# Oak regeneration and overstory density in the Missouri Ozarks

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**Abstract**: Reducing overstory density is a commonly recommended method of increasing the regeneration potential of oak (*Quercus*) forests. However, recommendations seldom specify the probable increase in density or the size of reproduction associated with a given residual overstory density. This paper presents logistic regression models that describe this relation for a forest in the Ozark Highlands of Missouri that has been managed for 40 years by the single-tree selection system. In general, density of oak reproduction of a given size increases with decreasing residual stand basal area. However, the corresponding increase in the reproduction density at all levels of overstory density indicates low predictability of individual stands. The models nevertheless describe the average trend in the highly stochastic regeneration process. They also suggest that stand densities must be kept low (e.g., basal areas <14 $m^2 \cdot ha^{-1}$) to sustain the requisite recruitment of reproduction into the overstory under the single-tree selection method.

**Résumé** : La réduction de la densité du couvert est une méthode communément recommandée pour augmenter le potentiel de régénération des forêts de chênes (*Quercus*). Toutefois, les recommandations spécifient rarement l'augmentation probable de la densité ou de la taille de la régénération associée à un niveau donné de densité résiduelle du couvert. Cet article présente des modèles de régression logistique qui décrivent cette relation pour une forêt des plateaux de l'Ozark, au Missouri, qui a été aménagée depuis 40 ans sous un régime de futaie jardinée par pied d'arbre. De façon générale, la densité de la régénération de chêne d'une dimension donnée augmente avec une réduction de la densité résiduelle du couvert. Cependant, l'augmentation correspondante de la densité de la régénération à tous les niveaux de densité du couvert indique un faible pouvoir prédictif au niveau des peuplements individuels. Les modèles décrivent néanmoins les tendances moyennes du processus hautement stochastique de régénération. Ils suggèrent aussi qu'on devrait conserver une faible densité (c.-à-d., surfaces terrières <14 $m^2 \cdot ha^{-1}$) des peuplements si on veut maintenir le recrutement nécessaire au sein du couvert principal dans le cadre du système de jardinage par pied d'arbre.

[Traduit par la Rédaction]

## Introduction

Controlling overstory density is a commonly recommended method for encouraging oak regeneration (Loftis 1990; Johnson 1993). It also may be the least expensive and most easily accomplished treatment and may even produce revenue. Silviculture texts commonly recommend preparatory cuts to encourage regeneration (Smith 1986; Matthews 1989; Oliver and Larson 1996). Although these texts describe the general nature of potential treatments, they usually leave specifics to local silviculturists. Ideally, forest managers should be able to define the probable tradeoffs between reduction in overstory density and establishment and growth of advance reproduction. A quantitative tool describing this relationship can be useful in decision making.

Oak regeneration is a continual process involving the birth and death of seedlings, recurrent shoot dieback, and the formation of seedling sprouts and sprouts from stumps of cut trees (Sander 1971). Seedlings, seedling sprouts, and stump sprouts are common forms of oak reproduction throughout the range of oaks in the eastern United States (Sander 1971). The relative importance of each form depends on site factors, maturity of the parent stand, disturbance intensity during the previous harvest, sprouting capacity and growth rate of the advance reproduction, and other factors.

In relatively xeric oak forests like those of the Ozark Highlands of Missouri, oak reproduction accumulates beneath the parent stand over several decades (Liming and Johnston 1944). This reproduction recurrently dies back to the root collar and resprouts for many years. Stem and root ages therefore may differ greatly. Consequently, sapling and small pole-size trees may be as old as dominant trees. Stem size is thus a poor indicator of stem age, and stem age is likely to be a poor indicator of biological age (i.e., age from germination). Sprouts from large advance reproduction and small overstory trees nevertheless can grow rapidly after release from overstory suppression. However, the potential for sprouting from cut overstory trees declines with increasing tree diameter and age (Johnson 1977).

In the Ozark Highlands, the non-oaks seldom become canopy dominants except for short periods after heavy canopy disturbance (Dey 1991; Shifley et al. 1995; Loewenstein 1996). In other regions, non-oaks are often potential canopy dominants, and a very different stand dynamic occurs. There, non-oak species compete with the oaks for canopy dominance. Moreover, many of these non-oaks are more shade tolerant than oaks, and this usually results in the successional displacement of

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oaks. This case is much more common in more mesophytic parts of the oak range.

A wide range of responses has been observed in released oak reproduction (Schlesinger 1978; McGee and Bivens 1984). Those studies indicate that oak reproduction responds to release from overstory shade, but rate of growth varies greatly depending on size and apparent physiological condition of the tree. It has long been noted that oak reproduction grows better under high than low light (Büsgen and Münch 1929; Assmann 1971; Fischer 1981; Kozlowski et al. 1991). Reducing overstory density and thereby increasing light in the understory is one method of increasing oak regeneration potential.

As with all regeneration methods, silviculturists need a way to predict amount and size of reproduction resulting from overstory treatments in Missouri oak forests. Such predictions are potentially valuable tools for understanding how to manipulate overstories for successful regeneration. We conducted a study to develop predictive models for estimating the probability of occurrence of a given density oak reproduction greater than a specified size in relation to overstory density.

## Study site

The study site is located within the Current River drainage of the Ozark Highlands of southern Missouri. The history of this 36 000-ha forest includes exploitive logging near the turn of the century and again between the 1920s and the late 1940s. Records show that, by the early 1950s, stand basal area ranged from 5 to 10 $m^2 \cdot ha^{-1}$. Species in the red oak group predominated and included scarlet oak (*Quercus coccinea* Muenchh.), black oak (*Quercus velutina* Lam.), northern red oak (*Quercus rubra* L.), and southern red oak (*Quercus falcata* Michx.). Over the past 40 years those species have declined in relative abundance, but white oak (*Quercus alba* L.) and shortleaf pine (*Pinus echinata* Mill.) have increased (Loewenstein 1996). Black oak site index ranged from 16.8 to 27.4 m with a mean of 21.3 m (50-year base) (Larsen 1980). During this time, the forest has been managed using the single-tree selection method. The cutting cycle is approximately 20 years, and management units averaged 259 ha. Timber removals were based on an assessment of each tree's soundness, vigor, spacing, species, and quality potential. During the 40-year management period, the forest-wide diameter distribution has conformed to the negative exponential function. During that time, the average $q$ for the diameter distribution ranged from 1.60 to 1.65 for 5-cm diameter classes. Basal area for trees ≥12.7 cm diameter at breast height increased from 8 $m^2 \cdot ha^{-1}$ in 1957 to 14 $m^2 \cdot ha^{-1}$ in 1992. For the current forest-wide quadratic mean diameter of 22 cm, an overstory basal area of 14.7 $m^2 \cdot ha^{-1}$ would fully utilize the growing space based on Gingrich's (1967) stocking equation.

## Methods

Data for the study were collected from 800-$m^2$ plots systematically located across a 36 000-ha forest. In 1992 and 1993, we measured reproduction and overstory trees on a stratified random sample of 102 plots selected from among a larger set of 488 systematically located plots. We stratified the selected plots by three overstory density classes, three slope position classes, and four aspect classes. Our goal was to select three plots in each category. However, for 6 of the 36 categories only two plots occurred in the original set of plots. Reproduction, defined as trees >15 cm tall and <4 cm diameter at breast height, was measured on a 78.7-$m^2$ plot centered within each larger plot. Measurements included heights of each reproduction stem (height measured to the nearest 3 cm) and breast height diameters of all overstory trees measured to the nearest 2.5 mm.

We used logistic regression to estimate from overstory density the probability of obtaining at least $x$ reproduction stems per hectare of $y$ size class. This approach required defining "success" criteria associated with $x$ and $y$. Models accordingly were fit by logistic regression based on defined success criteria. Logistic regression has been used to predict future stocking after clearcutting given the advanced reproduction (Sander et al. 1984; Johnson and Sander 1988). The equation is of following form:

$$P_s = \frac{\exp(b_0 + b_1\mathrm{BA})}{1 + \exp(b_0 + b_1\mathrm{BA})}$$

where $P_s$ is the probability of occurrence of a specified minimum density and size class of reproduction, BA is overstory basal area ($m^2 \cdot ha^{-1}$), and coefficients $b_0$ and $b_1$ are estimated from the data.

In logistic regression, the observed value of the dependent variable, $P_s$, is binary (1 for plots that equal or surpass the criteria, 0 for plots that do not). However, the estimates are continuous and constrained to the interval 0–1. We defined three success criteria based on minimum threshold heights: ≥0.8, ≥1.4, and ≥2.0 m. Four classes of reproduction density were also defined for each of two species groups: oaks and all species. For the all-species group, the density success criteria were ≥600, ≥1200, ≥2500, and ≥5000 reproduction stems/ha. The success criteria for oaks were ≥125, ≥250, ≥500, and ≥1000 reproduction stems/ha. For each species group, we then derived separate regressions for each combination of height and density (e.g., ≥0.8 m and ≥600 stems).

## Results and discussion

For both species groups, the probability of occurrence of successful reproduction density decreased as threshold densities increased for both species groups (Table 1). For all success criteria and species groups, success probabilities increased with decreasing overstory density (Figs. 1 and 2). Probabilities for the all-species group increased at a faster rate than did probabilities for oak reproduction with respect to decreasing overstory density. The all-species group was largely made up of species that seldom become canopy dominants in the Ozark Highlands (e.g., *Cornus florida* L., *Sassafras albidum* Nutt., *Nyssa sylvatica* Marsh., *Cercis canadensis* L., *Amelanchier arborea* Michx. f., and *Crataegus* spp.). For a given threshold height, probabilities for the all-species group were approximately five times that of the oaks. For both species groups, large variance was associated with reproduction density even after the effect of stand density was removed (Table 2). The models nevertheless describe the trends in average success probability.

For oak reproduction, the data show that, for overstory basal area greater than 20 $m^2 \cdot ha^{-1}$, none of the plots met any of the size and density success criteria. For stands in the midrange of overstory density, the probability of exceeding threshold oak reproduction densities ranged from 0.01 to 0.6. Although oak reproduction on some of those plots attained acceptable densities, there was great uncertainty associated with attaining any specified density within a given plot. The probability of attaining threshold reproduction densities for the all-species group ranged from 0 to 1 at midrange overstory densities. For stands with low overstory density, probabilities ranged from 0.2 to 0.9 for oaks and 0.2 to 1 for the all-species group.

The general trend for reproduction of both species groups is to increase density and size with decreasing overstory density. This trend is consistent regardless of threshold density or size class. This relation is also consistent with current theories of plant response to available light and growing space (Kozlowski et al. 1991; Oliver and Larson 1996). However, in our study, reproduction density and size under any given overstory density varied greatly. This variation indicates that, on a given plot, almost any combination of reproduction size and density can occur. The regression models nevertheless describe the most likely rate of decrease in reproduction density and size with increasing overstory density. Time since cutting was also considered as a possible variable but was not found to be a significant predictor in any model. For the all-species group, equivalent probabilities occur for the threshold densities that are about five times greater than those for the oaks. This reflects the successional status of non-oaks in the Ozark Highlands, which seldom become canopy dominants.

Non-oaks often produce greater numbers of seedlings than oaks. However, numerical superiority indicates long-term dominance only if the mortality and growth rates of the co-occurring species are similar. It is more likely that different species have different life histories: some are prolific seed producers and (or) sprouters, some are not; some have high survival rates, others do not; and some have high growth rates, and others do not. The ultimate fate of a species depends on the combination of these traits and how that combination is expressed in competition with other species occurring on the same site.

These equations can be used to guide decisions about the reduction of overstory density during the treatment of Ozark upland-oak stands to encourage regeneration. One might consider the current overstory density and the current probability of success at a level of advanced reproduction desired. Then, by considering either a desired level of advanced reproduction, one can determine the basal area reduction needed to obtain a high probability of success at that level.

Another approach would be to consider the current level of regeneration success and then evaluate the change in success probability that would be obtained by a contemplated basal area reduction. This change in overstory density can be evaluated as the relative difference a unit change overstory density can contribute to the reproduction population. The equations can be used to identify the level of overstory densities needed to substantially influence advanced reproduction. The results presented contain implications for management that warrant further consideration.

Historically, the forest we studied in the Ozark Highlands was frequently disturbed at irregular intervals but with unequal intensity. Before 1880, the most common disturbance was windthrow and fire. After settlement by Europeans, timber cutting and domestic grazing (cattle and hogs) also became important disturbances. Oaks are well suited to frequent varying disturbance, and regeneration depends on episodic disturbance. Overstory density treatments therefore should be implemented before the reproduction is needed.

To sustain an uneven-aged management system, sufficient advance reproduction must be available for recruitment into the smallest diameter class of the overstory's reverse-J diameter distribution. To sustain oak diameter distributions similar to those of the past 40 years, approximately 250 oaks/ha of oak reproduction ≥1.4 m would be needed to maintain the smallest diameter class (4–7 cm). The logistic regression model for a reproduction density of ≥250 stems/ha (Fig. 1*b*) indicates that, for an overstory basal area of 6.5 $m^2 \cdot ha^{-1}$, 50% of the 78.7-$m^2$ plots will equal or exceed the regeneration success criterion and half will not. However, on the average, each plot can be expected to include 250 reproduction stems of the requisite size. Uneven-aged forests are very heterogeneous at small spatial scales. A companion study of this forest (Loewenstein 1996) showed that the smallest area having an 80% or greater chance of conforming to the forest-wide negative-exponential diameter distribution of overstory trees was 2500 $m^2$. Analogously, it may be unrealistic to expect the reproduction in all or most 78.7-$m^2$ sample spaces to conform to a forest-wide average.

**Table 1.** Observed numbers of plots above and below the specified height and density classes of reproduction ($n$ = 102).

| Reproduction height class (m) | Reproduction density class (no./ha) | Observed no. of plots: Below threshold | Observed no. of plots: Above or equal to threshold |
|---|---|---|---|
| | **Oak seedlings** | | |
| ≥0.8 | ≥125 | 49 | 53 |
| | ≥250 | 64 | 38 |
| | ≥500 | 73 | 29 |
| | ≥1000 | 87 | 15 |
| ≥1.4 | ≥125 | 66 | 36 |
| | ≥250 | 72 | 30 |
| | ≥500 | 83 | 19 |
| | ≥1000 | 96 | 6 |
| ≥2.0 | ≥125 | 72 | 30 |
| | ≥250 | 81 | 21 |
| | ≥500 | 93 | 9 |
| | ≥1000 | 97 | 5 |
| | **All seedlings** | | |
| ≥0.8 | ≥600 | 5 | 97 |
| | ≥1200 | 10 | 92 |
| | ≥2500 | 41 | 61 |
| | ≥5000 | 87 | 15 |
| ≥1.4 | ≥600 | 16 | 86 |
| | ≥1200 | 40 | 62 |
| | ≥2500 | 75 | 27 |
| | ≥5000 | 93 | 9 |
| ≥2.0 | ≥600 | 35 | 67 |
| | ≥1200 | 63 | 39 |
| | ≥2500 | 87 | 15 |

Unfortunately, managing stands at densities of 6.5 $m^2 \cdot ha^{-1}$ is normally unacceptable. The recommended minimum density for oak forests of the Central Hardwood Region is usually set at 14.7 $m^2$ when quadratic mean diameter is 22 cm. This equates to 58% stocking on Gingrich's (1967) stocking chart and represents the minimum stocking level for complete utilization of growing space by the overstory when trees are spatially well distributed. The predictive model (Fig. 1*b*) indicates that, for an overstory density of 14.7 $m^2 \cdot ha^{-1}$, the reproduction stocking criterion of 250 trees/ha ≥1.4 m tall would be equaled or exceeded on only one third of plots (78.7 $m^2$) at any given time; two thirds of the plots would be understocked. Reducing the height criterion to 0.8 m increases the success probability to about

**Fig. 1.** (*a*–*c*) The estimated probability of occurrence of specified height and density classes of oak reproduction at a scale of 78.7 $m^2$ in relation to overstory basal area. Based on the logistic regression parameter estimates given in Table 2. Observed values for each plot (0 or 1) are shown as a stack of dots at the top and bottom of each figure. The minimum observed value is drawn as a broken line.

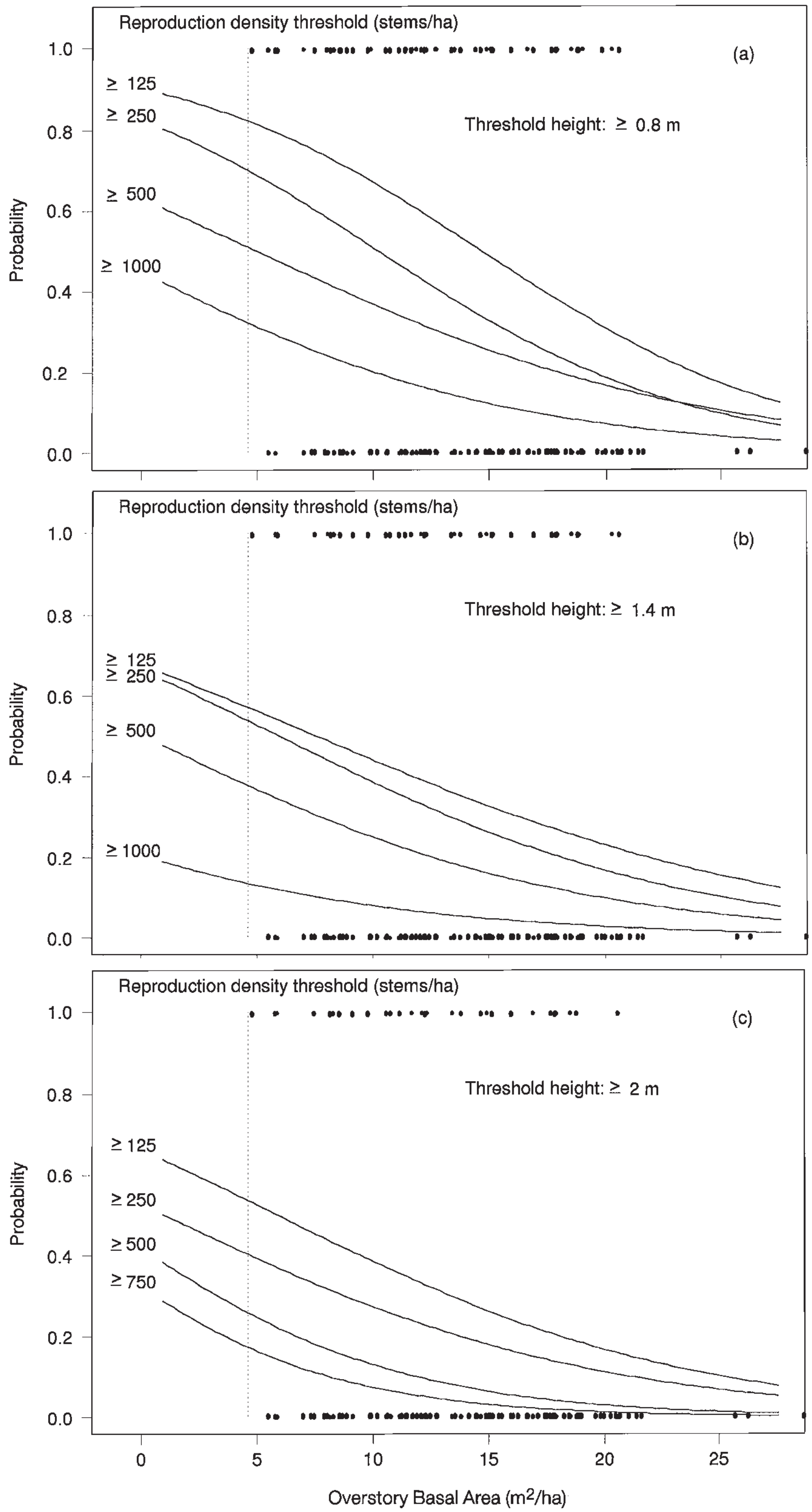


**Table 2.** Logistic regression parameter estimates for estimating from overstory basal area the probability of occurrence of specified reproduction height and density classes at a spatial scale of 78.7 $m^2$ (eq. 1).

| Reproduction height class (m) | Reproduction density class (no./ha) | $b_0$ | $b_1$ |
|---|---|---|---|
| | | **Oak seedlings** | |
| ≥0.8 | ≥125 | 2.2383 (0.7086)* | –0.1521 (0.0477)* |
| | ≥250 | 1.5513 (0.0496)* | –0.1510 (0.0496)* |
| | ≥500 | 0.5413 (0.6950) | –0.1073 (0.0499)* |
| | ≥1000 | –0.1897 (0.8553) | –0.1183 (0.0649) |
| ≥1.4 | ≥125 | 0.7383 (0.6630) | –0.0971 (0.0464)* |
| | ≥250 | 0.6841 (0.6934) | –0.1143 (0.0499)* |
| | ≥500 | 0.0178 (0.7867) | –0.1114 (0.0586) |
| | ≥1000 | –1.3514 (1.2497) | –0.1083 (0.0966) |
| ≥2.0 | ≥125 | 0.6773 (0.6931) | –0.1138 (0.0498)* |
| | ≥250 | 0.1159 (0.7612) | –0.1089 (0.0562) |
| | ≥500 | –0.3229 (1.0567) | –0.1573 (0.0860) |
| | ≥1000 | –0.7331 (1.3679) | –0.1787 (0.1167) |
| | | **All seedlings** | |
| ≥0.8 | ≥600 | 6.2123 (1.8016)* | –0.1993 (0.0957)* |
| | ≥1200 | 4.9144 (1.2921)* | –0.1712 (0.0726)* |
| | ≥2500 | 2.6139 (0.7393)* | –0.1533 (0.0482)* |
| | ≥5000 | 1.6709 (0.8424)* | –0.2369 (0.0687)* |
| ≥1.4 | ≥600 | 4.5185 (1.0907)* | –0.1826 (0.0632)* |
| | ≥1200 | 2.2248 (0.7079)* | –0.1237 (0.0461)* |
| | ≥2500 | 2.0860 (0.8067)* | –0.2389 (0.0635)* |
| | ≥5000 | 1.0104 (1.1379) | –0.2803 (0.1049)* |
| ≥2.0 | ≥600 | 2.4023 (0.7295)* | –0.1203 (0.0467)* |
| | ≥1200 | 1.8958 (0.7135)* | –0.1734 (0.0511)* |
| | ≥2500 | 1.3623 (0.9400) | –0.2517 (0.0810)* |
| | ≥5000 | –1.1287 (1.7280) | –0.1925 (0.1516) |

**Note**: Values in parentheses are the SEs of parameter estimates.
*Parameter estimate is significantly different from 0 ($p \leq 0.05$).

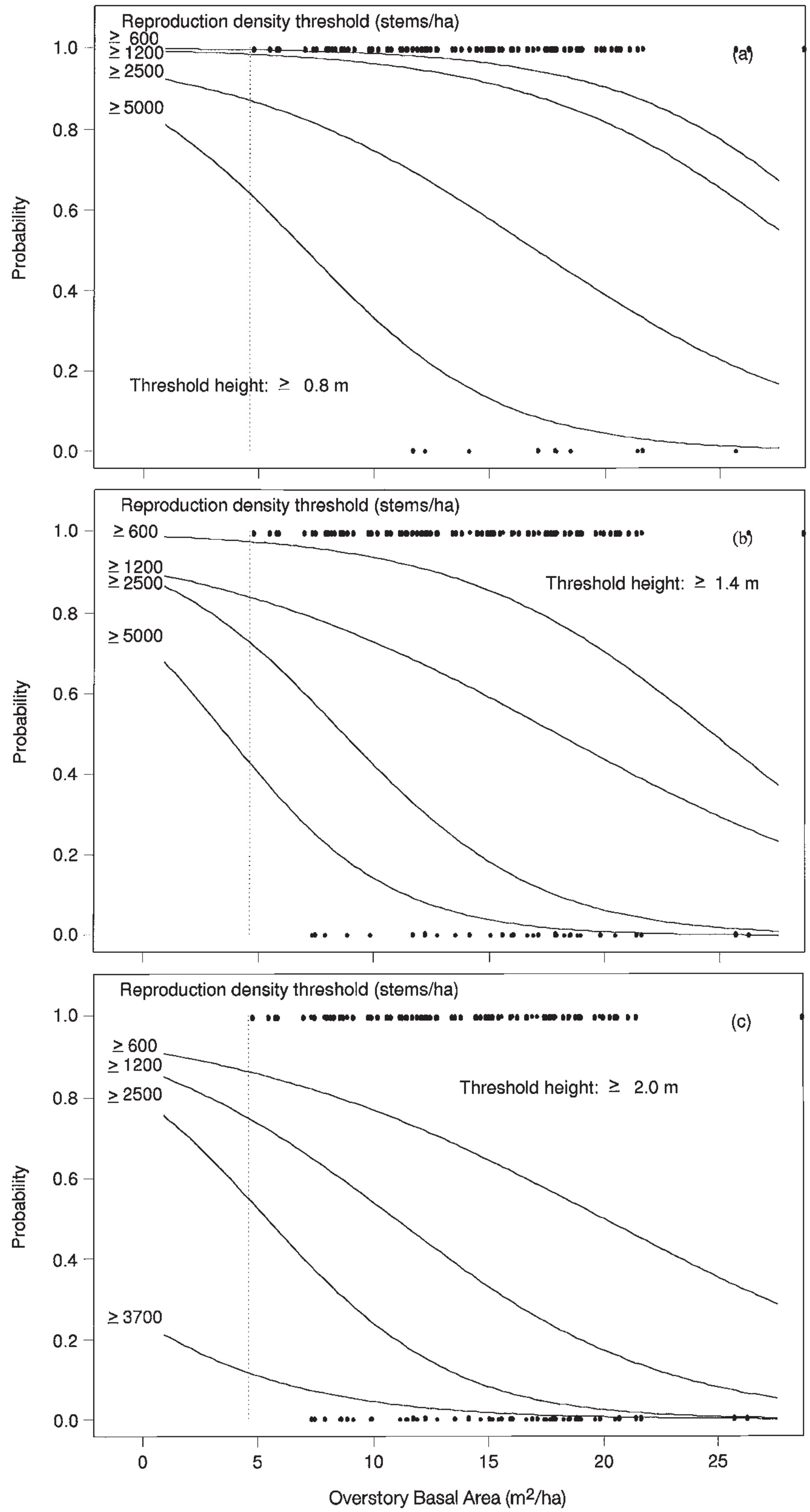
0.38 (Fig. 1*a*), which is still short of the required minimum acceptable probability of 0.5. Not accounting for reproduction <1.4 m tall nevertheless may seriously underestimate the potential recruitment of reproduction into the overstory.

Oak seedling sprouts with large basal diameters (and thus large root systems) frequently are less that 1.4 m tall. Moreover, there is much unexplained variation in the relation between height growth and basal stem diameter of oak reproduction (Sander 1971; Johnson 1979). Predicting the height growth of oak reproduction is so stochastic that regeneration models are often based on probabilistic methods (e.g., Sander et al. 1984; Dey et al. 1996). The predictive models in Fig. 1 thus may underestimate the recruitment potential of oak reproduction into the overstory by not including smaller reproduction, especially seedling sprouts with large basal diameters but no measurable diameter at breast height. The latter condition complicates relating the negative exponential distribution of overstory diameters to the reproduction. The relative stability of the forest's oak diameter distribution during the 40-year management period nevertheless provides indirect evidence of sufficient recruitment of reproduction in the past. The forest, however, is now at its highest average density since the start of management. The sufficiency of the forest's oak regeneration potential under the current prevailing density therefore remains unknown over the longer term. The models presented nevertheless establish a clear relation between overstory density and reproduction and emphasize the importance of this relation in managing oak forests.

## Conclusions

Silvicultural control of regeneration is often limited to controlling stand density. The predictive models presented show that density and size of reproduction increase with decreasing overstory density. The models provide general guides to average expected outcomes in relation to overstory density. However, because the outcomes are highly stochastic, the models should be considered descriptive of current states and not necessarily predictive of future states. The models nevertheless show that relatively low overstory densities are necessary for maintaining high densities of large advance oak reproduction in the Ozark Highlands. This reflects the adaptation of oaks to disturbance.

**Fig. 2.** (*a–c*) The estimated probability of occurrence of specified height and density classes of the reproduction of all species at a scale of 78.7 $m^2$ in relation to overstory basal area. Based on the logistic regression parameter estimates given in Table 2. Observed values for each plot (0 or 1) are shown as a stack of dots at the top and bottom of each figure. The minimum observed value is drawn as a broken line.



The relations observed in this study are consistent with oak's relative intolerance to shade.

In oak-dominated forests such as the Ozark Highlands where non-oak hardwoods are largely relegated to a subordinate canopy position, the non-oaks largely act to slow the reemergence of the oaks rather than to permanently displace the oaks from dominance. Although all the non-oak hardwoods in this study can rapidly capture growing space after heavy reductions in overstory density, they are short lived as canopy dominants.

When Ozark oak forests are managed as uneven-aged stands, the models presented provide a general guide to the expected relation between reproduction and overstory density at a spatial scale of 78.7 $m^2$. The models indicate that extremely low overstory densities may be necessary for maintaining populations of oak reproduction that are sufficient for sustaining the desired negative exponential diameter distribution of overstory trees. However, the models presented may overestimate the density of "large" oak reproduction needed because they do not consider the possible contribution of "small" seedling sprouts to stand regeneration potential. Also, because the forest is currently at its highest overstory density since the start of management, the sufficiency of its present state of regeneration in unknown over the longer run.

The models presented nevertheless point out the importance of overstory density in initiating and sustaining reproduction in uneven-aged oak forest in the Ozark highlands. The relationships illustrate the extent the advance reproduction of a Missouri Ozark forest can be altered by overstory reduction.

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