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Stand conditions and tree characteristics affect quality of longleaf pine for red-cockaded woodpecker cavity trees

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Abstract

We measured resin flow of longleaf (*Pinus palustris* Mill.) pines in red-cockaded woodpecker (*Picoides borealis* Vieillot) clusters in the Angelina National Forest in Texas, and the Apalachicola National Forest in Florida. Sample trees were categorized as active cavity trees, inactive cavity trees and control trees. Sample trees were further categorized by stand position as either edge or interior trees.

Longleaf cavity trees in Texas and Florida had similar resin flow characteristics. Active cavity trees on forest edges had the highest resin flow, whereas active cavity trees in forest interiors had the lowest. Trees experiencing both low and high levels of red-cockaded woodpecker activity and competition from other trees had low resin flow, whereas intermediate stress typically resulted in high resin flow.

Results from this study indicate that the best active red-cockaded woodpecker cavity trees, from a resin flow perspective, are on or near forest edges. This may explain the woodpecker's observed tendency to excavate new cavities near edges even when interior basal area has been reduced and midstory has been controlled. Our results suggest that pines managed as potential cavity trees should be experiencing minimal competition, and that a mosaic of patches in red-cockaded woodpecker habitat may be preferable to more uniform conditions.

Keywords: Endangered species; Resin flow; Red-cockaded woodpecker; Longleaf pine; Edge effect; Stand structure

1. Introduction

The red-cockaded woodpecker, *Picoides boreali* (Vieillot) has been listed as an endangered species since 1970 (US Department of the Interior, Fish and Wildlife Service, 1970). With populations occurring in a variety of pine and pine–hardwood ecosystems of the southeastern United States, the red-cockaded woodpecker is unique in that it excavates roosting and nesting cavities exclusively in living pines. Old-growth longleaf pine (*Pinus palustris* Mill.) is favored when available (US Department of the Interior, Fish and Wildlife Service, 1985), but shortleaf (*Pinus echinata* Mill.), loblolly (*Pinus taeda* L.), slash (*Pinus elliottii* Engelm.), Virginia (*Pinus virginiana* Mill.) and pitch (*Pinus rigida* Mill.) pines

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also are readily used (Hooper et al., 1980; Kalisz and Boettcher, 1991). Red-cockaded woodpecker populations in Texas (Conner and Rudolph, 1989) and southwide (Costa and Escano, 1989; James, 1995) have generally been declining because of loss and fragmentation of habitat (Lennartz et al., 1983a; US Department of the Interior, Fish and Wildlife Service, 1985; Conner and Rudolph, 1991). Recent population trends have been encouraging, however. Population decline in some areas has been reversed along with development of artificial cavity technology, aggressive hardwood control and basal area reduction (James, 1995; Conner et al., 1995).

In addition to excavating its cavities in living pines, red-cockaded woodpeckers peck small holes, called resin wells, around cavity entrances causing a copious flow of resin down and around the boles of their cavity trees. The resin serves as a barrier against rat snakes, *Elaphe* spp., a major woodpecker predator (Jackson, 1974; Rudolph et al., 1990a), but has little effect on cavity competitors (Rudolph et al., 1990b). The oleoresin system of southern pines also is presumed to be the primary defense mechanism against bark beetle attack and colonization by fungi (Lorio et al., 1990).

Resin in southern pines is produced in a system of resin ducts (Koch, 1972; Schmitt et al., 1988). Horizontal and vertical ducts occur in both early and late sapwood. Horizontal ducts occur in the phloem. Resin ducts also occur in foliage, but are not continuous with the resin system in the stem. Far fewer ducts occur in the early sapwood. Ducts begin to be concentrated at the transition between early and latewood (Blanche et al., 1992). Resin ducts are relatively large intercellular spaces lined with thin-walled epithelial cells where the resin is secreted. Resin ducts and resin production are primarily the results of tissue differentiation because of the greater number of ducts and greater volume of resin produced later in the growing season after early height and diameter growth slow (Lorio, 1986; Lorio and Sommers, 1986; Lorio et al., 1990; Blanche et al., 1992). According to the growth–differentiation balance theory originally proposed by Loomis (1932), and expanded upon by Lorio (1986), growth and resin production are competitors for photosynthates. When soil moisture is abundant early in the growing season, height, diameter, and vegetative growth are favored. When moderate soil moisture deficits limit growth, differentiation is favored. In all southern pine species, the general seasonal trend of resin flow is low flow from late September through early March, increased flow from mid-March to early April, high flow peaking in July or August, then declining rapidly to seasonal lows in December and January (Blanche et al., 1992). Researchers evaluating resin flow have observed the highest resin flow in mid to late summer, when temperatures and seasonal moisture deficits are highest, and radial and foliar growth are reduced (Lorio et al., 1990; Blanche et al., 1992).

Resin flow from a wound may be of two general types: (1) preformed; (2) traumatic/hypersensitive response (Hodges et al., 1979; Paine et al., 1985; Nebeker et al., 1988). When a pine is first wounded in tissue that has not been previously traumatized, the ensuing flow of resin is preformed, that is, it was in the resin ducts at the time of wounding and flowed from the disrupted resin ducts. The formation of resin ducts and resin flow volume may be stimulated by trauma and fungal inoculation (hypersensitive response) (Paine et al., 1985). This results in higher localized resin flow from the traumatic resin ducts. The extent of traumatic tissue formation depends on the extent and duration of the wounding. The hypersensitive response serves to seal off invading fungi. Low level bark beetle attacks may fail, not only because the beetles are killed by resin, but because the fungi the beetles carry also are neutralized. In addition, recovery after fire damage is aided by the resin system (Spurr and Barnes, 1980).

Southern pines vary greatly in resin production abilities, both among and within species. Generally longleaf and slash pines produce more resin for a longer time than loblolly and shortleaf (Wahlenberg, 1946). Longleaf and slash were in fact the only important species to the naval stores industry. Resin flow varies greatly within pine species as a function of tree, site, stand density, and genetic factors (Mason, 1971; Hodges et al., 1979; Blanche et al., 1992; Bowman and Huh, 1995; Ross et al., 1995).

A mature longleaf pine forest, where frequent fires keep hardwoods restricted to wetter areas, produce an open stand habit and maintain species and community structure mosaics on a landscape scale, is considered by most red-cockaded woodpecker investigators and managers to be the optimum forest type

for red-cockaded woodpeckers (Lennartz et al., 1983b; Locke et al., 1983; US Department of the Interior, Fish and Wildlife Service, 1985; Conner and Rudolph, 1989). Longleaf, in addition to being fire-resistant, also is highly resistant to southern pine beetles, the primary cause of mortality of Texas loblolly and shortleaf pine cavity trees (Conner et al., 1991a; Rudolph and Conner, 1995). Annual cavity tree mortality in Texas loblolly and shortleaf pines is twice that of longleaf (Conner and Rudolph, 1995a). Although cavities in longleaf pine take longer to excavate, they also are used much longer (Conner and Rudolph, 1995a).

Resin flow in pine trees has been studied in the context of the naval stores industry and also in the evaluation of southern pine beetle attack dynamics to commercial timber stands. Little research, however, has focused on red-cockaded woodpecker cavity trees. Resin production and flow in red cockaded woodpecker cavity trees is critical in that it serves to protect the birds against rat snake predation and the trees against insects and diseases. The purpose of this study was to evaluate resin flow in longleaf pine red-cockaded woodpecker cavity trees according to woodpecker utilization and stand position.

2. Methods

2.1. Study areas

Resin flow data were collected periodically during the growing seasons of 1987 through 1989 in red-cockaded woodpecker cavity tree clusters in the southern portion of the Angelina National Forest near Jasper, Texas. Yearly trips were made in late July or early August 1988 through 1991 to the Wakulla District of the Apalachicola National Forest in northern Florida.

The Angelina National Forest is about 45 km east of Lufkin, Texas in Angelina, Jasper, San Augustine, and Nacogdoches Counties. Its 61 988 ha are divided into northern and southern portions of roughly equal size by Sam Rayburn Reservoir. The southern portion of the Angelina National Forest is dominated by longleaf pine on Tehran (loamy, siliceous, thermic Grossarenic Paleudult) and Letney (loamy, siliceous, thermic Arenic Paleudult) series soils (USDA Soil Conservation Service, 1982). Hardwood basal area was low at less than 5 m^2 ha^{-1} (approximately 20 ft^2 $acre^{-1}$), and pine basal area ranged from 14 to 23 m^2 ha^{-1} (about 60–100 ft^2 $acre^{-1}$) in the study areas. Pine and hardwood midstory was generally moderate, but heavy in a few scattered areas (most data collection occurred before implementation of court-ordered midstory control). Understory was primarily bluestem grasses (*Andropogon* spp.) with a significant poison ivy (*Toxicodenron radicans*) component.

The Apalachicola National Forest is about 30 km south of Tallahassee, Florida. Soils in the study areas are primarily Leon (sandy, siliceous, thermic Aeric Haplaquod) and Talquin (sandy, siliceous, thermic Entic Haplaquod) series soils (USDA Forest Service, 1984). Overstory was entirely longleaf pine at basal areas ranging from 1 to 17 m^2 ha^{-1} (about 4–75 ft^2 $acre^{-1}$), averaging less than 14 m^2 ha^{-1} (about 60 ft^2 $acre^{-1}$). Midstory was sparse. Understory was dense, dominated by saw palmetto (*Serenoa repens*), runner oak (*Quercus pumila*), *Ilex* spp. and *Vaccinium* spp. Swamps were interspersed throughout the study areas.

2.2. Sample tree categories

Because sampling resin flow requires tree wounding, sample size in both locations was restricted to guard against the possibility of damaging a scarce resource. Total number of trees sampled was 40 in Texas and 96 in Florida (Table 1). Trees sampled within red-cockaded woodpecker stands were categorized as forest edge or forest interior trees. Edge trees were 20.1 m (66 ft.) or less from a significant forest opening (about 0.25 ha or greater) with little or no crown competition. Other trees were classified as interior trees.

Table 1
Sample size by location, stand position and cavity tree type

Cavity tree type	Texas		Florida	
	Edge	Interior	Edge	Interior
Active	8	4	21	12
Inactive	3	14	19	10
Control	3	8	19	15

In addition to stand position, the following red-cockaded woodpecker activity categories were assigned: trees currently used for nesting and roosting (Active); trees previously used for nesting and roosting but not currently used (Inactive); and trees having external characteristics similar to cavity trees but no evidence of red-cockaded woodpecker activity (Control).

Many of the sample trees could not be aged exactly with an increment borer because of heart rot (*Phellinus pini*). Tree ages in both study areas ranged (approximately) from 60 to 150 years, with most over 80 years old.

2.3. Tree measurements

Tree measurements taken in all study areas included height, height to lowest live branches and diameter at breast height (DBH). Live–crown ratio (LCR) was computed as the percentage of the total height of the tree covered with living branches.

2.4. Resin flow

Resin flow was measured by driving a 2.54 cm diameter circular arch punch (after Lorio and Sommers, 1986; Lorio et al., 1990) to the interface of xylem and phloem at approximately 1.4 m above ground on the bole. Holes were punched between 07:00 and 10:00 h to minimize effects of diurnal variation in resin flow (Nebeker et al., 1988). Triangular metal funnels were placed under the wounds to divert exuded resin into clear plastic graduated tubes. Resin flow was recorded 8 and 24 h after wounding. After 24 h readings were taken, funnels and tubes were removed and the bark plug replaced. Resin flow was measured on 13 different occasions from July 1987 through November 1989 in the Angelina National Forest, using the same trees each time. Resin flow in the Apalachicola National Forest was measured on four occasions, late July to early August, 1988 through 1991, also repeating measurements.

2.5. Analyses

Data from Texas and Florida were analyzed separately. Analysis of variance using a repeated measures design (because the same trees were used repeatedly for resin flow measurements) (SPSS Inc., 1983) with $\alpha = 0.05$, was used for each data set to test the null hypothesis of no differences among cavity tree types and stand position with respect to resin flow. Analysis of variance with $\alpha = 0.10$ (because of restricted sample size) was used in evaluating height, diameter at breast height, and live crown ratio of sample trees. The Least Significant Difference (LSD) method of comparing treatment means (Montgomery, 1984) was used when analyses of variance were statistically significant.

3. Results

3.1. Tree measurements

Tree height, diameter at breast height (DBH), and live–crown ratio (LCR) did not vary significantly among longleaf cavity tree categories in either the Angelina National Forest or the Apalachicola National Forest (Tables 2 and 3). Live crown ratio was significantly higher in all sample tree categories for edge trees in the Angelina National Forest (Table 3). Although no other edge versus interior comparisons of tree measurements were statistically significant, in general edge trees were slightly shorter than interior trees, but had larger DBH and LCR. Such differences are commonly associated with within-stand competition (Smith, 1986).

Table 2
Height (*HT*), diameter at breast height (DBH), and live–crown ratio (LCR) by stand position and red-cockaded woodpecker cavity tree type of longleaf pine sample trees in the southern Angelina National Forest, Texas. Values are means with standard deviations in parentheses

Stand type	Edge				Interior			
	N	*HT* (m)	DBH (cm)	LCR [a] (%)	*N*	*HT* (m)	DBH (cm)	LCR (%)
Active	8	22.4 (1.8)	51.6 (9.4)	48.4 (14.9)	4	25.4 (2.1)	46.2 (8.4)	31.5 (16.5)
Inactive	3	21.3 (0.3)	50.3 (2.5)	60.9 (6.7)	14	23.3 (2.0)	49.3 (7.1)	35.7 (6.8)
Control	3	25.6 (4.2)	45.5 (3.3)	41.6 (9.3)	8	25.1 (2.6)	49.5 (6.6)	33.8 (9.8)

[a] Edge live–crown ratio is significantly larger than interior ($\alpha = 0.10$).

Table 3
Height (*HT*), diameter at breast height (DBH), and live-crown ratio (LCR) by stand position and red-cockaded woodpecker cavity tree type of longleaf pine sample trees in the Wakulla District of the Apalachicola National Forest, Florida. Values are means with standard deviations in parentheses

Cavity tree type	Edge				Interior			
	N	*HT* (m)	DBH (cm)	LCR (%)	*N*	*HT* (m)	DBH (cm)	LCR (%)
Active	21	17.4 (3.4)	37.8 (4.8)	45.7 (10.4)	12	18.3 (4.7)	33.5 (4.3)	40.6 (8.8)
Inactive	19	16.5 (4.3)	35.8 (5.1)	43.8 (14.6)	10	19.3 (4.4)	36.3 (7.1)	37.6 (9.1)
Control	19	18.6 (3.3)	34.0 (4.6)	48.8 (8.2)	15	19.8 (3.0)	33.8 (5.6)	45.6 (13.1)

No differences in tree measurements were found among sample trees in the Apalachicola National Forest in Florida. Stands surveyed were much more open than Texas longleaf stands, with total basal area ranging from 8 to 16 m^2 ha^{-1} (30–60 ft^2 $acre^{-1}$) in most of the stand interiors. As a result, competition has been low with crown size and DBH only minimally affected. Site quality on the Aeric and Entic Haplaquods of the Florida study area is poorer than on the Arenic and Grossarenic Paleudults in Texas, and is reflected in the smaller Florida trees.

3.2. Resin flow

Resin flow in longleaf sample trees in the Angelina National Forest varied significantly among cavity tree types (Table 4), but the way in which it differed varied by stand position. Active red-cockaded woodpecker trees on or near forest edges had much higher resin flow at both 8 and 24 h than inactive or control trees. The reverse was true in stand interiors, with active red-cockaded woodpecker trees having lower resin flow than inactive or control trees. Interior active cavity trees exhibited about one-third of the resin flow of the edge active trees. Interior inactive cavity and control trees, however, had roughly twice the resin flow of corresponding edge sample trees.

Similar trends were seen in longleaf sample trees in the Wakulla district of the Apalachicola National Forest in Florida (Table 5) at both 8 and 24 h. Although no significant variation in resin flow was detected among edge trees, interior trees exhibited the same kind of variation among cavity tree types as interior longleaf trees in Texas (Table 4). Control trees had the highest resin flow among interior trees, followed by inactive trees, and then the active trees. As in Texas, active edge cavity trees had significantly higher resin flow than interior active trees. Inactive cavity trees on edges in Florida also had higher resin flow than interior inactive trees.

Table 4
Eight and 24 h resin flow in milliliters by position in stand and cavity-tree type, longleaf pines in southern Angelina National Forest, Texas. *N* refers to the number of trees sampled on 13 different occasions during 1987–1989. Means and standard deviations are from all sampling events

Cavity tree type	Edge trees			Interior trees		
	N	8 h (ml)	24 h (ml)	*N*	8 h (ml)	24 h (ml)
Active	8	6.8a * (5.2)	10.2a * (8.2)	4	2.3b (2.5)	3.6b (3.4)
Inactive	3	1.5b (1.8)	2.4c (2.8)	14	3.7b (2.8)	5.3b (4.0)
Control	3	2.5b (1.9)	4.1b (3.0)	8	5.5a (4.0)	9.0a (6.5)

Within columns, means followed by the same letter are not significantly different at $\alpha = 0.05$ (repeated measures analysis).
Asterisks indicate that the means of edge trees differ significantly from corresponding interior trees ($\alpha = 0.05$).

Table 5
Resin flow in milliliters at 8 and 24 h by cavity-tree type and stand position of longleaf pines in the Wakulla District of the Apalachicola National Forest, Florida. Sampling was carried out once a year in late July–early August 1988 through 1991. *N* refers to the number of trees sampled. Means and standard deviations are from all sampling events

Stand type	Edge trees			Interior trees		
	N	8 h (ml)	24 h (ml)	*N*	8 h (ml)	24 h (ml)
Active	21	4.7a * (3.9)	6.3a * (5.3)	12	3.2b (3.0)	4.2b (4.0)
Inactive	19	5.8a * (4.8)	8.4a * (7.9)	10	4.2ab (4.0)	6.2ab (6.4)
Control	19	5.8a (4.5)	7.9a (6.6)	15	5.4a (3.6)	8.0a (5.8)

Within columns, means followed by the same letter do not vary significantly at $\alpha = 0.05$ (repeated measures analysis).
Asterisks indicate that means of edge trees differ significantly from corresponding interior trees ($\alpha = 0.05$).

4. Discussion

4.1. Tree measurements

Tree vigor and stand health among southern pines have often been expressed in terms of radial increment or the ratio of radial increment to leaf area or sapwood radius (Waring and Pitman, 1980; Blanche et al., 1985; Matson et al., 1987). Vigorous trees, according to these indices, are presumed to have greater resistance to bark beetle attack. High vigor (relatively fast radial growth) is typically associated with thinning or low basal area. Diameter at breast height (DBH) and live–crown ratio (LCR) are considered to be good indicators competition effects on trees in a particular stand relative to other trees in that stand (Spurr and Barnes, 1980; Smith, 1986). Diameter growth is strongly controlled by stand density, with maximum growth at low density. Live crown ratio also is greatest when stand density is low.

Generally a live–crown ratio of 40% or greater is associated with satisfactory growth and vigor among southern pines, whereas live–crown ratio of less than 30% results in a reduction of vigor from which a tree may not recover, even after thinning (Smith, 1986). Such a reduction in vigor may increase susceptibility to death from insects, diseases and fire. Live–crown ratio of less than 40% among interior trees in the Angelina National Forest would indicate significant crown competition and generally lower vigor among these trees (Walker and Wiant, 1966; Smith, 1986). Among Florida sample trees, only interior inactive cavity trees had less than 40% average LCR.

Concepts of health and vigor developed in relatively young pine stands managed for timber production may not be entirely applicable in red-cockaded woodpecker clusters, however. Trees utilized by red-cockaded woodpeckers are generally the oldest in any given area, exhibit very slow radial increment even at low basal area and are often infected with red heart fungus (Conner and Rudolph, 1995a; Rudolph et al., 1995). Compared with fast-growing, thrifty pines in stands managed for optimum wood production, no red-cockaded woodpecker cavity trees would seem healthy. Among woodpecker cavity trees, the ability to produce a copious resin flow in the face of continual wounding by the woodpecker is beneficial both to the tree and the bird. Resin flow is therefore a more suitable measure of health and vigor among these trees than indices based on radial increment. Conditions resulting in rapid radial growth in younger stands may well result in higher resin flow even when height growth has ceased and radial growth has slowed because of age, however.

4.2. Resin flow

Trees in stand interiors typically experience more intense moisture competition because of root closure while crown closure results in smaller crowns and less light (Kramer and Kozlowski, 1979; Spurr and Barnes, 1980; Smith, 1986). Such competition increases with basal area in mature pine stands, and has been shown to influence resin flow (Mason, 1971). A pine tree's internal water status has also been shown to affect resin flow (Lorio et al., 1990). Red-cockaded woodpecker resin-well pecking and cavity excavation may trigger both a localized wound response and generalized allocation of photosynthates to resin production similar to that seen in turpentining (Walker and Wiant, 1966). Such woodpecker activity may stimulate a robust resin flow in trees under relatively low levels of competitive stress. Trees under high stress from moisture and crown competition may experience reduced flow with the added stress of resin well pecking. Trees under low stress with no woodpecker activity may also exhibit low resin flow when tested in the manner of this study because photosynthates are being allocated to other processes.

In the longleaf clusters of the southern Angelina National Forest in Texas, stand position and red-cockaded woodpecker activity status apparently interacted to influence resin flow (Table 3). Control trees and inactive red cockaded woodpecker trees on forest edges were under generally low stress as a combined result of low levels of moisture competition, relatively high light availability, high LCR and an absence of continual wounding. Resin production was generally low as a result. Once cavities are excavated by the woodpeckers, with associated daily wounding for resin flow, these types of trees are able to respond with high resin production in a manner similar (but not quite as dramatic) as turpentining (Walker and Wiant, 1966). Among interior trees, the inactive cavity trees and control trees were at a moderate level of stress, and had moderately higher

resin flow than corresponding edge trees even though their crowns were smaller (Table 1). Interior active trees were overly stressed by the added burden of red-cockaded woodpecker resin well pecking resulting in the lowest resin flow. Control trees in the interior, because of the absence of wounding, had the highest resin flow among interior trees.

Similar trends were seen among Apalachicola National Forest longleaf, but differences were not as dramatic as in Texas because of more open stand conditions (Table 4). Edge active trees had significantly higher resin flow than interior active trees. Also, control trees had the highest resin flow among interior trees, whereas active trees had the lowest.

Results of resin flow measurements conducted both in Texas and Florida strongly indicate that stand conditions favored by red-cockaded woodpeckers also are favorable for resin flow in active cavity trees. Such a relationship is apparent both among the longleaf sample trees in the Angelina National Forest in Texas and the Apalachicola National Forest in Florida. The balance in photosynthate allocation for resin production and other plant processes is apparently affected by red-cockaded woodpecker cavity excavation and resin-well pecking in conjunction with other stresses experienced by the trees. Even the relatively light competition among interior trees in the Apalachicola National Forest had a negative effect on resin flow when combined with the continual wounding associated with active red-cockaded woodpecker cavity trees. Woodpecker activity under such stand conditions may slow growth as has been observed with turpentine trees (Walker and Wiant, 1966), making the trees less competitive and more likely to die from insect and disease attack.

It is notable that the same relationship was seen among interior longleaf sample trees in Texas. In both cases, the interior active cavity trees had the lowest resin flow among interior trees (Tables 3 and 4). Also in both cases resin flow in edge active cavity trees was significantly higher than in corresponding interior trees. Edge active cavity trees should be more resistant to insects and diseases than interior trees as a result. They should provide greater protection against rat snake predation of eggs or birds in nest cavities as well. This may at least partially explain the red-cockaded woodpecker's observed tendency to excavate new cavities near forest openings even when interior midstory conditions and basal area should be optimal (Conner and Rudolph, 1995b). In both of our own study areas, roughly two-thirds of the active cavity trees were edge trees (Tables 1 and 2).

Bowman and Huh (1995) investigated resin flow in red-cockaded woodpecker stands in wet site slash pine in southwest Florida and in mesic site slash and longleaf pine in south central Florida. In both study areas they found that red-cockaded woodpecker cavity excavation was most frequent in trees with 'crown–bole ratios' (live–crown ratio) associated with maximum resin flow. These results, together with the results of our study and observations by Conner and O'Halloran (1987), strongly indicate that red-cockaded woodpeckers actively choose trees most likely to be high resin producers in a given area, and suggest that management to favor both natural cavity excavation and artificial cavity technology (Allen, 1991; Carter and Engstrom, 1995) should be site-specific in producing stand conditions likely to result in an adequate number of high resin producing trees. One generalization from the data is that edge trees make superior red-cockaded woodpecker cavity trees. Another is that optimum pine basal area in red-cockaded woodpecker cavity tree clusters dominated by longleaf pine may be lower than previously thought.

Disturbances in southern pine forests create a mosaic of patches in the larger forest matrix (Forman and Godron, 1986), with most of these patches being relatively small (Chrismer et al., 1995). Patches may be created by fire, lightning, bark beetles, storms, or management activity. Pine trees on the edge of patches typically expand both crown and roots into suddenly available adjacent patches (Spurr and Barnes, 1980; Smith, 1986; Forman and Godron, 1986). Light, water, and nutrients are made more abundant to the edge trees by disturbance. Enhanced ability of edge trees to produce resin when stressed may be a response to disturbance that makes the trees generally more resistant to future disturbance, particularly southern pine beetles and fire.

Results from this study imply that management to favor the red-cockaded woodpecker by increasing the health of the forest ecosystems in which they are native should mimic natural disturbances when practical, particularly in and immediately around wood-

pecker clusters. Judicious use of prescribed fire at natural frequencies and seasons is almost universally advocated by foresters and wildlife biologists (Krusac et al., 1995). Fire serves to keep stands open and favor pine regeneration, particularly longleaf pine. It helps to create a mosaic of plant communities and forest stand structures on the scale of a landscape, as fire does not burn uniformly over large areas (Spurr and Barnes, 1980).

Where red-cockaded woodpecker populations and habitat allow, a varied mosaic of relatively small clearings may be preferable to more uniform conditions. In addition to optimizing edge, these small patches, in concert with low to moderate interior basal area, would serve to guard against the spread of both southern pine beetle and damaging crown fires while assuring adequate regeneration.

A number of silvicultural options are available in southern pine management where red-cockaded woodpeckers must be considered. Walker (1995) provides a comprehensive treatment of the subject. Generally, management to favor the birds must provide both open stands and a sustained yield of mature trees for cavities. Silvicultural systems implied by the preceding discussion are group selection, small scale even-age management and two-age (irregular) variations of seedtree/shelterwood systems (Smith, 1986; Conner et al., 1991b). The concept of full stocking should be reconsidered where two-age and uneven-age management is being used primarily to benefit the red-cockaded woodpecker. Longleaf pine is very intolerant of shade, especially past the sapling stage. Too many trees may lead to suppression and poor stand health. Also, open grown trees are more windfirm (Spurr and Barnes, 1980). The purpose of management in and immediately around woodpecker clusters is not optimum wood production, but rather producing a particular kind of stand. Such management will play an important role in creating an insect, disease and fire resistant mosaic of forest ecosystems in red-cockaded woodpecker habitat management areas.

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