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Forest Ecology and Management 193 (2004) 399–412
Forest Ecology and Management
www.elsevier.com/locate/foreco

Simulated cavity tree dynamics under alternative timber harvest regimes

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Received 24 September 2003; received in revised form 3 December 2003; accepted 1 February 2004

Abstract

We modeled cavity tree abundance on a landscape as a function of forest stand age classes and as a function of aggregate stand size classes. We explored the impact of five timber harvest regimes on cavity tree abundance on a 3261 ha landscape in southeast Missouri, USA, by linking the stand level cavity tree distribution model to the landscape age structure simulated by the LANDIS model. Over 100 years, mean cavity tree density increased constantly under all timber harvest regimes except for even-aged intensive management. This was due in large part to the continued maturation of the numerous stands that were >70 years old at the start of the simulations. However, compared to the no harvest (control) regime, the uneven-aged, the mixed, the even-aged long rotation, and the even-aged intensive harvest regimes reduced the cavity tree density by 9–11, 11–13, 15–18, and 28–34%, respectively, as more old stands were cut. Forest managers and planners can use this information to evaluate the practical consequences of alternative timber harvest regimes and consider the need for activities such as cavity tree retention.

Keywords: Cavity tree density; LANDIS; Timber harvest; Even-aged management; Uneven-aged management; Missouri; Ozarks

1. Introduction

The past decades have seen a fundamental shift in forest management philosophy from commodity-based resource management to ecologically sustainable management of forest resources—managing landscape patterns and ecological processes in a holistic manner to provide for sustained ecological functioning while deriving commodities and amenities (Diaz and Bell, 1997). This type of management requires an understanding of ecosystem patterns and processes and the ability to predict, at multiple spatial and temporal scales, ecosystem response to management practices. Implementation is guided by the results of experiments, by observation and adaptation of previous management results, and by computer simulation.

In the Central Hardwood Region of the east-central United States, significant effort has been made to understand the impacts of alternative forest management practices on multiple ecosystem components simultaneously. This has been approached through synthesis and simulation (e.g., Thompson et al., 1992, 1995; Shifley et al., 2000; McShea and Healy, 2002) as well as through landscape scale experimental

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doi:10.1016/j.foreco.2004.02.008

studies such as the Missouri Ozark Forest Ecosystem Project (MOFEP). The MOFEP experiment was launched in 1990 to investigate the impacts of forest management practices, namely even-aged management with harvest by intermediate thinning and clear-cutting, uneven-aged management with harvest by single-tree and group selection, and no harvest, on multiple biotic and abiotic ecosystem attributes at multiple spatial scales (Brookshire and Shifley, 1997; Shifley and Kabrick, 2002). Response variables include vegetation composition and structure, mast production, the abundance and dynamics of wildlife communities, fungal communities, herbivorous insects, down wood, decay rates, nutrient cycling, and tree cavities (Jensen et al., 2002).

The abundance of tree cavities is an indicator of habitat quality for many species of wildlife, and availability of cavity trees (both live trees and snags) in forests managed for timber is of concern for wildlife conservation in this region and elsewhere. Timber harvesting tends to decrease the abundance of cavity trees and cavity-dependent wildlife species (e.g., Conner et al., 1975; Cline et al., 1980; McComb and Noble, 1980; Mannan and Meslow, 1984; Zarnowitz and Manuwal, 1985; Wilson, 1996; Fan et al., 2003a,b) because timber harvests usually target large trees which are likely to become cavity trees. This is especially the case in the Central Hardwood Region where most cavity trees are large, live trees, and only about 10% of cavity trees are snags (Fan et al., 2003a). Retention of current and potential cavity trees during harvest can be important for wildlife management because it partially offsets the reductions in the cavity resource due to timber harvest. Resource managers and planners must quantitatively evaluate effects of timber management regimes on cavity trees to assess tradeoffs between wildlife and timber goals and to understand how those tradeoffs change over time across a landscape. Cavity tree abundance is highly variable among forest stands (or inventory plots), even when the stands (or plots) are similar in many other respects (Carey, 1983; Fan et al., 2003a,b). Therefore, a large spatial scale such as a landscape (e.g., thousands or tens of thousands of ha in extent) is appropriate for analyzing broad trends in the relationship of timber management to cavity tree availability.

The objective of our study was to simulate and analyze the effects of alternative timber management practices on cavity tree dynamics across a real landscape for 100 years, the duration of a typical timber harvest rotation in this region. We investigated the dynamics of cavity tree abundance under five alternative timber harvest regimes and quantified the effect on cavity tree availability on the landscape. We also compared results for a cavity model based on 10-year stand age classes with a more parsimonious model based on four broad stand size classes, and we evaluated the ability of these models to predict observed cavity tree abundance for an independent data source.

2. Methods

2.1. Study area

We studied a 3261 ha portion of the Mark Twain National Forest located in the Ozark Highlands of southeast Missouri, USA (Fig. 1). This forested region, heavily logged and burned in the early 1900s, is now covered by second-growth forests <100 years old. White oak (*Quercus alba* L.), post oak (*Q. stellata* Wangenh.), black oak (*Q. velutina* Lam.), scarlet oak (*Q. coccinea* Muenchh.), hickory (*Carya* spp.), and shortleaf pine (*Pinus echinata* Mill.) are the predominant species. Current forest conditions (age, forest cover type, ecological landtype, stand boundaries) are known and have been mapped for this landscape (Shifley et al., 2000). We used this information to set the initial conditions for landscape simulations described in subsequent sections.

2.2. Cavity tree abundance on a landscape

Stand age and/or stand size class are important variables that affect cavity tree distribution (e.g., Carey, 1983; Allen and Corn, 1990), and the mean cavity tree abundance on a forest landscape can be estimated as a function of the stand age or size classes present on the landscape (Fan et al., 2003a,b). To simulate cavity tree dynamics under different management scenarios over a long temporal scale (e.g., 100 years), two components are required: (1) the stand age or size structure over time on the landscape and (2) the frequency distribution of cavity trees per ha by stand age or size class.

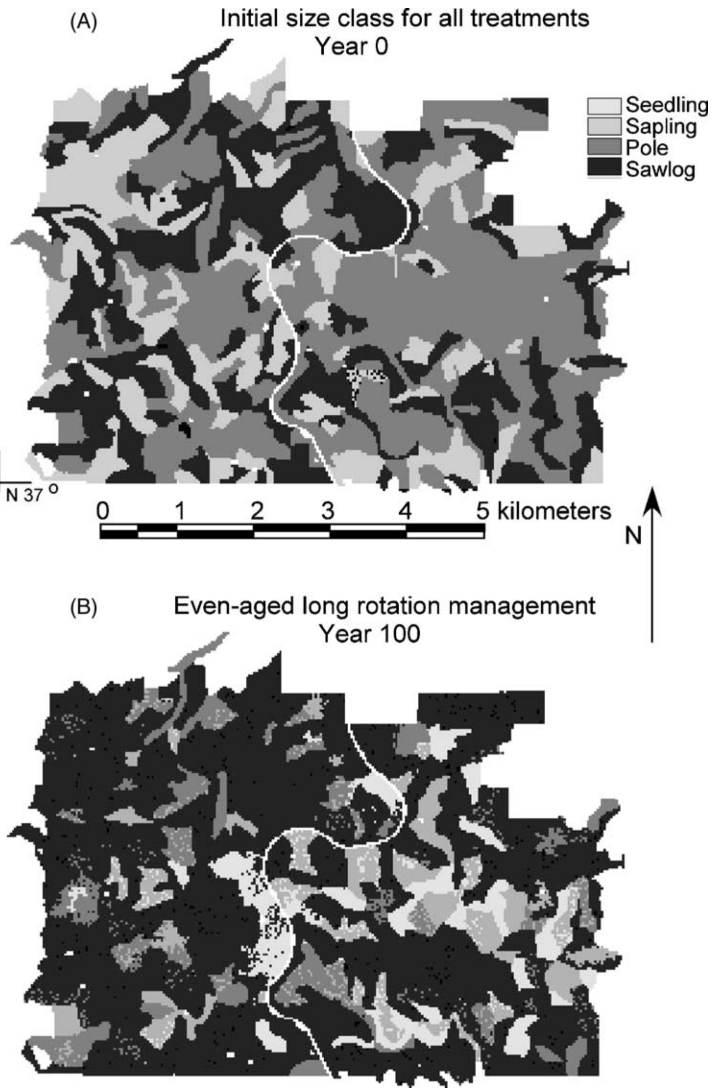

Fig. 1. (A) Initial forest size structure on the 3261 ha landscape that was used to examine changes in cavity tree abundance due to differing management practices. (B) Forest size structure after 100 years of simulation under the even-aged long rotation alternative, one of five alternatives examined (see Table 1 and Fig. 2). Additional description of this landscape and simulated vegetation change can be found in Shifley et al. (2000).

2.3. Distribution of cavity trees by stand age class

The 1989 Missouri statewide forest inventory conducted by the Forest Inventory and Analysis Unit (FIA) of North Central Research Station, US Department of Agriculture, Forest Service, was a systematic survey of all timberland in the state (Hahn and Spencer, 1991; Spencer et al., 1992; Miles et al., 2001). Over 141,000 trees on 4052 plots (aged from 1 to 155 years) were sampled. Both tree level attributes (e.g., species, dbh, decay class, live/dead) and stand-level characteristics (e.g., stand age, size class, slope, aspect, forest type) were recorded (Anonymous, 1986). For each tree >12 cm in diameter at breast height, the size of the largest cavity visible from the ground (if any) was recorded. Cavities smaller than 2.5 cm in their narrow dimension were excluded.

Live or dead trees with a cavity were classified as cavity trees. Sampling protocols did not enumerate multiple cavities per tree. Ground-based cavity inventories typically miss some cavities and some cavity trees (Healy et al., 1989; Jensen et al., 2002). Consequently, the recorded number of cavity trees is generally considered a conservative estimate of the true number.

Fan et al. (2003a) described the relationship between the mean cavity tree density per ha and stand age class (10-year) for these data. Fan et al. (2003a) further used the classification and regression tree (CART) model (Breiman et al., 1984; Steinberg and Colla, 1997) to classify the FIA plots into three size classes: seedling/sapling ($\leq$30 years old), poletimber (31–50 years), and sawtimber (>50 years) based on the observed frequency of plots with and without cavity trees. They subsequently used a Weibull function to describe the frequency distribution of cavity tree density within each size group. In this study we further used CART to classify the sawtimber size class into two subclasses: small sawtimber (51–70 years) and large sawtimber (>70 years) based on the fact that cavity tree density still varied substantially within the sawtimber size class. We then calculated the mean and variance of cavity tree density for each of the four size classes: seedling/sapling, poletimber, small sawtimber, and large sawtimber. We subsequently used that information and the total area per size class for a given landscape (or for simulated future landscape conditions) with Eqs. (3)–(5) (defined in the next section) to predict cavity tree density on the landscape (referred to later as the four size-class method of prediction).

As an alternative to the four size-class method of prediction, we fit the relationship of mean cavity tree density per ha (y) and the 10-year stand age class described by Fan et al. (2003b) using the Richard's function (Richards, 1959):

$$y = 21.5710(1 - e^{-0.0174\times\text{ageclass}})^{0.9076} \quad (R^2 = 0.92, P < 0.0001) \qquad (1)$$

Eq. (1) adequately quantified the mean cavity tree density by stand age class, and an analysis of regression residual errors revealed no patterns requiring remedial measures. Fitting Eq. (1) separately by forest cover type resulted in no appreciable improvement in R^2, so we applied Eq. (1) across all forest types. As with the four size-class method, we used the fitted mean cavity tree density for each age class and the size (in ha) of the corresponding age class to predict cavity tree dynamics on current and simulated landscapes (referred to later as the 10-year age-class method).

We applied both the 10-year age-class method and the simpler four size-class method to estimate cavity tree density for our 3261 ha landscapes. We compared the differences resulting from the two methods. We also compared predictions from both of these methods to observed cavity tree density from ground-based cavity inventories (Jensen et al., 2002) conducted as part of the Missouri Ozark Forest Ecosystem Project (Shifley and Kabrick, 2002).

2.4. Harvesting regimes and landscape age (size) structure

Uneven-aged (single-tree selection, group selection) and even-aged (clearcut, shelterwood, seed tree) management systems (Nyland, 1996) are used to meet specific management objectives. Even-aged systems typically promote shade-intolerant species while uneven-aged systems tend to favor regeneration of shade-tolerant species and maintain continuous high forest cover.

At the landscape scale, long-term change in forest structure resulting from natural disturbances and from even-aged, uneven-aged, and no harvest management regimes has been simulated using the LANDIS model (Mladenoff et al., 1996; Mladenoff and He, 1999; He and Mladenoff, 1999; He et al., 1999; Gustafson et al., 2000). LANDIS simulates forest age structure and tree species cover (presence or absence by species group) on mapped (i.e. spatially explicit) landscapes. Shifley et al. (2000) previously used LANDIS to simulate forest landscape change under five timber harvesting regimes applied to our 3261 ha landscape (Table 1). They described how landscape size and age patterns changed under the five alternatives and the anticipated effect on timber, down wood, and habitat characteristics. Treatments included even-aged management with rotation ages of 100 and 200 years, uneven-aged management with 5% of the area put in group openings each decade (roughly comparable to a 200-year rotation), a mixture of even-aged and uneven-aged management, and a no-harvest control. In this study, we analyzed the same harvest regimes on that

Table 1
Summary of the five harvest regimes[a]

Criteria	Harvest regime				
	Even-aged intensive	Even-aged long rotation	Uneven-aged	Mixed	No harvest
Area harvested per decade (%)	10	5	5	5	0
Method of harvest	Clearcut	Clearcut	Group selection[b]	Clearcut and group selection[b,c]	Not applicable
Equivalent rotation age (years)	100	200	200	200	Not applicable
Minimum harvest age (years)	50	80	50	50	Not applicable
Stand selection criteria	Oldest first	Oldest first	Oldest first	Oldest first	Not applicable

[a] Adapted from Shifley et al. (2000); fire disturbance was simulated with a 300-year mean return interval; major wind disturbance (blowdown) was simulated with an 800-year mean return interval for each harvest regime.
[b] Group selection openings had a mean size 0.2 ha.
[c] Clearcut on NE slopes; group selection on SW slopes, ridges, and floodplains.

landscape to examine the potential impact on the cavity tree abundance at the landscape level.

The 3261 ha forest landscape was represented as a grid of 30 m × 30 m pixels populated by four species groups (white/post oaks, black/red/scarlet oaks, shortleaf pine, red/sugar maples) based on ecological land type and stand inventory data that had been collected previously. Each pixel has an associated ecological landtype and was assigned an initial species group and age class (10-year). We used LANDIS to simulate the change in species and age within each pixel under different management activities and natural disturbance (fire and windthrow) for 100 years. LANDIS results were reported in a suite of output files that could be summarized and mapped. We used the cavity prediction models (Section 2.3) to estimate the number of cavities for different age classes (and for the four aggregate size classes) as they changed through time in response to the simulated management alternatives. The total number of pixels by each age class or size class i under different management scenarios j in decade k (P_{ijk}) can be counted and mapped directly from the LANDIS output and the area (A_{ijk}, in ha) can be calculated by (2):

$$A_{ijk}\,(\text{ha}) = P_{ijk} \times \frac{30^2}{10\,000} \qquad (2)$$

2.5. Estimating cavity tree abundance across the landscape

We assumed that the probability density distribution of cavity trees within a given age class (or size class) did not change over the course of the simulation. The cavity tree abundance on a landscape, in terms of cavity tree density (CTD, i.e. number of cavity trees/ha), variance, and approximate $100(1-\alpha)\%$ confidence interval (CI) can be calculated, respectively, as

$$\text{CTD}_{jk} = \frac{1}{A}\sum_{i=1}^{n} A_{ijk} Y_i \qquad (3)$$

$$\text{var}(\text{CTD}_{jk}) = \frac{1}{A^2}\sum_{i=1}^{n} A_{ijk}^2 \,\text{var}(Y_i) \qquad (4)$$

$$\text{CI} = \text{CTD}_{jk} \pm Z_{\alpha/2}\sqrt{\text{var}(\text{CTD}_{jk})} \qquad (5)$$

where CTD_{jk} is the mean cavity tree density per ha under management scenario j in decade k; n is the number of age or size classes, A and A_{ijk} are the size (ha) of the entire landscape and the component age class (or size class) i under management scenario j in decade k, respectively; Y_i is the mean cavity tree density of age class i; and $Z_{\alpha/2}$ is the $(1-\alpha/2)$th percentile of the standard normal distribution.

2.6. Effect of timber harvest on cavity tree density

Although LANDIS is a stochastic model and the spatial pattern of disturbances on the landscape can vary from run to run for a given simulation scenario, the aggregate stand size class distribution for large landscapes varies little for repeated runs of the same simulation scenario. Our past experiences with large landscapes in this region demonstrated that the coefficient of variation for hectares by size class ranged from 1 to 5% for five repeated simulations of a given management scenario. Therefore we used the outcome of a single simulation run for each management alternative to estimate the cavity tree density (Eq. (3)) and the variance (Eq. (4)). We let the subscript $j = 0, 1, 2, 3$, and 4 in Section 2.5 represent the no harvest, even-aged intensive, even-aged long rotation, uneven-aged, and mixed harvest regimes, respectively (Table 1). Taking the no harvest regime as the control, the effect of any other timber harvest regime j ($j = 1, 2, 3$, and 4) on the cavity tree density on a landscape in decade k was evaluated by the decrease of cavity tree density, H_{jk}, relative to no harvest:

$$H_{jk} = \frac{\mathrm{CTD}_{0k} - \mathrm{CTD}_{jk}}{\mathrm{CTD}_{0k}} \times 100\% = \left(1 - \frac{\mathrm{CTD}_{jk}}{\mathrm{CTD}_{0k}}\right) \times 100\% \qquad (6)$$

Given the independence of any two harvest regimes, the approximate mean, variance, and $100(1-\alpha)\%$ confidence interval of H_{jk} can be calculated, respectively, using Taylor approximations:

$$\begin{aligned} E[H_{jk}] &= \left(1 - \frac{\mathrm{CTD}_{jk}}{\mathrm{CTD}_{0k}}\right) \times 100\% + \frac{\partial^2 H_{jk}}{\partial(\mathrm{CTD}_{jk})^2}\,\mathrm{var}(\mathrm{CTD}_{jk}) + \frac{\partial^2 H_{jk}}{\partial(\mathrm{CTD}_{0k})^2}\,\mathrm{var}(\mathrm{CTD}_{0k}) \\ &= \left(1 - \frac{\mathrm{CTD}_{jk}}{\mathrm{CTD}_{0k}}\right) \times 100\% - \frac{\mathrm{CTD}_{jk}}{(\mathrm{CTD}_{0k})^3}\,\mathrm{var}(\mathrm{CTD}_{0k}) \end{aligned} \qquad (7)$$

$$\begin{aligned} \mathrm{var}(H_{jk}) &= \left[\frac{\partial H_{jk}}{\partial(\mathrm{CTD}_{jk})}\right]^2 \mathrm{var}(\mathrm{CTD}_{jk}) + \left[\frac{\partial H_{jk}}{\partial(\mathrm{CTD}_{0k})}\right]^2 \mathrm{var}(\mathrm{CTD}_{0k}) + 2\frac{\partial H_{jk}}{\partial(\mathrm{CTD}_{jk})}\frac{\partial H_{jk}}{\partial(\mathrm{CTD}_{0k})}\,\mathrm{cov}(\mathrm{CTD}_{jk}, \mathrm{CTD}_{0k}) \\ &= \frac{1}{(\mathrm{CTD}_{0k})^2}\,\mathrm{var}(\mathrm{CTD}_{jk}) + \frac{(\mathrm{CTD}_{jk})^2}{(\mathrm{CTD}_{0k})^4}\,\mathrm{var}(\mathrm{CTD}_{0k}) \end{aligned} \qquad (8)$$

$$\mathrm{CI} = E[H_{jk}] \pm Z_{\alpha/2}\sqrt{\mathrm{var}(H_{jk})} \qquad (9)$$

We applied these formulae to test the hypothesis that cavity tree density for the four manipulative harvest regimes did not differ from the no harvest regime.

2.7. Comparison of the four size-class method and the 10-year age-class method

Section 2.3 introduced two methods of estimating cavity tree density by stand age: (1) estimation based on 10-year age classes and (2) estimation based on four size classes (seedling/sapling, pole timber, small sawlog, large sawlog). In many practical applications the second method based on only four size classes is easier to apply with data that are typically available across large landscapes. The difference (D_{jk}) between the two methods in estimated landscape level cavity tree density, variance, and approximate $100(1-\alpha)\%$ confidence interval can be evaluated by

$$D_{jk} = \mathrm{CTD}_{jk1} - \mathrm{CTD}_{jk2} \qquad (10)$$

$$\mathrm{var}(D_{jk}) = \mathrm{var}(\mathrm{CTD}_{jk1}) + \mathrm{var}(\mathrm{CTD}_{jk2}) \qquad (11)$$

$$D_{jk} \pm Z_{\alpha/2}\sqrt{\mathrm{var}(D_{jk})} \qquad (12)$$

where CTD_{jk1} and CTD_{jk2} are the estimated landscape-level cavity tree density for scenario j in decade k by the first and second approaches, respectively. We used these relationships to test the null hypothesis that cavity tree abundance estimated by the 10-year age-class method did not differ from that estimated using the four size-class method.

3. Results

At the start of the simulation (year 0), the cavity tree density estimated by the 10-year age-class method was 12.8 trees/ha. By year 100, cavity densities with this method were estimated to be 19.0, 17.0, 16.6, and 15.5 trees/ha for increases of 48, 33, 30, and 21% for the no harvest, uneven-aged, mixed, and even-aged long rotation regimes, respectively (Fig. 3A). The cavity tree density at year 0 estimated by the four size-class method was 12.5 trees/ha. By year 100, it reached 17.6, 16.0, 15.7, and 14.9 for net increases of 41, 28, 26, and 19% for the no harvest, uneven-aged, mixed, and even-aged long rotation regimes, respectively (Fig. 3B). For the even-aged intensive regime,

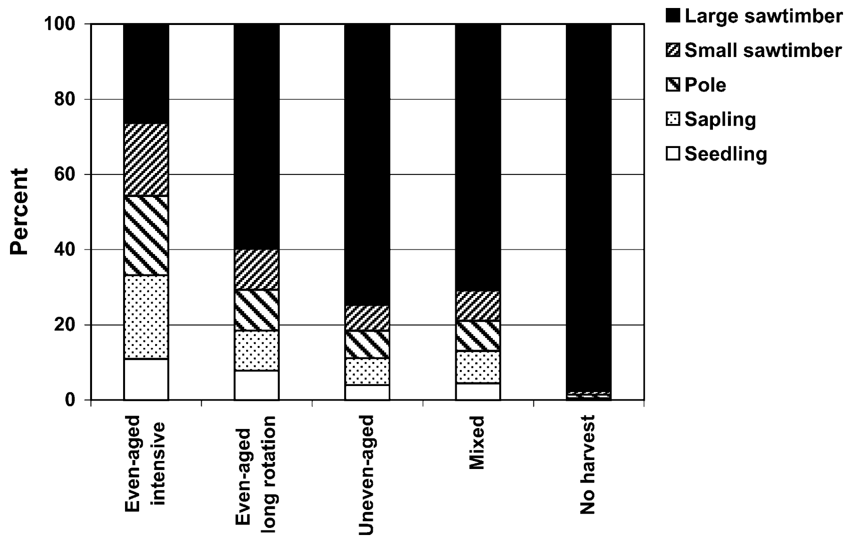

Fig. 2. Proportion of landscape by stand size class after 100 years of simulation for the five management alternatives. The even-aged long rotation, uneven-aged, and mixed harvest regimes each harvest approximately 5% of the area each decade, and they are similar in their proportions of area by age class. However, they differ in spatial arrangement of age classes across the landscape.

the cavity tree density estimated by both methods had almost no change over the 100-year simulation, and at year 100 the landscape still maintained 12.6 cavity trees/ha.

The choice of timber harvest method altered the age class and size class distribution on the landscape (Figs. 1 and 2) and cavity tree densities followed accordingly. For a given simulation year, cavity tree density decreased with increasing harvest intensity (Fig. 3). The no harvest regime had the greatest cavity tree density, followed by the uneven-aged, the mixed, the even-aged long, and the even-aged intensive regimes. Compared to the no harvest regime, the other four timber harvesting regimes significantly ($\alpha = 0.05$) reduced the mean cavity tree density after year 20 based on the 10-year age-class method (Fig. 4A). The effect of timber harvest on cavity tree density increased with time. By year 100, the even-aged intensive, even-aged long, mixed, and uneven-aged regimes reduced the mean cavity tree density relative to the no harvest alternative by 34, 18, 13 and 11%, respectively (Fig. 4A).

With the four size-class method, the reduction in cavity densities became statistically significant ($\alpha = 0.05$; the 95% CI does not include 0) for even-aged intensive (>year 20), and even-aged long rotation (>year 40) harvest regimes showing 28 and 15% reductions, respectively, relative to no harvest (Fig. 4). By year 100, the mixed and the uneven-aged regimes resulted in an 11 and 9% reduction in cavity tree density, respectively, relative to no harvest. However, the reduction was not statistically significant because of the large variance (Fig. 4B).

Compared to the 10-year age-class method, the four size-class method tended to predict a lower cavity tree density for the no harvest, uneven-aged, mixed, and even-aged long regimes after year 30, but the difference was not statistically significant ($\alpha = 0.05$) (Fig. 5). There was no difference in the estimated cavity tree density for the even-aged intensive regime between these two methods (Fig. 5). Compared to the observed cavity tree density on six hundred and forty-eight 0.2 ha plots (131 total ha) on the independent MOFEP study, both the 10-year age-class method and the four size-class methods used in our study overestimated the observed cavity tree density by 12.5%.

4. Discussion

Stand age or tree size (measured in terms of dbh or basal area) is the most important single predictor of cavity tree availability (Carey, 1983; Allen and Corn, 1990; Fan et al., 2003a,b). This allowed us to explore

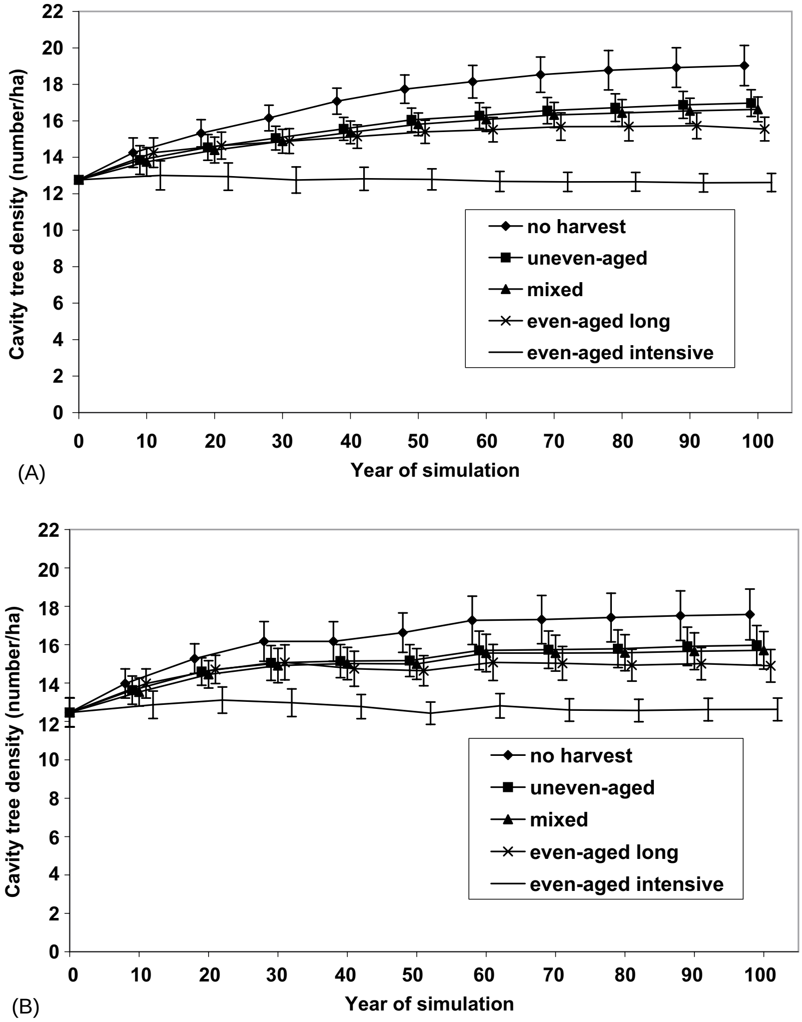

Fig. 3. Estimated cavity tree density over time in response to the five harvest-regimes described in Table 1. (A) Results for the model based on 10-year age classes. (B) Results for the model based on four size classes.

the dynamics of cavity tree density at the landscape level by linking the stand (plot) level cavity tree density models to the landscape age (or size) structure simulated by LANDIS in a deterministic manner described by Eq. (3).

An underlying assumption when using this modeling approach to predict future changes in cavity tree abundance is that the factors affecting cavity abundance are relatively constant over time. The cavity model derived from Fan et al. (2003a) and applied here for landscape-scale cavity tree estimates is based on conditions observed during a 1989 state-wide, systematic inventory of timberland in Missouri (Spencer et al., 1992) and a 1992–1994 inventory of old-growth forests (Fan et al., 2003b; Spetich, 1995). If disturbance factors such as insect outbreaks or drought-induced oak decline are likely to occur over large portions of the landscape within the time horizon of the simulation and affect the rates of tree mortality and cavity formation, the estimated cavity tree abundance will need to be revised accordingly. This caveat applies to most forest simulation models used to forecast change for several decades or more and is a consequence of having relatively short periods of

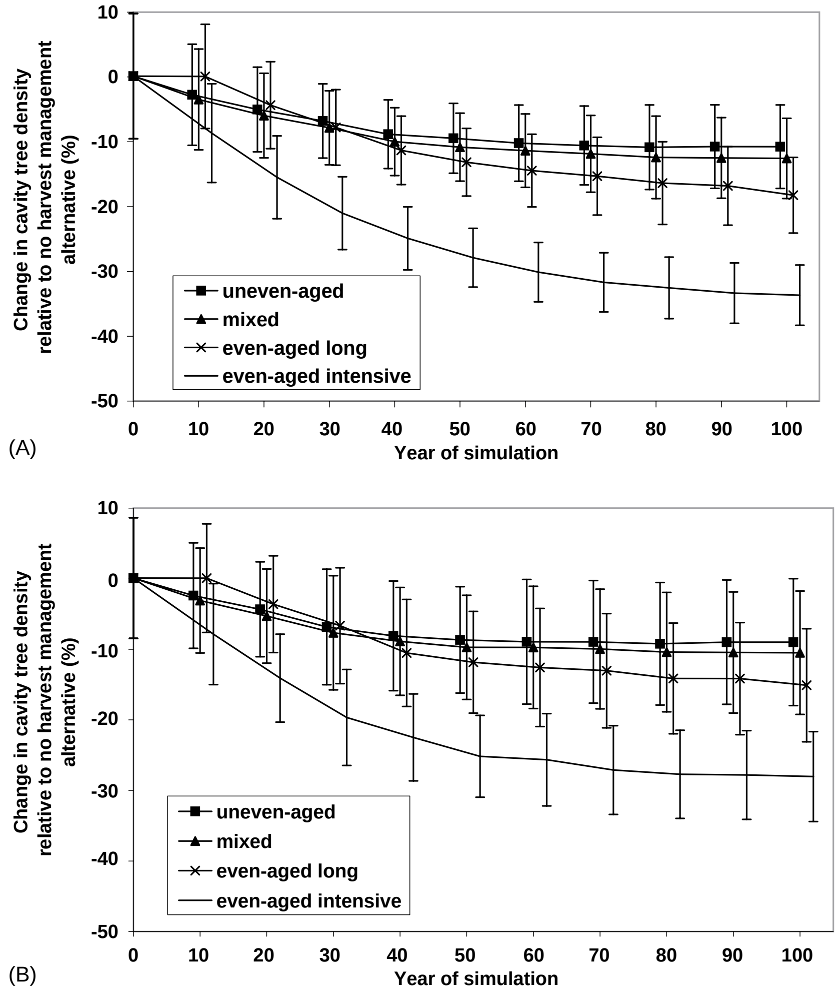

Fig. 4. Percent reduction in cavity trees per ha relative to the no harvest alternative. Plotted values are $-E[H]$ as defined in Eq. (7). The error bars show the 95% confidence intervals for the percent decrease in cavity trees. Differences are statistically significant ($\alpha = 0.05$) when the confidence intervals (error bars) do not include zero. (A) Results for model based on 10-year age classes. (B) Results for the model based on four size classes.

observation from which to infer long-term outcomes. Given the scarcity of cavity data of any sort and the unpredictability of catastrophic events, the typical response to this problem is to recognize that cavity estimates are conservative and will underestimate the impact of catastrophic disturbances.

Formally, Eq. (3) is an unbiased estimator of the cavity tree density on a landscape because the estimated mean cavity tree densities (the $Y_i^{'}$s) for different age classes are normally distributed and are the unbiased estimators of the unknown true means under large number theory. In reality, the size of a landscape or a component (e.g., an age class) cannot always satisfy the sample size required by large number theory. Thus, the estimated cavity tree density from Eq. (3) is, more often than not, positively biased by a density distribution that is skewed to the left for cavity trees at the stand (or patch) level (Fan et al., 2003). Because the true cavity tree density on this 3261 ha landscape is unknown, we were unable to directly evaluate the scale of the bias. However, we were able to estimate the bias using an independent cavity tree data set from the Missouri Ozark Forest Ecosystem Project (MOFEP) (Jensen et al., 2002; Jensen, 2000;

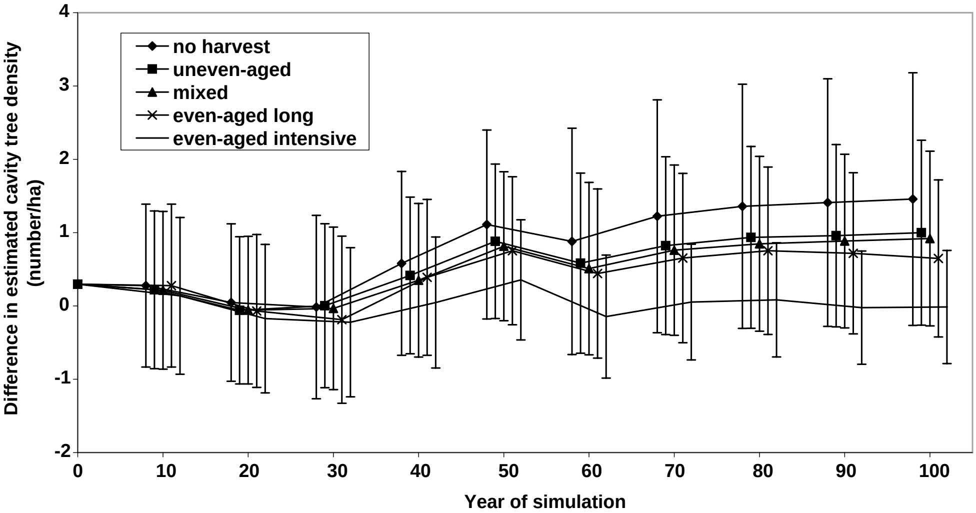

Fig. 5. Difference in predicted cavity tree density (cavity trees per ha) for the model based on 10-year age classes (Eq. (1)) and the model based on four stand size classes. Mean cavity tree estimates from the 10-year age class model were generally greater, but only by about 1 cavity tree/ha. The 95% confidence intervals (error bars) include zero, so differences resulting from the choice of model were not statistically significant ($\alpha = 0.05$).

Roovers, 2000). The observed cavity tree density for the 131 ha MOFEP study area (648 0.2 ha plots) was 12.8 trees/ha (Jensen et al., 2002) compared to the predicted 14.4 trees/ha. Our comparison of the observed and predicted cavity tree densities for individual age classes indicated that the overestimation mainly occurred in age classes that comprised less than 10% of the landscape area. Over all age classes, the degree of overestimation decreased as the area (ha) of individual age classes increased. This result indirectly suggests that any overestimation for the cavity tree density on the 3261 ha landscape should not exceed 12.5% because that landscape and its component age classes are at least 10 times larger than the MOFEP landscape. A computationally intensive solution to overcome the bias problem is to predict the cavity tree density using a stochastic approach based on the actual probability density function of cavity trees per ha (Fan et al., 2003a). This requires randomly drawing an estimate of the number of cavity trees per ha multiple times from a probability density and averaging the results.

When cavity tree estimates (or associated cavity prediction models) are derived using ground-based observations as is the case here, the estimated (or predicted) cavity tree densities are conservative and generally underestimate the true number of cavity trees that would be found if trees were climbed or felled and given closer scrutiny. Healy et al. (1989) working in oak sawtimber in Massachusetts found that ground-based cavity tree inventories missed 20% the true number of cavity trees. Jensen et al. (2002) working in upland oak forest in the Missouri Ozarks found that cursory ground-based cavity tree inventories missed about half the cavity trees that were subsequently identified by intensive ground-based scrutiny with the aid of binoculars. However, Jensen et al. also found that their intensive cavity surveys tended to overestimate the true number of cavity trees by including trees with small, visible deformities that upon close inspection after felling turned out not to be cavity trees. The proportion of correctly identified cavity trees ranged from approximately 60–100%, depending on species. Thus, our estimates (and predictions) of cavity tree density are conservative relative to the true number of cavity trees. Actual cavity tree densities could be roughly 25% higher than model estimates (i.e., assuming the observed number of cavity trees is about 80% of the true number). For relative comparisons of cavity tree density among alternative harvest regimes, this underestimation is of little consequence. For applications where the absolute number of cavity trees is of interest, estimated values can be adjusted upward.

One factor that can affect cavity tree density but is not reflected either implicitly or explicitly by the age-cavity tree density model in Section 2.3 is species composition (or forest type). Differences among species in susceptibility to cavity formation and subsequently in cavity tree distribution have been observed (McClelland et al., 1979; McComb et al., 1986; Franklin et al., 1987). For instance, Fan et al. (2003b) classified American beech (*Fagus grandifolia* Ehrh.), sugar maple (*Acer saccharum* Marsh.), and red maple(*A. rubrum* L.) as species most susceptible to cavity formation, hickories as intermediately susceptible species, and most oaks, yellow-poplar (*Liriodendron tulipifera* L.) and shortleaf pine as least susceptible species. This suggests that prediction accuracy may be improved if species composition is incorporated with stand age or stand size class. However, detailed information on species composition is usually not available across large landscapes. Moreover, we found that forest cover type is not an adequate substitute for species composition when estimating cavity tree abundance. Incorporating both age and forest type in the model (Eq. (1)) did not improve performance in terms of R^2 compared to the model with age as the only variable.

Cavity formation is the outcome of a large number of stochastic events, and tree and stand attributes are only indictors of the underlying processes. In the context of cavity trees, selection of the ''best'' prediction model in the traditional way (including all variables that are statistically significant) may not be practical, particularly when the model is intended for broad application across landscapes with limited site-specific data. Fire and grazing, two processes that contribute to cavity formation, have decreased in frequency since 1940. This may introduce some additional uncertainty into estimates of future cavity abundance.

As pointed out by many previous studies (e.g., Conner et al., 1975; Cline et al., 1980; McComb and Noble, 1980; Mannan and Meslow, 1984; Zarnowitz and Manuwal, 1985; Wilson, 1996; Fan et al., 2003a,b), timber harvest will typically reduce the availability of cavity trees and may affect populations of cavity-dependent wildlife. In the coming decades cavity tree abundance is likely to increase on this forest landscape as stands continue to age; disturbance events now regenerate less acreage annually than they did a century ago when the region was heavily timbered and grazed. Our pairwise comparison of differences in cavity tree density by decade for a no-harvest management regime versus the four other timber harvest regimes show the relative effect of timber harvest methods on cavity abundance over time (Fig. 4).

Differences in cavity tree abundance due to timber harvest regimes were related to harvest intensity (or rotation length). The even-aged intensive harvest regime held the mean number of cavity trees per ha near the initial (year 0) level of approximately 13 cavity trees/ha. Under all other harvest regimes the cavity tree density increased, and the greatest increase was associated with no harvest. By year 100, the mean cavity tree density for the even-aged intensive management regime (Table 1) was approximately 30% below the level for the no harvest regime (Fig. 4). Over the same simulation period, cavity tree densities for the even-aged long rotation management, uneven-aged management, and mixed management regimes (Table 1) were 10–20% below the no harvest regime (Fig. 4). In general, longer rotations increased the mean forest age and the mean number of cavity trees per ha across the landscape.

The harvest regimes affect timber output as well as cavity abundance. By year 100, the even-aged intensive, the even-aged long, the mixed, and the uneven-aged harvest regimes are expected to produced roughly 79, 33, 30, and 26% more timber (cumulative harvest plus residual) than the no harvest regime (Shifley et al., 2000). Greater harvest volumes were correlated with a greater reduction in cavity trees. Consequently, resource planners and managers must assess the tradeoff between the two goals of timber production and cavity tree preservation as habitat for wildlife species. For a given timber sale, practices such as retention of cavity trees, potential cavity trees, and snags can be used to reduce the impact on the cavity resource. Moreover, intensive management for timber in some areas may allow other areas of a landscape to be devoted to development of cavity-rich habitat. A landscape or multi-landscape scale perspective is required to explore these alternatives.

The cavity estimation model based on four stand size classes (seedling/sapling, poletimber, small sawtimber, large sawtimber) was a useful alternative to the model based on up to seventeen 10-year age classes.

These four stand size classes identified by the classification and regression tree model (Fan et al., 2003a) correspond closely to size classes typically used in timber management. These broad size classes are much easier to estimate across a large landscape than are 10-year stand age classes. Therefore, a cavity estimation model based on broad size classes is often more practical for resource managers to implement. In this study, the cavity estimation model based on 10-year age classes and the model based on four stand size classes represent a full and a constrained model, respectively. The two methods produce similar, but not identical estimates of cavity density (Fig. 5). Differences are partially attributable to the discrepancy between the age range of the Missouri FIA plots used to calibrate the size class model and that of the simulated landscape under the simulated harvest regimes. The Missouri FIA data include very few plots >120 years in age. Therefore in the model based on four size classes the cavity tree density for the largest size class (large sawtimber with age >70 years) was estimated primarily from plots in stands between 70 and 100 years old. Naturally, compared to the 10-year age-class method, it underestimated the cavity tree levels for stands >120 years in age. If a landscape is dominated by stands <120 years old, both models produce nearly identical results. And as indicated by Eqs. (4) and (8), the prediction error in terms of variance or confidence intervals will decrease with increasing landscape size and statistical power to reject null hypotheses comparing management effects will be improved.

5. Conclusions

Sustainable forest management to satisfy multiple objectives requires understanding patterns and processes of forest change at multiple spatial and temporal scales, including the large-scale, long-term effects of management actions. At landscape or regional scales, computer simulation using models provides a framework with which to integrate information about many resources and can be a useful tool for management planning. Such models allow exploring/comparing alternative scenarios that cannot be tested experimentally. Simultaneously comparing the impact of alternative management scenarios on multiple ecosystem attributes such as patch size, length of edge, age structure, timber harvest volume, residual timber volume, down wood, mast production (e.g., Shifley et al., 2000; Sullivan, 2001), and cavity tree abundance (this study) can help resource managers and planners evaluate and revise their management guidelines from different perspectives and mitigate undesirable outcomes.

We demonstrated that it is possible to link an appropriately formulated cavity tree model to a spatially explicit landscape simulation model, LANDIS, to explore the ramifications of alternative harvest regimes on estimates of future cavity tree abundance. This approach allows other ecosystem attributes to be modeled and analyzed simultaneously, thus providing a framework for integration of knowledge.

For our landscape comprised primarily of maturing hardwood forests we found that cavity tree abundance is likely to remain constant or increase over time for many common timber harvest regimes. Under intensive even-aged management (approximately 100-year rotation length) cavity tree abundance is expected to remain near current levels of 12–13 cavity trees/ha. For less intensive timber harvest regimes we projected that cavity tree abundance would increase by 20–50% as forests age over the next century. The adequacy of a given level of cavity tree abundance can only be interpreted in the context of specific wildlife habitat objectives. For many applications a relatively simple model estimating cavity tree abundance based on four broad forest size classes can produce results comparable to a more complex model based on forest age classes.

Acknowledgements

Gary Brand, Patrick Miles, and Thomas Schmidt of the Forest Inventory and Analysis Unit of the North Central Research Station, St. Paul, MN provided access to the cavity data collected during the 1989 Missouri statewide inventory. Randy Jensen and John Kabrick of the Missouri Department of Conservation provided the independent cavity test data from the Missouri Ozark Forest Ecosystem Project. Bill Dijak helped create the landscape-scale simulations of forest structure that we used to examine the effect of timber harvest on cavity abundance over time.

Eric Gustafson, Gary Wang, and Hong He provided helpful comments on an earlier version of this paper. We thank them all.

References

Allen, A.W., Corn, J.G., 1990. Relationships between live tree diameter and cavity abundance in a Missouri oak-hickory forest. N. J. Appl. For. 7, 179–183.

Anonymous, 1986. North Central Region forest inventory and analysis field instructions, Missouri. U.S. Dept. Agric., For. Serv., North Central For. Exp. Stn.

Breiman, L., Friedman, J.H., Olshen, R.A., Stone, C.J., 1984. Classification and Regression Trees. Wadsworth and Brooks, Monterey, CA, USA.

Brookshire, B.L., Shifley, S.R. (Eds.), 1997. Proceedings of the Missouri Ozark Forest Ecosystem Project Symposium: An Experimental Approach to Landscape Research. Gen. Tech. Rpt. NC-193. U.S. Dept. Agric., For. Serv., North Central For. Exp. Stn.

Carey, A.B., 1983. Cavities in trees in hardwood forests. In: Proceedings of the Snag Habitat Management Symposium. Gen. Tech. Rpt. RM-99. U.S. Dept. Agric., For. Serv., Rocky Mountain For. and Range Exp. Stn., pp. 167–184.

Cline, S.P., Berg, A.B., Wight, H.M., 1980. Snag characteristics and dynamics in Douglas-fir forests, western Oregon. J. Wildl. Manage. 44 (4), 773–786.

Conner, R.N., Hooper, R.G., Crawford, S.H., Mosby, H.S., 1975. Woodpecker nesting habitat in cut and uncut woodlands in Virginia. J. Wildl. Manage. 39, 144–150.

Diaz, N.M., Bell, S., 1997. Landscape analysis and design. In: Kohm, K.A., Franklin, J.F. (Eds.), Creating Forestry for the 21st Century: The Science of Ecosystem Management. Island Press, Washington, DC, pp. 255–270.

Fan, Z., Larsen, D.R., Shifley, S.R., Thompson III, F.R., 2003a. Estimating cavity tree abundance by stand age and basal area, Missouri, USA. For. Ecol. Manage. 179, 231–242.

Fan, Z., Shifley, S.R., Spetich, M.A., Thompson III, F.R., Larsen, D.R., 2003b. Distribution of cavity trees in midwestern old-growth and second-growth forests. Can. J. For. Res. 33, 1481–1494.

Franklin, J.F., Shugart, H.M., Harmon, M.E., 1987. Tree death as an ecological process. Bioscience 37, 550–556.

Gustafson, E.J., Shifley, S.R., Mladenoff, D.J., Nimerfro, K.K., He, H.S., 2000. Spatial simulation of forest succession and timber harvesting using LANDIS. Can. J. For. Res. 30, 32–43.

Hahn, J.T., Spencer, J.S., 1991. Timber resource of Missouri, statistical report, 1989: an analysis. Resour. Bull. NC-119. U.S. Dept. Agric., For. Serv., North Central For. Exp. Stn.

He, H.S., Mladenoff, D.J., 1999. Spatially explicit and stochastic simulation of forest landscape fire and succession. Ecology 80, 80–99.

He, H.S., Mladenoff, D.J., Boeder, J., 1999. An object-oriented forest landscape model and its representation of tree species. Ecol. Model. 119, 1–19.

Healy, W.M., Brooks, R.T., De Graaf, R.M., 1989. Cavity trees in Saw timber-size oak stands in central Massachusetts North. J. Appl. For. 6, 61–65.

Jensen, R.G., 2000. Appendix A, woody vegetation protocols. In: Shifley, S.R., Brookshire, B.L. (Eds.), Missouri Ozark Forest Ecosystem Project: Site History, Soils, Landforms, Woody and Herbaceous Vegetation, Down Wood, and Inventory Methods for the Landscape Experiment. Gen. Tech. Rpt. NC-208. U.S. Dept. Agric., For. Serv., North Central Res. Stn., pp. 134–148.

Jensen, R.G., Kabrick, J.M., Zenner, E.K., 2002. Tree cavity estimation and verification in the Missouri Ozarks. In: Shifley, S.R., Kabrick, J.M. (Eds.), Proceedings of the Second Missouri Ozark Forest Ecosystem Project Symposium: Post-treatment Results of the Landscape Experiment. Gen. Tech. Rpt. NC-227. U.S. Dept. Agric., For. Serv., North Central Res. Stn., pp. 114–112.

Mannan, R.W., Meslow, E.C., 1984. Bird populations and vegetation characteristics in managed and old-growth forests, northeastern Oregon. J. Wildl. Manage. 48, 1219–1238.

McClelland, B.R., Frissell, S.S., Fischer, W.C., Halvorson, C.H., 1979. Habitat management for hole-nesting birds in forests of western larch and Douglas fir. J. For. 77, 480–483.

McComb, W.C., Noble, R.E., 1980. Effects of single tree selection cutting upon snag and natural cavity characteristics in Connecticut. In: Proceedings of the Fish Wildlife Conference, Transactions Northeastern Section, vol. 37, Wildlife Society, pp. 50–57.

McComb, W.S., Bonney, S.A., Sheffield, R.M., Cost, N.D., 1986. Den tree characteristics and abundance in Florida and South Carolina. J. Wildl. Manage. 50, 584–591.

McShea, W.J., Healy, W.M. (Eds.), 2002. Oak Forest Ecosystems Ecology and Management for Wildlife. The Johns Hopkins University Press, Baltimore, MD.

Miles, P.D., Brand, G.J., Alerich, C.L., Bednar, L.F., Woudenberg, S.W., Glover, J.F., Ezell, E.N., 2001. The Forest Inventory and Analysis Database Description and Users Manual, Version 1.0. Gen. Tech. Rpt. NC-218. U.S. Dept. Agric., For. Serv., North Central Res. Stn.

Mladenoff, D.J., He, H.S., 1999. Design and behavior of LANDIS, an object-oriented model of forest landscape disturbance and succession. In: Mladenoff, D.J., Baker, W.L. (Eds.), Advances in Spatial Modeling of Forest Landscape Change: Approaches and Applications. Cambridge University Press, Cambridge, UK, pp. 125–162.

Mladenoff, D.J., Host, G.E., Boeder, J., Crow, T.R., 1996. LANDIS: a spatial model of forest landscape disturbance, succession, and management. In: Goodchild, M.F., Steyaert, L.T., Parks, B.O. (Eds.), GIS and Environmental Modeling: Progress and Research Issues. GIS World Inc., Ft. Collins, Co., pp. 175–180.

Nyland, R.D., 1996. Silviculture Concepts and Application. McGraw-Hill, New York.

Richards, F.J., 1959. A flexible growth function for empirical use. J. Exp. Bot. 10 (29), 290–300.

Roovers, L.M., 2000. Appendix C, woody vegetation characteristics by site and plot. In: Shifley, S.R., Brookshire, B.L. (Eds.), Missouri Ozark Forest Ecosystem Project: Site History, Soils, Landforms, Woody and Herbaceous Vegetation, Down Wood, and Inventory Methods for the Landscape Experiment. Gen. Tech. Rpt. NC-208. U.S. Dept. Agric., For. Serv., North Central Res. Stn.

Shifley, S.R., Kabrick, J.M. (Eds.), 2002. Proceedings of the Second Missouri Ozark Forest Ecosystem Project Symposium: Post-treatment Results of the Landscape Experiment. Gen. Tech. Rpt. NC-227. U.S. Dept. Agric., For. Serv., North Central Res. Stn.

Shifley, S.R., Thompson III, F.R., Larsen, D.R., Dijak, W.D., 2000. Modeling forest landscape change in the Missouri Ozarks under alternative management practices. Comput. Electron. Agric. 27, 7–24.

Spencer Jr., J.S., Roussopoulos, S.M., Massengale, R.M., 1992. Missouri's forest resource, 1989: an analysis. Resour. Bull. NC-139. U.S. Dept. Agric., For. Serv., North Central For. Exp. Stn.

Spetich, M.A., 1995. Characteristics and spatial pattern of old-growth forests in the Midwest. Ph.D. Dissertation. Purdue University, West Lafayette, IN, 276 pp.

Steinberg, D., Colla, P., 1997. CART—Classification and Regression Trees. Salford Systems, San Diego, CA.

Sullivan, N.H., 2001. An algorithm for a landscape level model of mast production. Ph.D. Dissertation. University of Missouri, Columbia.

Thompson III, F.R., Lewis, S.J., Green, J., Ewert, D., 1992. Status of neotropical migrant landbirds in the Midwest: identifying species of management concern. In: Finch, D.M., Stangel, P.W. (Eds.), Status and Management of Neotropical Migratory Birds. Gen. Tech. Rpt. RM-229. U.S. Dept. Agric., For. Serv., Rocky Mountain For. and Range. Exp. Stn., pp. 145–158.

Thompson III, F.R., Probst, J.R., Raphael, M.G., 1995. Impacts of silviculture: overview and management recommendations. In: Martin, T.E., Finch, D.M. (Eds.), Ecology and Management of Neotropical Migratory Birds. Oxford University Press, New York, NY, pp. 201–219.

Wilson, J.D., 1996. Missouri breeding bird changes: 1967–1995. In: Proceedings of the Missouri's Forest, Fish, and Wildlife Conference, Osage Beach, MO.

Zarnowitz, J.E., Manuwal, D.A., 1985. The effects of forest management on cavity-nesting birds in northwestern Washington. J. Wildl. Manage. 49 (1), 255–263.