac{\text{RBA}}{\sum \left( \frac{D_{\text{max}} - D_i}{w} \right)} \]  

where RBA is the selected residual basal area in ft² per acre for a specified range of tree diameters represented by the guiding curve, BA is the basal area of the tree of d.b.h. \( D \) in ft², \( q \) (which is the reciprocal of the antilog of \( b \) in eq. 1) is the selected stand structure represented by the guiding curve, \( D_{\text{max}} \) is the maximum tree d.b.h. represented by the guiding curve, and \( w \) is d.b.h. class width in inches. Equation 2 is convenient for calculating guiding curves using computer spreadsheets.

(90 percent of total residual stocking) and a \( q \) of 1.2 to 1.3 for 1-inch d.b.h. classes (1.4 to 1.7 for 2-inch classes). We recommend harvesting trees across the widest possible range of diameters to ensure maximum control of stand structure. Although non-merchantable subcanopy trees occupy a small amount of growing space (about 5 ft² of basal area per acre on the average), they make up a silviculturally significant component of stand stocking because of their relatively large numbers and associated effects on stand regeneration and bole quality.

The recommended guiding curves are generally consistent with the regeneration dynamics of the oak forests of Ozark Highlands. We therefore offer them as a reasonable basis for sustaining oaks and other valuable canopy dominants using the single-tree selection method in that region.
Table 2.—Number of trees in 1-inch d.b.h. classes for a residual basal area of 45 ft² per acre for three q values

<table>
<thead>
<tr>
<th>D.b.h.(In.)</th>
<th>1.2</th>
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<th>1.3</th>
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<tbody>
<tr>
<td>2</td>
<td>24.2</td>
<td>35.3</td>
<td>49.1</td>
</tr>
<tr>
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<td>12</td>
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<tr>
<td>19</td>
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<td>0.6</td>
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<tr>
<td>20</td>
<td>0.9</td>
<td>0.6</td>
<td>0.4</td>
</tr>
</tbody>
</table>

1 Values were calculated using the method presented in table 1, footnote 2.

Table 3.—Number of trees in 2-inch d.b.h. classes for a residual basal area of 45 ft² per acre for four q values

<table>
<thead>
<tr>
<th>Diameter class</th>
<th>Number of trees per 2-inch class for q of</th>
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<tbody>
<tr>
<td></td>
<td>1.4</td>
</tr>
<tr>
<td>2</td>
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<td>2.8</td>
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<td>20</td>
<td>2.0</td>
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1 Values were calculated using the method presented in table 1, footnote 2.

LITERATURE CITED


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Larsen, David R.; Loewenstein, Edward F.; Johnson, Paul S.  
Successful application of the single-tree selection system in Ozark oak forests depends on sustaining adequate recruitment of reproduction into the overstory. In turn, this requires maintaining stand density at ecologically appropriate levels. The ecological requirements for oak recruitment are discussed and guiding curves are presented that meet those requirements.  

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KEY WORDS: Uneven-aged silviculture, stand structure, stand density, diameter distributions.
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