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Resin Flow in Loblolly and Shortleaf Pines Used by Red-Cockaded Woodpeckers

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Abstract

We measured resin flow in loblolly (*Pinus taeda* L.) and shortleaf (*Pinus echinata* Mill.) pines in stands used by red-cockaded woodpecker, *Picoides borealis* (Vieillot), in the Angelina and Davy Crockett National Forests in eastern Texas. We also measured resin flow in a mature loblolly pine stand not used by the woodpeckers. Resin flow varied by study area, species, and stand position. In woodpecker stands, pines experiencing low levels of competition seemed better able to tolerate the continual resin drainage associated with red-cockaded woodpecker resin well pecking. In the Angelina National Forest, all new cavity trees excavated during the study were on forest edges. In the non-woodpecker stand, edge trees had significantly better resin flow. These results indicate that the woodpeckers choose trees most likely to be good resin producers. They also indicate that silviculture in loblolly and shortleaf pine stands should favor edge and an open stand habit when red-cockaded woodpeckers are a major management consideration and that potential resin production can be measured in both cavity pines, and pines being considered for red-cockaded woodpecker introduction.

Keywords: Endangered species; Edge effect; National forests; Forest management

Introduction

Red-cockaded woodpeckers, federally listed as an endangered species [1], are unique among North American woodpeckers in that nesting and roosting cavities are excavated in living pine trees. Populations occur from Texas and Oklahoma, east to Florida and north to Virginia, but have declined or been extirpated because of habitat loss and fragmentation [2-5]. Population declines have been reversed in some areas with the use of artificial cavities, translocation of non-breeding birds from large populations to needy populations, aggressive hardwood control and basal area reduction [6-7].

Although longleaf pine (*Pinus palustris* Mill.) in relatively open stands is considered optimal habitat [8], shortleaf (*P. echinata* Mill.) and pitch pines (*P. rigida* Mill.) also are readily used [9,10]. In Texas the majority of red-cockaded woodpecker clusters (called colonies in older literature) occur in loblolly (*P. taeda*) and shortleaf pine stands [3,11].

Attack by southern pine beetles (*Dendroctonus frontalis* Zimmermann) is the primary cause of cavity tree mortality in Texas loblolly and shortleaf pine stands [12,13]. Trees favored by the woodpeckers tend to be the oldest in the stand, ranging from 60-130 years old among loblolly and shortleaf pines, and are characterized by slow radial growth, disintegrating crowns and red-heart rot (*Phellinus pini*) infection [3,14,15]. Such characteristics may place southern pine trees at high risk of attack by southern pine beetles and other phloem boring insects even when bark beetle populations are relatively low [16].

A potentially important area of interaction among red-cockaded woodpeckers, southern pine beetles and southern pines is the resin system of pine trees used as hosts by both the woodpeckers and beetles [17-20]. Red-cockaded woodpeckers peck small holes, called resin wells, around cavity entrances that create a cascade of pine resin on the bole around and beneath cavity entrances. This flow of fresh, sticky resin serves as a barrier against rat snakes, Elaphe sp., a major nest predator [21,22]

A primary pine tree defense against bark beetle attack is resin in preformed resin flow [12,16-20,23-29]. Bark beetles, particularly during endemic periods, are often unable to invade and kill southern pines with high resin flow [29]. Severe trauma, such as a lightning strike may temporarily immobilize resin production and flow and at the same time release host odors, particular alpha-pinene, an important component of pine resin [24]. Freshly excavated red-cockaded woodpecker cavity trees suffer disproportionate bark beetle attacks [12,13]. It is hypothesized that extensive resin-well pecking may cause the trees to resemble lightning struck trees under some circumstances [12] and may negatively affect resin production and flow in concert with other stresses [14,24].

Little research has focused on resin flow, an important defense in red-cockaded woodpecker cavity trees or mature to senescent trees in quasi old-growth stands. A better understanding of resin flow on the relative susceptibility of loblolly and shortleaf pine cavity trees can aid in developing more effective long-term management that incorporates red-cockaded woodpecker recovery into multiple use forestry. This study focuses on mature loblolly and shortleaf pine stands in Texas

National Forests that are used or may potentially be used by red-cockaded woodpeckers.

Methods

Study sites

Resin data from red-cockaded woodpecker clusters dominated by loblolly and shortleaf pine were collected in 1991-1993 from the Bannister Wildlife Management Area of the Angelina National Forest and from the Davy Crockett National Forest. Both forests are located in eastern Texas. Data were also collected in the Angelina National Forest from a mature loblolly stand with no evidence of red-cockaded woodpecker nesting, roosting or foraging.

The Angelina National Forest (31°15' N, 94°15' W, 50 m elevation MSL) is about 45 km east of Lufkin, Texas in Angelina, Jasper, Nacogdoches, and San Augustine counties. Its 62,423 ha are divided by Sam Rayburn reservoir into northern and southern portions of roughly equal size. The Bannister Wildlife Management Area is on the northern portion. Red-cockaded woodpecker clusters in this area are on shrink-swell soils of the Woodtell (fine, montmorilonitic, thermic, Vertic Hapludalf) and Lacerda (very-fine, montmorillonitic, thermic Aquentic Chromudert) series. Loblolly and shortleaf pines dominate the overstory, with a small overstory hardwood component. Substantial hardwood midstory and medium to high pine basal area (19-22 m^2 ha^{-1}) existed at the time of the study. Midstory has since been controlled and pine basal area reduced.

The Davy Crockett National Forest (31.30 N, 95.10 W, 95 m elevation MSL) has 65,599 ha, and is situated in Houston and Trinity counties about 45 km west of Lufkin, Texas. Moswell series soils (very-fine, montmorillonitic, thermic, Vertic Hapludalf) were predominant in the study areas. The forest canopy was composed of loblolly and shortleaf pines at basal areas ranging from 19 to 28 m^2 ha^{-1}. Hardwood midstory was substantial in all stands surveyed. As in the Angelina National Forest, pine basal area was subsequently reduced and hardwood midstory controlled in compliance with court-ordered management.

To study the edge effect on resion production without woodpecker influence, a non-woodpecker stand in the Angelina National Forest was also selected. It was dominated by loblolly pine at an interior basal area exceeding 24 m^2 ha^{-1}. A substantial mature white oak (*Quercus alba* L.) component also was present in the canopy at about 7 m^2 ha^{-1} basal area. Midstory was sparse because of low light. The understory consisted primarily of American beech (*Fagus grandifolia* Ehrh.) and Florida maple (*Acer barbatum* Michx.).

Sample trees

Trees in the red-cockaded woodpecker clusters used for sampling were categorized as forest edge or forest interior trees (Table 1). Edge trees were 20 m or closer to a significant forest opening (0.25 ha or greater) with little or no crown competition. Other trees were considered to be interior trees.

In addition to stand position, the following red-cockaded woodpecker activity categories were assigned: 1) active trees were currently used for nesting and roosting; 2) inactive trees were formerly used, but currently not used; and 3) control trees had no evidence of ever being used for woodpecker nesting or roosting, but did have external characteristics associated with cavity trees such as age, size, crown condition and evidence of heart rot. In the Angelina National Forest only, cavity trees excavated during the course of the study were added to those being samples and classified separately as new trees.

Cavity Tree	Edge Loblolly	Interior Loblolly	Edge Shortleaf	Interior Shortleaf
Angelina National Forest				
Active	5	4	5	4
Inactive	5	4	2	3
Control	4	9	2	3
New	3	0	3	0
Davy Crockett National Forest				
Active	2	0	4	5
Inactive	2	3	8	4
Control	4	2	6	9

Table 1: Sample sizes for resin sampling on stands with red-cockaded woodpecker activity in the Angelina and Davy Crockett National Forests in eastern Texas.

For the edge effect study without woodpecker influence, a total of 40 sample trees in the non-woodpecker stand in the Angelina National Forest were divided equally into two categories: edge trees were a distance of 20 m or less from a large, sharply delineated forest edge formed by a highway right-of-way and interior trees were 40 m or farther from this edge.

A number of sample trees in all of the study areas could not be aged with an increment borer because of heartwood decay. In the red-cockaded woodpecker stands, trees that could be aged ranged from 60 to 120 years, with most over 80. The trees that could be aged in the non-woodpecker area averaged 70 years.

Tree measurements

Tree measurements taken in all study areas included tree height (HT) measured with a clinometer, height to lowest live branches, crown width and diameter measured with a diameter tape at breast height (DBH, 1.4 m). Live-crown ratio (LCR) was computed as the percentage of the total height of the tree covered with live branches.

Resin flow

Resin flow was measured by driving a 2.54 cm diameter circular arch punch to the interface of xylem and phloem about 1.4 m above the ground on the bole. This is the depth of red-cockded woodpecker pecking to produce resin from resin ducts. Sampling holes were punched between 07:00 and 10:00 hrs to minimize diurnal variation effects [30]. Triangular metal funnels were placed under the wounds to divert exuded resin into clear plastic graduated tubes. Resin flow was recorded in ml 8 and 24 hours after wounding. After 24-four readings were completed, funnels and tubes were removed, and bark plugs replaced. At the non-woodpecker area, samples were taken at 1.4 m on all trees, and about 3.5 m on 10 edge and 10 interior trees.

Analyses

Data sets from each study area and each tree species were analyzed separately. For stands involving woodpecker activities, a series of analysis of variance (ANOVA) were performed to determine if there is any significant difference among the cavity tree types (active, inactive, control, and new) on HT, DBH, LCR, as well as resin production. These variables were also compared between the group of edge trees and interior trees.

For the non-woodpecker stands, the ANOVA was performed using a repeated measures approach because the same trees were used throughout the study for resin flow measurements [30]. ANOVA with α =0.05 was used to test the null hypothesis of no differences among cavity trees types and stand position with respect to resin flow, while α =0.10 was used to evaluate HT, DBH and LCR because of restricted sample size. The Least Significant Difference (LSD) method of means separation was used when the results of ANOVA were found statistically significant.

Results

Tree measurements

Among loblolly pines with woodpecker activities in the Angelina National Forest, active cavity trees in the forest interiors had significantly higher live-crown ratio than other interior trees (Table 2). Shortleaf pines in the forest interiors showed a similar relationship, with active and inactive woodpecker trees having higher live-crown ratios than the control trees (Tables 2 and 3).

Loblolly Pine								
	Edge				Interior			
Cavity Tree Type		HT	DBH	LCR		HT	DBH	LCR
		M	Cm	%		M	Cm	%
	N	(SD)	(SD)	(SD)	N	(SD)	(SD)	(SD)
Active	5	28	59.9	52.7	4	25.7	56.1	59.4a
		(2.3)	(4.8)	(7.6)		(2.0)	(6.8)	(9.9)
Inactive	5	28	58.9	54.8	4	30.5	54.4	44.4b
		(1.9)	(4.3)	(5.6)		(2.7)	(5.8)	(9.9)
Control	4	29	62.2	48.7	9	27.9	58.9	43.4b
		(3.3)	(10)	(10)		(2.6)	(4.6)	(7.2)
New	3	28	56.9	56.6	0			
		(3.1)	(9.1)	(9)				
Shortleaf Pine								
	Edge				Interior			
Cavity Tree Type		HT	DBH	LCR		HT	DBH	LCR
		M	Cm	%		M	Cm	%
	N	(SD)	(SD)	(SD)	N	(SD)	(SD)	(SD)
Active	5	27	45.7	43.8	4	27.6	53.3	49.4a
		(2.2)	(8.1)	(2.6)		(3.1)	(4.1)	(5.2)
Inactive	2	27	49.3	42.1	3	24.4	52.3	50.2a
		(2.6)	(3.3)	(2.4)		(4.8)	(13.0)	(4.2)
Control	2	26	45.7	53	3	26.8	51	43.1b
		(3.2)	(5.8)	(5.0)		(1.0)	(5.8)	(1.1)
New	3	31	53.6	48.2	0			
		(2.5)	(4.6)	(13.0)				
Nothing was significant unless annotation within a column where means followed by same letter do not differ significantly (α = 0.10).								

Table 2: Average height (HT), diameter at breast height (DBH) and live-crown ratio (LCR) of loblolly and shortleaf pine sample trees by cavity tree type and stand position, Angelina National Forest, Texas.

Loblolly Pine								
	Edge				Interior			
Cavity Tree Type		HT	DBH	LCR		HT	DBH	LCR
		M	Cm	%		M	Cm	%
	N	(SD)	(SD)	(SD)	N	(SD)	(SD)	(SD)
Active	2	28.2	58	37.8	0			
		(0.8)	(0.6)	(1.0)				
Inactive	2	29	64	40.5*	3	30	55.1	31.5
		(0.0)	(7.6)	(0.7)		-2.1	-17	-2.6
Control	4	26.9	58	49.0*	2	27	62	33.9
		(4.7)	(9.9)	(6.9)		(0.0)	(6.1)	(2.4)
Shortleaf Pine								
	Edge				Interior			
Cavity Tree Type		HT	DBH	LCR		HT	DBH	LCR
		M	Cm	%		M	Cm	%
	N	(SD)	(SD)	(SD)	N	(SD)	(SD)	(SD)
Active	4	26.6	50	46.5*	5	25	43.2	34
		(2.7)	(8.1)	(6.9)		(3.0)	(6.1)	(5.5)
Inactive	8	26.4	52	36.6*	4	28	47	29.2
		(1.3)	(8.9)	(7.9)		(3.0)	(6.8)	(6.9)
Control	6	25.2	47	40.1*	9	27	51	35.9
		(2.0)	(4.3)	(7.8)		(2.6)	(4.3)	(11.0)
Nothing was significant expect the annotation * where the mean of edge trees significantly differs from that of corresponding interior trees (α=0.10).								

Table 3: Average height (HT), diameter at breast height (DBH) and live-crown ratio (LCR) of loblolly and shortleaf pine sample trees by cavity tree type and stand position, Davy Crockett National Forest, Texas.

Among the Davy Crockett National Forest sample trees, edge trees of both species had significantly larger crowns (P<0.10) than corresponding interior trees (Table 3).

No other significant differences were found. It is notable, however, that all new cavity trees excavated by woodpeckers during the course of this investigation were on forest edges of the Angelina National Forest and had relatively high live-crown ratios (Table 2). These new cavity tree also exhibited high initial resin flow rates (Table 4).

Loblolly Pine						
	Edge			Interior		
Cavity Tree Type	N	8 hours (SD)	24 hours (SD)	N	8 hours (SD)	24 hours (SD)
Active	5	2.2b*	3.2b*	4	5.3a	7.2a
		(1.9)	(3.0)		(4.7)	(6.9)
Inactive	5	5.7a*	7.8a*	4	3.1b	4.2b
		(6.6)	(8.5)		(2.9)	(4.3)
Control	4	2.3b*	3.5b*	9	3.6b	5.3ab
		(2.7)	(3.8)		(3.4)	(4.9)
New	3	4.7a	7.6a	0		
		(3.4)	(6.1)			
Shortleaf Pine						
	Edge			Interior		
Cavity Tree Type	N	8 hours (SD)	24 hours (SD)	N	8 hours (SD)	24 hours (SD)
Active	5	2.9b	4.4b	4	3.3b	4.5b
		(2.7)	(4.0)		(3.1)	(4.3)
Inactive	2	3.1b*	5.3b*	3	6.4a	8.7a
		(3.0)	(4.9)		(6.3)	(8.8)
Control	2	4.9b	8.2ab	3	3.6b	6.1ab
		(4.9)	(9.1)		(3.6)	(6.3)
New	3	7.9a	11.4a	0		
		(5.0)	(7.5)			

*Edge mean significantly differs from corresponding interior mean (α = 0.05). Within columns, means followed by same letter do not differ significantly (α = 0.05).

Table 4: Average eight and twenty-four-hour resin flow (ml) for loblolly and shortleaf pine sample trees in northern Angelina National Forest, 1986–1989.

Resin yield

Resin flow varied by forest, pine species, cavity tree type and stand position. Among loblolly pines in the Angelina National Forest, new cavity trees and inactive trees had the highest resin flow on the edges, whereas active trees were the highest resin producers among interior trees (Table 4). Edge active and control trees had lower resin flow than corresponding interior trees, but inactive edge trees had significantly higher resin flow than the corresponding interior trees.

Among the Angelina National Forest shortleaf pines, the only similarity was that new trees also were among the highest resin producers (Table 4). The only significant edge versus interior comparison was with inactive cavity trees, where the interior sample trees exhibited higher resin flow.

Inactive trees in the forest interior had higher resin flow than control trees among loblolly pines in the Davy Crockett National Forest (Table 5).

Loblolly Pine						
	Edge			Interior		
Cavity Tree Type	N	8 hours (SD)	24 hours (SD)	N	8 hours (SD)	24 hours (SD)
Active	2	8.9a	13.3a	0		
		(5.3)	(9.2)			
Inactive	2	8.6a*	15.1a*	3	5.2a	7.9a
		(5.2)	(10.2)		(3.8)	(5.6)
Control	4	5.7a	9.5a*	2	3.5a	4.6b
		(5.6)	(9.7)		(3.5)	(4.6)
Shortleaf Pine						
	Edge			Interior		
Cavity Tree Type	N	8 hours (SD)	24 hours (SD)	N	8 hours (SD)	24 hours (SD)
Active	4	2.4ab*	3.6b*	5	4.9a	7.9ab
		(3.3)	(4.7)		(5.1)	(8.5)
Inactive	8	1.8b	2.5b	4	2.8b	5.3b
		(2.6)	(3.5)		(3.2)	(4.9)
Control	6	3.5a	6.3a	9	4.7a	8.0a
		(2.7)	(5.2)		(4.4)	(7.1)

*Edge mean significantly differs from corresponding interior mean (α =0.05). Within columns, means followed by same letter do not differ significantly (α =0.05).

Table 5: Average eight and twenty-four-hour resin flow (ml) for loblolly and shortleaf pine sample trees in the Davy Crockett National Forest, 1989-1990.

Inactive edge trees had higher resin flow than inactive interior cavity trees. The only other significant comparison was for control trees at 24 hours, with edge trees having the higher resin flow. Highest resin flow among shortleaf pines in the Davy Crockett National Forest was observed in interior active and control trees (Table 5). Interior active trees had significantly higher resin flow than edge active trees.

Edge effect

Forty trees without woodpecker activities were selected and categorized into edge tree or interior tree in order to determine edge effect influenced soley by forestry practices. No differences in any tree measurements were seen in this non-woodpecker stand in the Angelina National Forest (Table 6).

For resin flow, edge trees consistently produced significantly higher resin than interior trees at both 1.4 and 3-5 m, with the single exception of 1.4 m results on September 18, 1992 (Tables 7). When multiple date data were combined, it reconfirmed that edge trees produced more resin than interior trees significantly (Table 8).

Tree Variable	N	Edge (SD)	N	Interior (SD)
HT (m)	20	32.3 (3.0)	20	31.1 (1.8)
DBH (cm)	20	56.9 (12.2)	20	53.1 (9.1)
LCR (%)	20	24.6 (5.4)	20	26.1 (5.4)

Table 6: Average Height (HT), diameter at breast height (DBH) and live-crown ratio (LCR) of loblolly pine sample trees by stand position in non-red-cockaded woodpecker stand, Angelina National Forest, Texas.

			Eight Hours		Twenty-four Hours	
Sampling Date	Sample Height	N	Edge Mean (SD)	Interior Mean (SD)	Edge Mean (SD)	Interior Mean (SD)
10/26/1991	1.4 m	20/19	4.0 (2.5)	2.5 (2.1)	6.6 (3.5)	4.2 (3.0)
	3-5 m	10-Sep	4.1(3.1)	2.0 (3.0)	6.5 (5.4)	3.0 (4.0)
02-07-1992	1.4 m	20	1.3 (1.4)	0.5 (0.8)	2.9 (3.0)	1.2 (1.9)
	3-5 m	10	2.2 (1.8)	0.4 (1.0)	4.2 (3.5)	1.0 (2.2)
3/13/1992	1.4 m	20	2.7 (1.8)	1.5 (1.7)	4.4 (3.3)	2.6 (3.2)
	3-5 m	10	3.6 (2.0)	1.6 (1.7)	5.8 (3.3)	2.7 (3.1)
04-10-1992	1.4 m	20	5.3 (3.9)	3.9 (3.6)	7.2 (5.8)	5.2 (4.8)
	3-5 m	10	7.5 (3.1)	3.6 (3.2)	8.5 (4.0)	5.2 (4.6)
06-02-1992	1.4 m	20	6.1 (4.5)	4.8 (6.1)	8.4 (6.4)	6.9 (7.9)
	3-5 m	10	8.3 (5.8)	3.0 (5.4)	12.7 (11.4)	4.1 (6.6)
6/30/1992	1.4 m	20	8.0 (4.8)	5.7 (6.7)	9.9 (6.1)	7.5 (9.6)
	3-5 m	10	7.5 (4.3)	4.0 (3.4)	8.4 (5.3)	5.4 (4.2)
08-11-1992	1.4 m	20	9.4 (6.2)	6.8 (9.7)	11.5 (7.9)	8.6 (12.1)
	3-5 m	10	11.5 (7.7)	5.5 (7.1)	15.4 (11.3)	6.8 (8.0)
9/18/1992	1.4 m	20	7.1 (4.3)	6.7 (8.0)	10.0 (5.8)	9.9 (11.3)
	3-5 m	10	7.2 (5.5)	5.3 (6.2)	9.5 (3.5)	8.1 (8.5)
11/13/1992	1.4 m	20	3.0 (2.6)	1.8 (2.8)	5.1 (4.5)	3.5 (5.6)
	3-5 m	10	3.1 (1.9)	1.6 (2.4)	5.4 (3.7)	2.7 (4.0)
2/19/1993	1.4 m	20	0.6 (0.7)	0.3 (0.4)	2.5 (2.6)	1.2 (1.3)
	3-5 m	10	1.4 (1.1)	0.3 (0.5)	4.4 (3.2)	2.0 (2.6)

All edge results significantly higher than corresponding interior results (α=0.05) at both sampling heights at 8 and 24 hours except 1.4 m results on September 18, 1992.

N is for each stand position, 40 trees total.

Table 7: Average eight- and twenty-four-hour resin flow (ml) by date, stand position, and height of sampling on tree bole, Angelina National Forest non-red-cockaded woodpecker stand dominated by loblolly pine, 60 to 80 year old, October 1991 to February 1993.

			Eight Hours	Twenty-four Hours
Stand Position	**Sample Height**	**Total Samples**	**Mean (SD)**	**Mean (SD)**
Edge	1.4 m	200	4.8 (4.5)a	6.9 (5.8)a
	3-5 m	98	5.6 (5.0)a	8.1 (7.0)a
Interior	1.4 m	199	3.4 (5.6)b	5.0 (7.5)b
	3-5 m	98	2.8 (4.2)b	4.1 (5.4)b
Within columns, means followed by same letter do not differ (a=0.05).				

Table 8: Average eight- and twenty-four-hour resin flow (ml), all sampling dates combined, by stand position and sample height, sample taken for non-red-cockaded woodpecker area in the Angelina National Forest, October 1991 to February 1993.

Discussion

A copious resin flow, particularly during the breeding season, in the face of environmental stresses, including resin-well pecking, may be a viable indicator of health for red-cockaded woodpecker cavity trees [19,20,28]. Red-cockaded woodpeckers select cavity trees if there is sufficient resin production from resin well pecking [11]. This may be particularly true in shortleaf and loblolly pine stands, species that usually exhibit lower resin flow than longleaf pine [19] and are more susceptible to bark beetle mortality [12,13,28]. Theoretically, trees with large crowns should be better able to support a larger volume of sustained resin flow than trees with smaller crowns, and thinning has been associated with higher resin flow in younger trees [31,32], but this was not true in our study.

In the Davy Crockett National Forest, interior shortleaf pine trees had significantly smaller crowns than corresponding edge trees, but active and inactive cavity trees had significantly higher resin flow. Loblolly pines in the same forest also had larger crowns on edges, but these also had higher resin flow. Crown size did not vary by stand position in the Angelina National Forest, but resin flow did. Among loblolly pines, active and control edge trees had lower resin flow. Interior active loblolly pines had both larger crowns and higher resin flow. No such trends were seen in the shortleaf pine trees. New cavities established during the study were on forest edges, had live-crown ratios averaging above 45 percent and had the highest mean resin flow during the study. These observations indicate that red-cockaded woodpeckers actively choose trees that are likely to be high resin producers in a given stand [11,15,20,22].

Some of the variation in resin flow may be explained by the growth-differentiation balance [33,34] as a generalized way of understanding and predicting plant development and behavior. According to this concept, growth predominates when all internal and external factors are favorable. Water availability is seen as crucial in the growth-differentiation balance [33,34]. When water is slightly limiting but other factors such as light, temperature and photosynthate supply are not, then differentiation is favored.

Red-cockaded woodpeckers are known to select pines for cavity trees that yield high volumes of resin [11]. Generally live-crown ratio of 40 percent or greater is associated with satisfactory growth and vigor, whereas live-crown ratio of less than 30 percent results in a loss of vigor from which trees may not recover even after thinning [35]. Such a reduction of vigor may lead to increased risk of death from insects, diseases and fire.

Resin flow in all study areas varied by tree species, stand position and red-cockaded woodpecker activity. Seasonal factors such as soil moisture deficits, photoperiod and cold-hardening; competitive stresses related to stand position; and a response to continual wounding by the woodpeckers are environmental factors known to influence resin flow [36] that may have influenced resin flow in this study. Genetic factors in loblolly pine act within individual pines to increase (or decrease) growth. In our study we found high (or low) resin producers remained in these categories [37].

In the non red-cockaded woodpecker study area, a more rigorous sampling of mature loblolly pines were categorized as edge or interior. Edge trees in the non-woodpecker stand clearly had significantly higher resin flow than the interior trees where stand position was clearly defined and was the only difference between the two tree categories. Especially interesting was the magnitude of sample differences 3 to 5 m up the bole from April through August 1992, a time for red-cockaded woodpecker nesting and fledging and when southern pine beetles may be particularly active. These substantial differences at 3 to 5 m up the bole (where most southern pine beetle attacks are initiated) indicate that the edge trees in this case are more beetle resistant [38]. These trees also would be superior from the perspective of the red-cockaded woodpeckers.

The added stress associated with red-cockaded woodpecker resin well maintenance may trigger additional resin flow, or ultimately result in lowered resin flow if moisture availability, photosynthetic surface, light availability and carbon demand created by continual resin drainage becomes non-sustainable. Edge trees typically have more resources available, enabling a sustained and higher resin flow for a greater period of time, with increased wounding having significantly higher resin flow in loblolly pine [37,38]. Resin well pecking in relatively dense stands may result in a diminished ability of the tree to resist insect attack and disease spread [13,23,37]. Loblolly pine responded with an increase in resin flow after mechanical wounding. This increased resin flow reflects translocation of resin and also an induced response of resin synthesis [32]. Newly excavated red-cockaded woodpecker cavity trees in our study exhibited higher resin flows on stand edges indicating an initial effect on resin allocation. These results may partially explain the red-cockaded woodpecker's observed preference for edge trees and low basal area. Resin well pecking in relatively dense stands may result in a diminished ability of the tree to resist insect attack and disease spread [12,26,28].

In all of the study areas, the gross seasonal trends in resin flow were exemplified by the non-woodpecker area. Resin flow at the beginning of the year is at a seasonal low. It begins to rise notably at about mid-March reaching seasonal highs in July and August. After September it declined quickly to seasonal lows. Relationships among sample tree categories tended to remain the same for each sampling period.

Management to favor red-cockaded woodpeckers in loblolly and shortleaf pine stands should be site specific, and produce and maintain an adequate number of high resin producing trees. Potential and active red-cockaded woodpecker trees can be sampled for resin production following the sampling methods used in this study. The sampling can follow the projected resin production over the season and recommendations made for resin status of each tree for potential for both future status of the tree and for installation of artificial cavities. Maintaining an open park-like stand, or providing some edge habitat should enhance resin production in pines potentially used by red-cockaded woodpeckers. Long-term management should emphasize windfirmness and a relatively open stand habit early in a pine stand's history. Silvicultural options for red-cockaded woodpecker management may include irregular seed-tree regeneration that may help to create two-age stand structures similar to some of the study areas [39,40]. Attempts at uneven-age management also must take the species' lack of shade tolerance past the sapling stage into account as well.

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References

1. US Department of the Interior, Fish and Wildlife Service, Washington, DC (1970) Listing of red-cockaded woodpecker as endangered. Federal Register 13 October 1970 35: 16047.
2. Conner RN, Rudolph DC, Bonner LH (1995) Red-cockaded woodpecker population trends and management on Texas national forests. Journal of Field Ornithology 66: 140-151.
3. Conner RN, Saenz D, Rudolph DC (2006) Population trends of red-cockaded woodpeckers in Texas. Bulletin Texas Ornithological Society 39: 42-48.
4. Conner RN, Rudolph DC (1991) Forest habitat loss, fragmentation, and red-cockaded woodpecker populations. Wilson Bulletin 103: 446-457.
5. James FC (1995) The status of the red-cockaded woodpecker in 1990 and the prospect for recovery. In: Kulhavy DL, Hooper RG, Costa R (eds), Red-cockaded Woodpecker: Recovery, Ecology and Management, Center for Applied Studies Publication, College of Forestry, Stephen F. Austin State University, Nacogdoches, Texas, USA, pp: 439-451.
6. Allen DH (1991) An insert technique for constructing artificial red-cockaded woodpecker cavities. USDA Forest Service General Technical Report SE-73, Southeastern Forest Experiment Station, Asheville, North Carolina, USA.
7. Carter JH, Engstrom RT (1995) Use of artificial cavities for red-cockaded woodpecker mitigation: two studies. In: Kulhavy DL, Hooper RG, Costa R (eds), Red-cockaded Woodpecker: Recovery, Ecology and Management, Center for Applied Studies Publication, College of Forestry, Stephen F. Austin State University, Nacogdoches, Texas, USA. pp: 372-379.
8. Conner RN, Rudolph DC (1995) Excavation dynamics and use patterns of red-cockaded woodpecker cavities: relationships with cooperative breeding. In: Kulhavy DL, Hooper RG, Costa R (eds), Red-cockaded Woodpecker: Recovery, Ecology and Management, Center for Applied Studies Publication, College of Forestry, Stephen F. Austin State University, Nacogdoches, Texas, USA, pp: 342-352.
9. US Department of the Interior, Fish and Wildlife Service, Washington, DC (1985) Red-cockaded woodpecker recovery plan. US Fish and Wildlife Service, Atlanta, GA, p: 88.
10. Hooper RG, Robinson Jr. AF, Jackson J (1980) The red-cockaded woodpecker: notes on life history and management. USDA Forest Service, General Report SA-GR 9, Southeastern Area, Atlanta, GA, USA p: 8.
11. Conner RN, Saenz D, Rudolph DC, Ross WG, Kulhavy DL (1998) Red-cockaded woodpecker nest cavity selection: relationships with cavity age and resin production. Auk 115: 447-454.
12. Conner RN, Rudolph DC, Kulhavy DL, Snow AE (1991) Causes of mortality of red-cockaded woodpecker cavity trees. Journal of Wildlife Management 55: 531-537.
13. Rudolph DC, Conner RN (1995) The impact of southern pine beetle induced mortality on red-cockaded woodpecker cavity trees. In: Kulhavy DL, Hooper RG, Costa R (eds). Red-cockaded Woodpecker: Recovery, Ecology and Management, Center for Applied Studies Publication, College of Forestry, Stephen F. Austin State University, Nacogdoches, Texas, USA. pp: 208-213.
14. Conner RN, Locke BA (1982) Fungi and red-cockaded woodpecker cavity trees. Wilson Bulletin 94: 64-70.
15. Conner RN, O'Halloran KA (1987) Cavity tree selection by red-cockaded woodpeckers as related to growth dynamics of southern pines. Wilson Bulletin 99: 398-412.
16. Mitchell JH, Kulhavy DL, Conner RN, Bryant CM (1991) Susceptibility of red-cockaded woodpecker colony areas to southern pine beetle infestations in East Texas. Southern Journal of Applied Forestry 15: 158-162.
17. Bowman R, Huh C (1995) Tree characteristics, resin flow, and heartwood rot in pines (*Pinus palustris*, Pinus eliottii) with respect to red-cockaded woodpecker excavation in two hydrologically distinct Florida flatwood communities. In: Kulhavy DL, Hooper RG, Costa R (eds). Red-cockaded Woodpecker: Recovery, Ecology and Management, Center for Applied Studies Publication, College of Forestry, Stephen F. Austin State University, Nacogdoches, Texas, USA, pp. 416-426.
18. Ross WG, Kulhavy DL, Conner RN (1995) Vulnerability and resistance of red-cockaded woodpecker cavity trees to southern pine beetle in Texas. In: Kulhavy DL, Hooper RG, Costa R (eds), Red-cockaded Woodpecker: Recovery, Ecology and Management, Center for Applied Studies Publication, College of Forestry, Stephen F. Austin State University, Nacogdoches, Texas, USA, pp. 404-414.
19. Ross WG, Kulhavy DL, Conner RN (1997) Stand conditions and tree characteristics affect quality of longleaf pine for red-cockaded woodpecker cavity trees. Forest Ecology and Management 91: 145-154.
20. Kulhavy DL, Rozelle KB, Ross WG, Unger DR, Conner RN (2015) Resin production in natural and artificial red-cockaded woodpecker cavity trees. Open Journal of Forestry 5: 364-374.
21. Rudolph DC, Kyle H, Conner RN (1990) Red-cockaded woodpeckers versus rat snakes: the effectiveness of the resin barrier. Wilson Bulletin 102: 14-22.
22. Rudolph DC, Conner RN, Turner J (1990) Competition for red-cockaded woodpecker roost and nest cavities: effects of resin, age and entrance diameter. Wilson Bulletin 102: 23-36.
23. Hodges JD, Elam WW, Watson WF, Nebeker TE (1979) Oleoresin characteristics and susceptibility of four southern pine beetle (Coleoptera: Scolytidae) attacks. Canadian Entomologist 111: 889-896.
24. Paine TD, Stephen FM, Cates RG (1985) Induced defenses against Dendroctonus frontalis and associated fungi: variation in loblolly pine resistance. In: Branham SJ, Thatcher RC (eds.), Integrated Pest Management Research Symposium: The Proceedings. USDA Forest Service General Technical Report SO-56, New Orleans, Louisiana, USA, pp. 167-169.
25. Conner RN, Rudolph DC, Saenz D, Coulson RN (1997) The red-cockaded woodpecker's role in the southern pine ecosystem, population trends and relationships with southern pine beetles. Texas, Journal of Science Supplement 49: 139-154.
26. Sullivan BT (2011) Southern pine beetle behavior and semiochemistry. In Coulson RN, Klepzig KD (eds.), Southern Pine Beetle II, USDA Forest Service, General Technical Report SRS-140,Southern Research Station, Ashville, North Carolina, USA. pp. 25-50.
27. Lorio PL Jr, Sommers RA, Blanche CA, Hodges JD, Nebeker TE (1990) Modeling pine resistance to bark beetles based on growth and differentiation balance principles. In: Dixon RK, Meldahl RS, Ruark GA, Warren WG (eds.), Process Modeling of Forest Growth Responses to Environmental Stress, Timber Press, Portland, Oregon, USA. pp. 402-409.
28. Conner RN, Saenz D, Rudolph DC, Ross WG, Kulhavy DL, et al. (2001) Does red-cockaded woodpecker excavation of resin wells increase risk of bark beetle infestation of cavity trees? Auk 118: 219-224.

29. Nebeker TE, Hodges JD, Honea CR, Blanche CA (1998) Preformed defensive system in loblolly pine: variability and impact on management practices. In: Payne TL, Saarenmaa J (eds), Proceedings: Control of Scolytid Bark Beetles, Virginia Polytechnic and State University, Blacksburg, VA, USA, pp. 147-162.

30. SPSS Inc. (1983) SPSSx User's guide. McGraw-Hill New York, New York, USA, p: 806.

31. Ruel JJ, Ayers MP, Lorio PL Jr (1998) Loblolly pine responds to mechanical wounding with increased resin flow. Canadian Journal of Forest Research 28: 596-602.

32. Mason RR (1971) Soil moisture and stand density affect oleoresin exudation flow in a loblolly pine plantation. Forest Science 17: 170-17740.

33. Lorio PL Jr (1985) Growth-differentiation balance: a basis for understanding southern pine beetle-tree interactions. Forest Ecology and Management 14: 259-273.

34. Lorio PL Jr, Sommers RA (1986) Evidence of competition for photosynthates between growth processes and oleoresin synthesis in Pinus taeda L. Tree Physiology 2: 301-306.

35. Spurr SH, Barnes BV (1980) Forest Ecology, 3rd edition, John Wiley, New York, USA, p: 687.

36. Blanche CA, Lorio PL Jr., Sommers RA, Hodges JD, Nebeker TE (1992) Seasonal cambial growth and development of loblolly pine: xylem formation, inner bark chemistry, resin ducts and resin flow. Forest Ecology and Management 49: 151-165.

37. Roberds JH, Strom BL, Hain FP, Gwaze DP, McKeand SE, et al. (2003) Estimates of genetic parameters for oleoresin and growth traits in juvenile loblolly pine. Canadian Journal of Forest Research 33: 2469-2476.

38. Tisdale RA, Nebeker TE (1992) Resin flow as a function of height along the bole of loblolly pine. Canadian Journal of Botany 70: 2509-2511.

39. Conner RN, Snow AE, O'Halloran KA (1991) Red-cockaded woodpecker use of seedtree/shelterwood cuts in eastern Texas. Wildlife Society Bulletin 19: 67-73.

40. Walker JS (1995) Potential red-cockaded woodpecker habitat on a sustained basis under different silvicultural systems. In Kulhavy DL, Hooper RG, Costa R (eds). Red-cockaded Woodpecker: Recovery, Ecology and Management, Center for Applied Studies Publication, College of Forestry, Stephen F. Austin State University, Nacogdoches, Texas, USA, pp. 112-130.