SUSTAINABLE FORESTRY FOR THE RED-COCKADED WOODPECKER'S ECOSYSTEM

FRANCES C. JAMES, Department of Biological Science, Florida State University, Tallahassee, FL 32306-1100

PAUL M. RICHARDS, School of Computational Science and Information Technology, Florida State University, Tallahassee, FL 32306-4120

CHARLES A. HESS, USDA Forest Service, Box 579, Apalachicola National Forest, Bristol, FL 32321

KEVIN E. MCCLUNEY, 1834 Jackson Bluff Road, Apartment 5D, Tallahassee, FL 32304

ERIC L. WALTERS, Department of Biological Science, Florida State University, Tallahassee, FL 32306-1100

MATTHEW S. SCHRADER, Department of Biological Science, Florida State University, Tallahassee, FL 32306-1100

Abstract: Unless implementation of the Technical/Agency Draft Revised Recovery Plan for the Red-cockaded Woodpecker (*Picoides borealis*) (Draft Recovery Plan) is accompanied by habitat management to assure the development of multi-age pine forests with their characteristically diverse herbaceous groundcover, the longleaf pine ecosystem in which the red-cockaded woodpecker probably evolved may be lost. That ecosystem exists today mostly as naturally regenerated stands in second-growth forests that have experienced minimal soil disturbance, a regular program of prescribed fire, and periodic harvest of sawtimber. On the well-managed Apalachicola Ranger District (ARD) of the Apalachicola National Forest (ANF), which harbors the only recovered population of red-cockaded woodpeckers, nesting habitat is characterized by an average of 220 trees/ha >10 cm diameter at breast height (dbh), of which about 75 are 10-25 cm dbh and >40 are larger than 35 cm dbh. Where the birds are most productive, the groundcover averages 65% herbaceous and patches of natural pine regeneration are interspersed throughout the area. Nevertheless, our transition matrix model suggests that even ARD pine forests have insufficient recruitment of sapling longleaf pine trees to assure the long-term sustainability of the ecosystem. On the Wakulla Ranger District (WRD) of the same forest, where the red-cockaded woodpecker population is declining, the density of pine trees is higher, the percentage of herbaceous groundcover is lower, and natural pine regeneration is minimal. If these forests are to be healthy and sustainable, a better balance is needed between the recruitment of young trees and harvest. The consequences of applications of the options recommended for harvest of timber in the Draft Recovery Plan (periodic thinning, irregular shelterwood, group selection, and single-tree selection) need additional study. Our data suggest a 3-part solution: (1) more prescribed fire; (2) a version of single-tree selection that emphasizes thinning from below; and (3) mini-group selection, a form of group selection that periodically removes trees from patches that have a radius equal to the height of dominant trees in the area.

Key words: basal area, dominant species, forestry, herbaceous groundcover, longleaf pine, matrix model, recruitment, red-cockaded woodpecker, size distribution, tree structure.

Here we address the subject of whether achievement of the target values for habitat characteristics described in the Draft Recovery Plan (U.S. Fish and Wildlife Service 2000) will assure that such habitat will be sustainable in the long term. More broadly, we discuss whether conservation biologists and managers should be placing more emphasis on managing for the specific demographic requirements of the dominant plant species in an ecosystem. In the case discussed here, that species of concentration is the longleaf pine, *Pinus palustris*.

The Draft Recovery Plan describes standards for the condition of good quality foraging habitat in terms of basal area of pine stands, densities of trees in general size classes, and the percentage of herbaceous vegetation in the groundcover. Basal area is defined as the cross-sectional area of trees greater than 10 cm dbh. According to the Draft Recovery Plan, good-quality red-cockaded woodpecker foraging habitat should have longleaf pine with a basal area between 9.2 and 13.8 m^2/ha (40-60 ft^2/ac). It should have fewer than 50 trees/ha 10-25-cm (~4-10-in) dbh with a combined basal area less than 2.3 m^2/ha and at least 45 trees/ha >35 cm (~14 in) dbh. The percentage of herbaceous groundcover should be at least 40%. Guidelines for the management of nesting habitat (the 4-ha or 10-ac area that includes the cluster of cavity trees) are similar but less specific. Would the achievement of these target values assure the long-term production of good quality habitat? In terms of the demography of the longleaf pine, the question is, "To what extent should management be directed toward the attainment of a stable size (and presumably age) distribution of pine trees?" In forestry terms, it is, "How much emphasis should be put on the achievement of a 'balanced' forest? Allowing for periodic harvest and even major disturbances like hurricanes, will future productivity of foraging habitat be assured?" The objectives of this paper are (1) to study covariation among the red-cockaded woodpecker's fitness, habitat characteristics, and the size and age structure of the pine forest and (2) to explore the consequences of various management options.

THE APALACHICOLA NATIONAL FOREST

The ANF, in northern Florida, is the largest national forest in the eastern United States. Its 2 districts (the WRD and the ARD) cover 240,000 ha (570,000 ac), of which 118,000 ha are in stands of managed pine and pine-hardwood. About half of the managed area is in slash pine (*Pinus elliottii*) plantations and longleaf pine plantations. The other half (61,400 ha) is in naturally regenerated stands, including >26,000 ha of mature longleaf sawtimber in >1000 stands and >12,000 ha of immature longleaf sawtimber in >750 stands.

Both the sandhills and the flatwoods habitats present in the forest have somewhat stressful conditions for plant growth. Many mature timber stands are estimated to have a canopy height of 21.3 m at 80 years (site index of 70, height in feet of an 80-year-old tree). As elsewhere in the geographic range of the longleaf pine, today's naturally regenerated mature sawtimber stands are dominated by the single pulse of regeneration that occurred approximately 80 years ago, after the old-growth forest was cut (Figure 1).

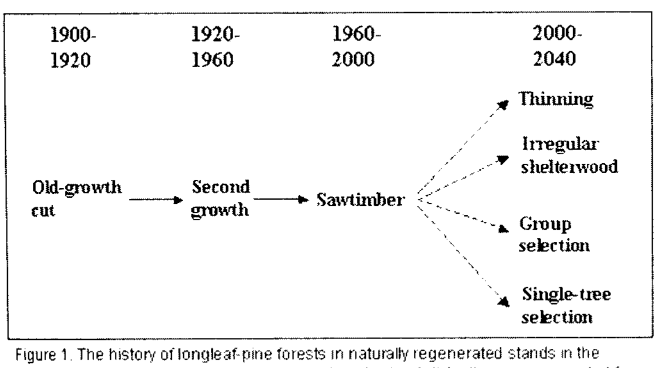

Figure 1. The history of longleaf-pine forests in naturally regenerated stands in the southern United States and four conventional methods of silviculture recommended for production of sawtimber and management of habitat for the red-cockaded woodpecker in the Draft Recovery Plan (U.S. Fish and Wildlife Service 2000).

The U.S. Forest Service (USFS) conducts a vigorous program of prescribed burning in the ANF, frequently burning >40,000 ha/year. Groups of pine stands are burned on a 3-5-year rotation in the more than 200 management compartments, each of which includes several stands. The smaller diameter of the average 80-year-old tree on the WRD (30 cm dbh) than on the ARD (35 cm dbh, James et al. 2001) may result from site differences or because more large faster-growing trees were harvested from the WRD to meet timber targets, a practice never officially recommended but not uncommon.

COVARIATION BETWEEN BIRDS AND HABITAT

In the ANF, habitat variables related to tree structure and groundcover are highly correlated with demographic variables for the woodpeckers (James et al. 2001). The group size and productivity of the birds are higher in places where densities of large trees are higher in their nesting habitat, the percentage of herbaceous vegetation in the groundcover is higher, and the densities of small trees are lower. Similar associations are found in other woodpecker populations in Florida (Hardesty et al. 1997b), North Carolina (Walters et al. 2002b), Louisiana (Wigley et al. 1999), and Arkansas (Hedrick et al. 1998). The idea that thinning from below (removal of many small trees, defined as trees 15-25 cm dbh) could change the size distribution of stands in the poorer nesting habitat on the WRD toward that of stands in the better habitat on the ARD (James et al. 2001) contributed to the development of the target standards for good-quality foraging habitat in the Draft Recovery Plan.

Two other features characterize the pattern of covariation between the birds and their habitat in the ANF. First, the area of foraging habitat that has at least some natural pine regeneration is positively related to red-cockaded woodpecker group size (James et al. 1997), and the amount of natural pine regeneration in nesting habitat is positively correlated with the density of family groups (James et al. 2001).

METHODS

Extent of Regeneration of Young Pines in Sawtimber

In 1993 we attempted to obtain habitat data in each stand of foraging habitat within a circle of 0.8-km radius in 9 random samples of 100 clusters on the ARD plus an additional random sample of 50 clusters on the WRD. Because of a combination of factors including difficult access and problems with past record keeping, we were able to locate only 114 of 150 clusters. We surveyed 669 of the 706 stands that qualified as foraging habitat in these 114 0.8-km radius circles. Of these stands, 447 (67%) were classified by the USFS as sawtimber (>23 cm dbh). Here we report the number of stands in which we found any evidence of seedling or sapling pines (<5 cm dbh) in the stands classified as longleaf pine sawtimber. We estimate the percentage of all longleaf sawtimber in the forest that is without seedlings or saplings (Table 1). We scored each stand for the presence or absence of any seedlings or saplings within 50 m of 1 observation point in each stand.

Table 1. The estimated proportion of the area of longleaf pine sawtimber in the Apalachicola National Forest with no seedlings or saplings (trees <5 cm dbh). The presence or absence of seedlings or saplings was recorded in each of 447 stands in 114 randomly selected Red-cockaded Woodpecker territories. Data are presented separately for the Apalachicola Ranger District (ARD) and the Wakulla Ranger District (WRD) and for mature sawtimber (MST) and immature sawtimber (IST). Numbers are rounded to the nearest 5.

District	Sawtimber Maturity	Area Sampled (ha)	Area with Seedlings or Saplings (ha)	% Area with No Seedlings or Saplings
ARD	MST	3645	1350	63%
ARD	IST	905	315	65%
WRD	MST	5070	1515	70%
WRD	IST	3460	845	76%
	Total	13080	4025	69%

Birds and Habitat

In 1996, we selected a random sample of 60 from the 200 management compartments in the ANF that contained active clusters of woodpeckers and selected 1 group of birds from each compartment. We monitored these groups from 1996 through 2001, banded all birds, and obtained habitat data in the stands where clusters occurred as described previously (James et al. 1997, 2001). Stands included the 4-ha clusters usually considered to be nesting habitat for the red-cockaded woodpecker, but the area sampled was selected to be representative of the entire stand at the core of the territory. Two samples for which the habitat data contained outliers were omitted from the analyses reported here. Estimates of stand structure and basal area in core stands were based on measurements of the diameters of living pines in 3 0.04-ha (0.1-ac) plots in each stand, which we selected by walking into the stand about 40 m from the edge in 3 different areas. Estimates of the composition of the groundcover were based on 2 randomly selected transects of 20 readings each in which the 15 most common plants were identified (http://bio.fsu.edu/htmls/fjindex.html). Here, we report only the percentage of groundcover that was herbaceous (grasses plus forbs, not woody shrubs or palmetto). These methods are described more fully by James and Shugart (1970). We estimated the density of saplings 1-5 cm dbh in these samples by counting the saplings visible within a 50-m radius circle. We obtained data for nesting habitat in 1996 and data for stands not in red-cockaded woodpecker territories in 2001. We used the same sampling methods for all habitat reported in Table 2. All of this work was part of a larger experimental study of fire ecology that will be reported elsewhere.

Size-Age Relationship for Longleaf Pine

In 1997, with a 6.25 mm diameter Suunto increment corer, 69 noncavity trees were cored in 10 stands on the WRD. Cores were sanded and mounted for determination of their ages. By counting tree rings to the appropriate radius and adding 7 years for the tree to reach breast height (1.3 m) (Thum 1998), we estimated the ages that 33 trees would have attained at 5 cm dbh. From dbh and age data from 69 cores, we estimated growth increment rates by size class. The equation we developed for predicting age (years) from size (dbh in centimeters) is

Table 2. Bird and habitat variables for 8 types of longleaf pine stands in 58 stands of nesting habitat and 11 stands that were not within Red-cockaded Woodpecker (RCW) territories. The 2 districts of the Apalachicola National Forest are the Apalachicola Ranger District (ARD) and the Wakulla Ranger District (WRD). Average fledglings are for the first nesting attempt. Values for bird variables are means with standard deviations in parentheses. For values for habitat variables, superscript letters identify significant statistical tests (see below). Numbers over 50 are rounded to the nearest 5. MST = mature sawtimber; IST = immature sawtimber; N = nesting; NT = not in RCW territories; RCW density = groups within 1.6 km; Small trees (ST) = trees 10–25 cm dbh/ha; Large trees (LT) = trees > 35 cm dbh/ha; pine saplings are 1– 5 cm dbh.

District/Maturity/ Habitat	n	RCW Group Size	Average Fledglings 1996-2001	RCW Group Density	Basal Area (m^2/ha)	Pines >10 cm/ha	Small Trees (ST)	Large Trees (LT)	ST Minus LT	% Herb. Ground-cover	Saplings/ha and Range
ARD/MST/N	32		1.5 (0.5)	6.0 (3.0)	12.2	220	75	42	26[ce]	65[df]	11
ARD/MST/N	26	>2[a]	1.6 (0.5)	6.1 (3.0)	12.3	220	70	41	26	65	13[b] (0–60)
ARD/MST/N	6	≤2	1.0 (0.3)	4.9 (3.0)	11.3	210	105	46	50	38	5 (0–70)
WRD/MST/N	26		1.1 (0.4)	3.7 (1.8)	11.4	240	140	17	125[c]	28[d]	6
WRD/MST/N	12	>2[a]	1.2 (0.4)	4.3 (1.9)	11.5	235	135	16	125	31	3[b] (0–40)
WRD/MST/N	14	≤2	0.9 (0.4)	3.1 (1.6)	11.2	240	145	17	125	28	7 (0–30)
WRD/MST/NT	6				19.1	380	189	19	150[e]	17[f]	4
WRD/IST/NT	5				14.2	290	91	8	91	23	4
District/Maturity/ Habitat	**n**	**Pine Sapl. /ha**	**Average Fledglings 1996-2001**	**RCW Group Density**	**Basal Area (m^2/ha)**	**Pines >10 cm/ha**	**Small Trees (ST)**	**Large Trees (LT)**	**ST Minus LT**	**% Herb. Ground-cover**	
ARD+WRD/MST/N	16	0	1.3 (0.5)	4.2 (2.1)	11.1	240	150	17	125[g]	29[h]	
ARD+WRD/NST/N	29	>10	1.4 (0.6)	5.9 (3.1)	12.1	223	92	33	58[g]	62[h]	
Recovery Standard					9.2–13.8		<50	>45			

Note: Mann Whitney U statistics and significance levels for comparisons described in the text. [a]92, $P < 0.05$; [b]94, $P < 0.05$; [c]660, $P < 0.001$; [d]90, $P < 0.001$; [e]174, $P < 0.002$; [f]13, $P < 0.001$; [g]229, $P < 0.06$; [h]66, $P < 0.002$. P values for all other comparisons were higher. These p values were not corrected for simultaneous comparisons.

Note: Five sites received artificial cavities, and six received translocated birds during the period reported here.

$$\text{age} = \left(-0.817 + \sqrt{(0.5 - 0.008\text{dbh})}\right) / -0.004$$
$$= 195.49 - \sqrt{28129.32 - 478.46(\text{dbh})}$$

The equation for annual diameter growth increment (in centimeters) is

diameter growth increment = 0.6983 - 0.0049 dbh - 0.00007 dbh^2

Natural Mortality Rate for Longleaf Pine

We obtained data from the Forest Inventory and Analysis (FIA) program for the average survival rates of longleaf pines by size class. Data were selected for Florida between 1987 and 1993. We then calculated an equation for annual percent mortality:

annual percent mortality = 10.076 - 0.8738 dbh + 0.0176 dbh^2

The Transition Matrix

To construct a transition matrix for longleaf pine stands, we used the above estimates for the relationship between annual diameter growth increment and annual percent mortality. We used 10 dbh size classes in 5-cm increments that start at 5-10 cm (midpoint 7.5 cm) and end at >50 cm.

We used annual diameter growth increment to estimate size-class duration (d_i) by dividing growth increments by the magnitude of the size-class interval (5 cm). Growth increments for size-classes 40-45, 45-50, and 50-55 cm had to be extrapolated.

Percent mortalities (as calculated above) were expressed in terms of annual survival (P_i) according to $P_i = 1 - (\text{mortality}/100)$. The diagonal ($P_i$) and subdiagonal ($G_i$) elements of the transition matrix are a function of annual survival, p_i, and size class duration, d_i. P_i is calculated as

$$P_i = \frac{p_i(1 - p_i^{d_i - 1})}{1 - p_i^{d_i}}$$

and G_i as

$$G_i = \frac{p_i^{d_i}(1 - p_i)}{1 - p_i^{d_i}}$$

where P_i is the probability of remaining in a stage i, and G_i is the probability of growing into the next stage (Crouse et al. 1987).

The population rate of increase, λ_d (i.e., the dominant eigenvalue of the transition matrix), and the stable stage distribution (i.e., the right eigenvector of the matrix associated with λ_d) are typically calculated from a complete transition matrix, one that includes fecundities in the top row of the matrix (Caswell 1989). We did not have estimates of fecundities associated with the different sizes of trees, so we used the method of Michod and Anderson (1980), who assumed a stable age structure, and a table of fecundities. Platt et al. (1988a) later used this approach to estimate the expected stable size (or age) structure of a forest given any λ and known survival and transition probabilities.

RESULTS

The Occurrence of Seedlings and Saplings in Longleaf Pine Stands

The 447 stands we sampled in 1993 covered an area of more than 13,000 ha. Some seedlings and saplings were evident in stands that covered 4,025 ha. We recorded no seedlings or 1-5-cm dbh saplings in 69% of the area of longleaf sawtimber in our random sample of 114 territories (Table 1).

In the sample of 33 tree cores from nesting habitat on the WRD, we estimated that the mean age of a 5-cm dbh tree was 17 years (SD 6.0). Our estimates of regeneration are therefore based on samples from trees <17 years old. Note, however, that the standard deviation is high.

Covariation of Bird and Habitat Variables, Including the Density of Sapling Longleaf Pines

In our samples of nesting habitat on the ARD where woodpecker groups consistently had at least 1 helper (group size >2) between 1996 and 2001 (Table 2, row 2), habitat conditions were close to recovery standards (Table 2, row 11). These groups had the highest number of other groups nearby, and the density of sapling pines was significantly higher than in clusters on the WRD where groups also had helpers (Table 2, rows 2 and 5, tests a and b). Where woodpecker groups did not have helpers (average group size ≤2) on the ARD, the median density of small trees (trees/ha 10-25 cm dbh) was higher and the percentage of herbaceous groundcover was lower than where groups had helpers, but these differences were not statistically significant at these sample sizes. In nesting habitat, the difference between the densities of large and small trees was lower on the ARD than on the WRD, and the percentage of herbaceous vegetation in the groundcover was higher (Table 2, rows 1 and 4, tests c and d). This discrepancy was even more extreme in comparisons between nesting habitat on the ARD and stands on the WRD that are not in woodpecker territories (Table 2, rows 1 and 7, tests e and f). In general, on the ARD and between the 2 districts, the group sizes and productivity of red-cockaded woodpeckers are higher in areas with fewer small trees, more large trees, more herbaceous groundcover, and more sapling pines (Table 2).

The maximum number of saplings per hectare was higher on the ARD (Table 2, column 14). Some sapling pines were present in some stands in all types of habitat, but those stands in which we found no saplings had larger differences between the densities of small and large trees and lower percentages of herbaceous groundcover than did stands with median densities of >10 saplings/ha (Table 2, rows 9 and 10, test g).

Spearman correlations between the density of saplings and other habitat variables in the nesting habitat of 38 groups where some regeneration occurred (saplings > 3/ha) again show that woodpecker group size, productivity, and density are strongly positively related to the density of saplings (Table 3). In addition, the habitat variable most highly correlated with levels of pine regeneration is the percentage of herbaceous vegetation in the groundcover, an indirect indicator of fire history. In fact, the percentage of herbaceous groundcover is the only habitat variable significantly related to variation in levels of pine regeneration (percentage herbaceous groundcover = 0.82 $\log_{10}$ saplings/ha, $n = 38$, $P < 0.0005$).

Table 3. Spearman correlations between the number of sapling pines/ha (1–5 cm dbh), bird variables, and other habitat variables, in nesting habitat that has more than 3 saplings/ha (n = 38). Bird data are averages between 1996 and 2001. Red-cockaded woodpecker (RCW) density = groups within 1.6 km; small trees (ST) = trees/ha 10–25 cm dbh; large trees (LT) = trees/ha > 35 cm dbh.

RCW Group Size	Fledglings 1996-2001	RCW Cluster Density	Basal Area (m^2/ha)	Pines >10 cm/ha	Small Trees (ST)	Large Trees (LT)	ST – LT	% Herb. Ground-cover
0.33	0.32	0.48	–0.03	–0.01	0.11	0.18	0.04	0.50

Table 4. Annual transition matrix for the average longleaf pine stand in red-cockaded woodpecker clusters in the Wakulla Ranger District of the Apalachicola National Forest, Florida, based on size-age relationships in these stands and average mortality in longleaf pine stands in Florida. The sum of each column is the estimated annual survivorship.

Size Class Midpoint	5–10	10–15	15–20	20–25	25–30	30–35	35–40	40–45	45–50	>50 cm
7.5	0.847	0	0	0	0					
12.5	0.108	0.865	0	0	0	0	0	0	0	0
17.5	0	0.116	0.881	0	0	0	0	0	0	0
22.5	0	0	0.117	0.890	0	0	0	0	0	0
27.5	0	0	0	0.110	0.898	0	0	0	0	0
32.5	0	0	0	0	0.102	0.905	0	0	0	0
37.5	0	0	0	0	0	0.093	0.906	0	0	0
42.5	0	0	0	0	0	0	0.073	0.903	0	0
47.5	0	0	0	0	0	0	0	0.049	0.890	0
52.5	0	0	0	0	0	0	0	0	0.027	0.864

Transition Matrix Model

The transition matrix (Table 4) gives estimates of the proportion of trees in 5-cm size classes that are expected to remain in the same size class until the next sampling time (diagonal elements) and the proportion that are expected to enter the next larger size class (subdiagonal elements). The theoretical stable size distribution was normalized and extrapolated to a theoretical population having the same total number of trees as our observed population on the WRD (Figure 2, dotted line). We compared this size distribution with the observed average size distributions for nesting habitat in the 2 districts. The major differences between the observed size distributions of trees in nesting habitat in the 2 districts (Figure 2) are that the density of small trees (10-25 cm dbh) is higher on the WRD, and the density of large trees (>35 cm dbh) is higher on the ARD, as was seen in Table 2. The theoretical stable size distribution is more similar in shape to the distribution on the ARD than to that on the WRD. The most obvious difference is that the theoretical distribution has a much higher density of trees in the recruitment (5-10-cm) size class. Although the density of recruits (5-10 cm) is higher on the ARD than on the WRD, it is not estimated to be sufficient to replace the larger trees, even on the ARD.

DISCUSSION

Throughout the geographic range of the longleaf pine (southeastern Virginia to eastern Texas), naturally regenerated second-growth stands that are considered to be in good condition today tend to be even-aged (Landers et al. 1990). Most are being managed for sawtimber by periodic thinning, a form of classical even-aged management (Walker 1995, Smith and Hawley 1986). Except for attempts to reduce fuel loads with prescribed fire, little regard has been shown for either natural regeneration (Kelly and Bechtold 1990) or the condition of the understory and groundcover communities (Outcalt and Sheffield 1996). Implementation of the guidelines for habitat management for the red-cockaded woodpecker in the Draft Recovery Plan, which mostly calls for lower stocking levels than the conventional 13.8 m^2/ha (60 ft^2/ac), will undoubtedly improve the ecological condition of the forests in today's overstocked stands. Our finding that 69% of the area of longleaf pine sawtimber in the ANF has no or minimal pine regeneration is conservative because we sampled only stands in red-cockaded woodpecker territories.

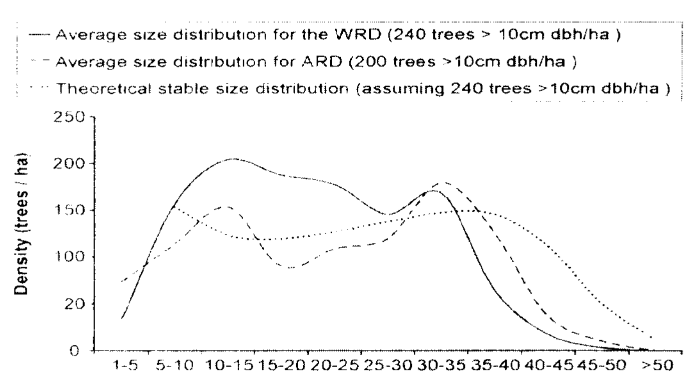

Figure 2. The average size distribution of pine trees in nesting habitat of red-cockaded woodpeckers in two districts of the Apalachicola National Forest, the Wakulla Ranger District (WRD) and the Apalachicola Ranger District (ARD), and the theoretical stable size distribution for the current density of trees in the WRD.

Removing trees where the groundcover is less than 30% herbaceous is dangerous because it can stimulate the resprouting of woody shrubs. On the basis of the values in Table 2, we think the percentage of herbaceous groundcover should be at least 30% before such harvest takes place, and the higher the percentage of herbaceous groundcover the better. This important point is ignored by McConnell (2002), who advocates cutting 0.8-ha patches without attention to the condition of the groundcover. Because the proportion of the groundcover that is herbaceous is so important to the health of the ecosystem, we recommend that future monitoring programs include it as a variable.

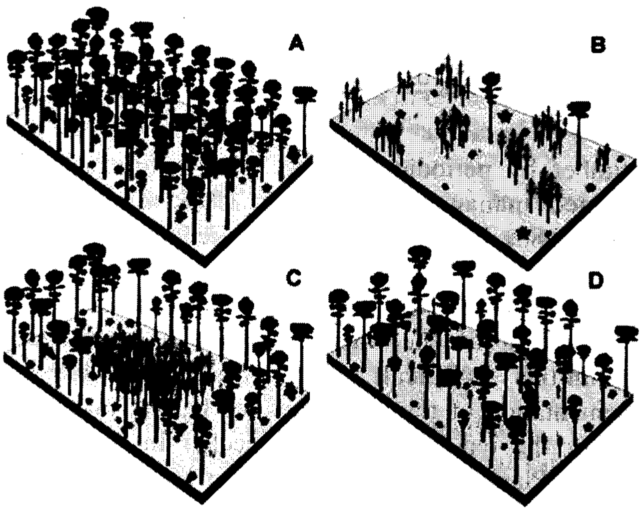

Figure 3. Diagrams for methods of silviculture recommended for management of habitat for the red-cockaded woodpecker in the Draft Recovery Plan (U.S. Fish and Wildlife Service 2000). Each quadrangle represents 0.2 ha (<0.5 acre). With periodic thinning (a), sawtimber stands are maintained at a full stocking level (250 trees > 10 cm dbh/ha, approximately 13.7 m^2/ha basal area). With irregular shelterwood (b), the stand is reduced to a basal area of about 6.9 m^2/ha to encourage one major pulse of regeneration and to achieve a two-age forest. With group selection (c) small patches of trees are removed periodically to produce individual patches of regeneration. Group selection would remove patches up to four times the size of those in the diagram (0.2–0.8 ha). Minigroup (or multiple-tree) selection, illustrated in Fig. 2c, as described in this paper, would remove smaller patches. With single-tree selection (d), the objective is to alter the size distribution and achieve a multiage forest by encouraging regeneration throughout the stand.

The ARD of the ANF is one of the best examples of a large area of mature sawtimber with an intensive prescribed burning program. Within this district, the red-cockaded woodpecker habitat that supports groups of birds that have helpers and that are consistently productive is the habitat that comes the closest to having sufficient regeneration of pines to promote a multi-aged forest (Table 2). However, we show that current levels of regeneration, even on the ARD (Table 2), are unlikely to be sustainable in the long term. This finding has important consequences for the longleaf pine ecosystem. If the naturally regenerated stands of sawtimber on the well-managed ARD have insufficient regeneration, other areas are likely to have even less. Once this problem has been acknowledged (Noel et al. 1998), managers and researchers need to consider options for using prescribed burning and silviculture to improve the rates of regeneration and recruitment after mast years and to provide multi-aged forests. New studies should be designed with replicates, controls, and feedback, so that policies can be shifted as the best alternatives emerge (Walters 1986, Walters and Holling 1990).

Because the general ecology of the longleaf pine is treated elsewhere (e.g., by Christensen 1981, Platt et al. 1988a, Hermann 1993, Abrahamson and Hartnett 1990, Glitzenstein et al. 1995, Conner et al. 2001a) and we are not discussing other species of pines (as do Rudolph and Conner 1996), we will limit our discussion to those demographic features of our data that are relevant to prescribed burning and silviculture.

Demography of the Longleaf Pine

Mature longleaf pines do not produce large numbers of cones every year (Boyer 1986), and regeneration occurs mostly in openings (Wahlenberg 1946). Only 3 mast years (1978, 1987, and 1996) have occurred in the ANF in the last 25 years (D. Farnsworth, U.S. Forest Service, personal communication). In those mast years seed production was abundant and widespread. Our samples of seedlings and saplings in 1993 and 1996 occurred 15 years after the 1978 mast year and 9 years after the 1987 mast year, respectively. We found that substantial regeneration was unlikely if the number per hectare of small trees (10-25 cm dbh) minus that of large trees (>35 cm dbh) (SL - LT) was greater than 125 and the percentage of herbaceous groundcover was less than 30 (Table 2, lines 9 and 10).

The age distribution of a stand of longleaf pine trees cannot necessarily be predicted from its size-class distribution. Recruitment and mortality are likely to occur in pulses, and although the process is poorly understood, individual tree growth is density dependent (Boyer 1993). The size distribution at any given time may not be a reliable indicator of the long-term dynamics of a stand of trees (Harper and White 1974, Platt et al. 1988a). Rates of growth and recruitment vary with habitat (Glitzenstein et al. 1995), and growth in the first 30 years is higher in open plantations than in natural stands (Boyer 1996). Saplings can persist in suppressed growth conditions for many years (Goelz and Leduc 2002). We will not fully understand the dynamics of recruitment in naturally regenerated stands of longleaf pine until more data on their age distributions are available. Young trees less than 10 cm dbh are expected to undergo a pulse of rapid initial growth, during which mortality is high, but between 10 and 40 cm dbh, growth is expected to be slow and mortality rates lower (Platt et al. 1988a, Platt and Rathbun 1993, Boyer 1990). These processes can distort the size distribution of a stand from the negative exponential size distribution that would be expected if growth and mortality rates by size class were constant. The resultant size distribution is expected to be wave-like (Platt and Rathbun 1993), as in Figure 2.

Silviculture

Both the Final Environmental Impact Statement for the Management of the Red-cockaded Woodpecker and Its Habitat on National Forests in the Southern Region (U.S. Forest Service 1995) and the Draft Recovery Plan allow the use of 4 methods of harvesting trees in red-cockaded woodpecker foraging habitat (Figures 1 and 3a-d): thinning, irregular shelterwood, group selection, and single-tree selection. Thinning (Figure 3a) is the removal of certain size classes of trees, preferably the least healthy ones and the small and medium sized ones (Engstrom and Baker 1995, Engstrom et al. 1996, Guldin and Baker 1998). Standard practice has been to allow even-aged stands of trees to grow to a basal area of about 16.1 m^2/ha (70 ft^2/ac) and then to thin them to 13.8 m^2/ha (60 ft^2/ac). This standard is thought to promote the maximum growth and yield of sawtimber (Smith and Hawley 1986). Note that in the Draft Recovery Plan the maximum recommended basal area is 13.8 m^2/ha. In typical stands, this condition is not expected to allow much regeneration or recruitment of young trees (Engstrom and Baker 1995, Engstrom et al. 1996). The irregular shelterwood method (Figure 3b), on the other hand, induces such a large pulse of regeneration that the result is a 2-aged forest. First the canopy trees are reduced to a basal area of about 6.9 m^2/ha (30 ft^2/ac). If the groundcover is in good condition, and is burned again prior to seedfall, it will be prepared to receive the next seed fall. With the irregular shelterwood method the canopy trees are retained indefinitely. Boyer (1997) remarked that the original harvest of longleaf pine early in the 20th century was unintentionally like a rangewide shelterwood cut. The first cut removed the largest trees and allowed massive regeneration to become established. The second cut removed nearly all of the remaining trees. Today's relicts are the few trees left unharvested within the regenerating cohort. Many of those that were more than 30 years old in 1930 are today's cavity trees. Group selection (Figure 3c) as described by the U.S. Forest Service (1995) and U.S. Fish and Wildlife Service (2000) involves cutting areas of 0.2-0.8 ha, which should be prepared to catch the next seed fall. As proposed, the minimum cut would be the full size of the diagrams in Figure 3, and the maximum cut would be 4 times the area of the diagram. We have used this diagram to illustrate mini-group selection (see below).

Single-tree selection (Figure 3d) is theoretically likely to produce an all-age forest at a smaller scale than is group selection. It is based on a long-term target distribution of tree sizes that has an inverse J-shaped (negative exponential) size distribution like the one in Figure 4 (Smith and Hawley 1986, Farrar and Boyer 1991, Farrar 1996, Boyer 1997). One objective is to produce regular regeneration after mast years. However, the conventional parameters with single-tree selection specify a residual basal area (13.8 m^2/ha, 60 ft^2/ac), a maximum diameter of trees to be retained (56 cm, 22 in), and the ratio of the number of pine stems in a given 2.5-cm (1-in) size class to that in the next smaller size class of 1/1.2 (Farrar 1996, Guldin and Baker 1998). As proposed in U.S. Forest Service (1995) and U.S. Fish and Wildlife Service (2000) guidelines, its target tree-size distribution (Figure 4) would have too many small trees (10-25 cm dbh) to allow regeneration (Figure 2, ARD; James et al. 2001) and too few large trees (>35 cm dbh) to provide good woodpecker habitat. The guideline parameter values for single-tree selection need to be changed, but so far only limited tests have been carried out (Farrar and Boyer 1991). In general, guidelines for densities of trees by size class are preferable to the conventional combination of basal area and total density of trees >10 cm dbh.

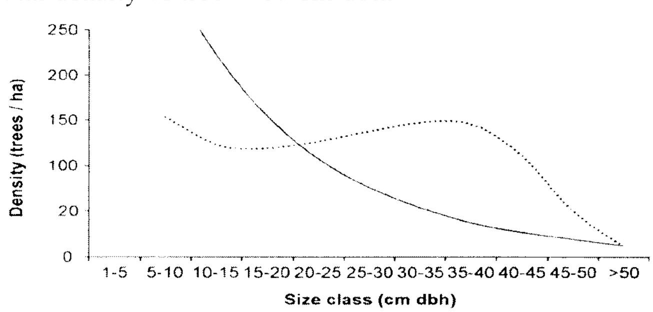

Figure 4. The target size distribution of pine trees in stands managed by single-tree selection (solid line) according to the method of Farrar (1996) with a maximum basal area of 13.8 m^2/ha, a maximum tree size of 56 cm dbh, and a q value of 1.2 (factor by which successively lower 2.5-cm (1-in) size classes increase in their densities of trees). The dotted line is the theoretical stable size distribution for the current density of trees on the WRD (see Fig. 2).

This review of the options recommended for the harvest of trees in red-cockaded woodpecker habitat leads to several questions. Should a target size distribution for a multi-aged forest be adopted? What should be its spatial scale? Would increased burning alone produce a multi-aged forest, making tree harvest unnecessary? How can we assure that we are accommodating the basic features of the life history of the longleaf pine? Would open multi-aged forests provide sufficient opportunities for harvest?

A Proposed Combination of More Prescribed Fire, Single-tree Selection, and Mini-group Selection

Single-tree selection and group selection, as types of uneven-aged management, seem best suited to achieving a multi-aged forest in longleaf pine ecosystems. Single-tree selection is more difficult to implement (McConnell 2002), and a comparison of Figures 2 and 4 suggests that the conventional parameters for single-tree selection may not promote the regeneration and recruitment needed to develop a sustainable age structure. Nevertheless, variants could easily be developed to suit ecological objectives, and over the period of several entries, single-tree selection with adjusted parameters and a vigorous program of prescribed burning could be the best ecological solution to the problems raised here. In practice in the ANF, single-tree selection could consist primarily of thinning from below.

Brockway and Outcalt (1998) studied canopy gaps in longleaf pine forests in sandhills habitat in the Ocala National Forest in north-central Florida, where overstory trees averaged 39 cm dbh and were ~24 m tall. They found that seedling survival was lower near established trees and concluded that fine-root competition probably lowers seedling survival for a distance of 12-16 m from the trunks of parent trees. The phenomenon of reduced survival of seedlings and saplings near dominant trees has also been documented elsewhere (e.g., by Platt et al. 1991; Platt and Rathbun 1993; Grace and Platt 1995a,b. Brockway and Outcalt (1998) suggested that their data could be used to develop a criterion for the minimum size of canopy gaps designed to promote regeneration. Similarly, Croker and Boyer's (1975) work could be used to develop a criterion for the optimal maximum size of canopy gaps. They argued that, because seeds from longleaf pines do not usually disperse farther than a distance equal to the height of the tree, seedlings should be expected mostly within that radius.

On the ANF, a typical stand of mature second-growth longleaf pine sawtimber (Figure 3a) has approximately 250 trees/ha >10 cm dbh and an average canopy height of ~20 m (Figure 3a). Brockway and Outcalt (1998) concluded that, in a forest where dominant trees were 24 m tall, the minimum size of a canopy gap created by harvest should be at least 30 × 30 m. According to Croker and Boyer's (1975) criterion, unless the objective were to create a somewhat permanent opening in the forest, the maximum size of a gap among trees 20 m tall should be 40 × 40 m (approximately 0.2 ha or 0.5 ac). We call this proposed regime mini-group selection. It creates gaps with a maximum radius of the height of the dominant trees in a stand. It is illustrated in Figure 3c.

The calculations above plus the findings reported in Table 2 suggest that mini-group selection might be a useful way to encourage regeneration and recruitment, provided that the groundcover is already >30% herbaceous and that single-tree selection could be used to reduce the density of suppressed trees in the 10-25-cm (4-10-in) size classes. If applied repeatedly, single-tree selection should also create gaps that promote recruitment. Clearly, researchers and managers will have to work together to study the consequences of various ways to introduce more age structure into longleaf pine forests. Under current market conditions for timber, implementation of ideal practices may not be economically feasible (Stephenson and Ritchie 2003). Regardless of the method of silviculture, the prescribed fire program and the condition of the groundcover will be the most important correlates of the level of regeneration.

INTERPRETATION OF THE TRANSITION MATRIX MODEL

Matrix models stem from a well-developed methodology (Caswell 2001:646-662, Tuljapurkar and Caswell 1997). They have been shown to produce useful generalities (DeAngelis et al. 1980), and they have been used extensively in forestry (Buongiorno and Michie 1980) and conservation biology (Crouse et al. 1987, Lande 1988a). See Heppell et al. (1994) for an application to the management of red-cockaded woodpecker populations.

Our matrix model was developed from 2 equations, 1 for the average rate of growth increment in longleaf pine trees and 1 for estimates of rates of mortality. The mortality rates, which were provided by the Forest Inventory and Analysis program, are based on data from plots in Florida whose locations are not released by the USFS. Some of the plots may have been harvested in the period sampled. Such harvest could account for the high mortalities in the larger size classes of trees.

The theoretical size distribution in Figure 2 is a first step toward predicting a target size distribution for a sustainable multi-aged forest and is the best estimate we can produce given the currently available data for the ANF. The model has important restrictive assumptions. Because it is set to $\lambda = 1$, it assumes that population density (trees/ha > 10 cm dbh) does not change. It also assumes that current vital rates are constant and predicts the constant frequency of trees that would occur in different size classes. Of course, population size and forest structure will be affected by variation in demographic factors and by whatever management is imposed, as discussed above. Given all these assumptions, we can compare the distributions of observed and predicted size distributions in Figure 2. The major difference is that the observed proportion of saplings (1-5 cm) is lower than the proportion needed to sustain the stable size distribution. Also, on the WRD, the proportion of small trees (10-25 cm) is much higher than in the stable distribution. Some caution is warranted. These differences may also mean (1) that the observed forest does not have a stable size distribution, (2) that the estimated demographic rates used in constructing the matrix model are not characteristic of the observed stands used for comparison, or (3) that the population of trees is changing in number. However, even a cautious interpretation of our model indicates that current management for sawtimber in the ANF is not sustainable. Platt et al. (1988a) and Platt and Rathbun (1993) developed a similar model for an old-growth longleaf pine forest in southwestern Georgia.

CONCLUSION

The young field of ecological forestry (Kohn and Franklin 1997) has not yet paid much attention to the coniferous forests of the southeastern United States (Noss et al. 1995), where the management of naturally regenerated longleaf pine forests is affecting the recovery of the red-cockaded woodpecker. Without management for sawtimber, we would undoubtedly have fewer red-cockaded woodpeckers today and probably fewer of the other 26 federally listed threatened and endangered species in this ecosystem (National Research Council 1998). Implementation of the habitat guidelines in the Draft Recovery Plan should improve the health of the longleaf pine ecosystem. However, we think that periodic thinning, as currently practiced, does not promote sufficient regeneration or recruitment of young pine trees. The irregular shelterwood method creates a 2-aged forest, not the desired multi-aged forest. Group selection, as advocated in the Draft Recovery Plan, creates openings that are too large. We recommend more vigorous burning and monitoring of the condition of the groundcover. When it is more than 30% herbaceous, we recommend a form of single-tree selection that emphasizes thinning from below in combination with mini-group selection. Mini-group selection allows harvest of patches of trees up to a radius equal to the height of canopy trees. If our findings apply to longleaf pine forests elsewhere, then currently recommended guidelines for the management of longleaf pine sawtimber in red-cockaded woodpecker habitat need further modifications if they are expected to provide a sustainable longleaf pine ecosystem.

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