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Snag dynamics and cavity occurrence in the South Carolina Piedmont

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Abstract

Standing dead trees, or snags, are natural components of forest stands and are important habitats for many wildlife species. We examined snag dynamics from 1982–1990 on 140 0.1 ha plots in the upper Piedmont of South Carolina. Plots were established in 10 stand type–age class combinations. Mean snag density was 28.4 snags/ha and mean snag diameter (DBH) and height were 20.3 cm and 9.9 m, respectively. Highest snag densities occurred in hardwood stand types; pine plantations had lower ($p \leq 0.05$) snag density than all other types. Within a particular stand type, snag densities, recruitment rates, and loss rates generally were lowest in the oldest age classes. Intermediate age classes of all stand types had higher snag densities and snag turnover rates than younger or older stands within that type. Young pine plantations had the lowest recruitment rate ($\bar{x}=1.79$ snags/ha/year) and old pine plantations had the lowest loss rate ($\bar{x}=1.59$ snags/ha/year) of all the stand type–age class combinations. Although twenty species of snags were observed, five species/species groups, shortleaf pine (*Pinus echinata*), red oaks (*Quercus* spp.), white oaks (*Quercus* spp.), loblolly pine (*P. taeda*), and yellow poplar (*Liriodendron tulipifera*), occurred most frequently. Snag DBH and cavities/snag were not significantly correlated. Stage of decay for cavity and noncavity snags ($r=0.97$ and 0.83, respectively; $p \leq 0.05$) and number of cavities/snag ($r=0.78$) increased with year since snag recruitment. Ten snag species contained cavities ($\bar{x}=0.1$ cavities/snag), but shortleaf pine accounted for 56% of the cavity years observed ($\bar{x}=0.18$ cavities/snag). Three other softwood species also contained equal to or above average numbers of cavities/snag. Approximately 30% of all snags fell within two years of recruitment, 55% within three years, and 95% within six years. Snag longevity was independent of diameter class ($p=0.67$). Hardwood snags, especially those in upland hardwood stands, appeared to persist longer than pine snags. As pine plantations managed on short rotations (<25 years) and older-aged stands (>50 years) of all types may not provide abundant snags in the South Carolina Piedmont, the potential for wildlife habitat might be enhanced if older, larger diameter trees, especially softwood species, are retained or designated as snag replacements.

Keywords: Forest management; Snags; Wildlife cavities; Wildlife management

1. Introduction

Standing dead trees, or snags, are natural components of forest environments resulting primarily from injury, fire, lightning, suppression, insects, disease, or weather extremes (Mannan et al., 1980; Raphael and

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White, 1984). In the southeastern United States, 45 species of birds require snags, cavities, or both (Hamel, 1992). Birds use snags as roosting, foraging, drumming, and perching sites, and the cavities associated with snags provide nesting sites during the breeding season and roosting sites throughout the year (Lanham and Guynn, 1996). Snags provide roosting sites for bats (Hamilton and Whitaker, 1979), and nesting, roosting, and foraging sites for other mammals (Loeb, 1996). Decaying snags also are an important source of downed woody debris (Graham, 1925; Thomas et al., 1979; Harmon et al., 1986), providing cover and foraging habitats for amphibians and reptiles (Aubry et al., 1988; Whiles and Grubaugh, 1993), small mammals (Hamilton and Whitaker, 1979), and invertebrates (Seastedt et al., 1989). Use of snags by different wildlife species and population densities of cavity nesters change with snag density, size, species, and degree of decay (Bull, 1983; Raphael and White, 1984; Runde and Capen, 1987).

In spite of the acknowledged value of snags to wildlife, resource managers only recently have attempted to quantify snag characteristics and dynamics in managed forests of the southeastern United States (Harlow and Guynn, 1983; McComb et al., 1986; Cain, 1996). Density of snags is a function of stand type and age, intensity of forest management, climate, and occurrence of natural disturbances. Clearcuts, improvement thinnings, short harvest rotations, removal of dead trees to reduce fire and safety hazards, and conversion of hardwood stands to intensively managed pine plantations normally decrease the availability and suitability of snags for wildlife (Mannan et al., 1980; McComb et al., 1986; Runde and Capen, 1987). As snags are more abundant in unmanaged stands (Cline et al., 1980), the typical long-term impact of intensive forest management is decreased snag availability (McComb et al., 1986).

In the southeastern United States, intensive timber management is expanding rapidly, but knowledge of snag resources and of management effects on snag-dependent wildlife is inadequate (Harlow and Guynn, 1983; Peitz et al., 1997). Existing information about the determinants of snag characteristics primarily comes from short-term data sets ($\leq$3 years). Longer studies (>5 years) are needed to better understand processes such as snag recruitment, decay and loss. Management of southern forests for both timber and wildlife production will require understanding the determinants of snag characteristics and dynamics as well as the factors that affect snag use by wildlife (McComb et al., 1986; Land et al., 1989). The objectives of our study were to:

1. quantify densities and characteristics of snags across a range of stand types and ages within the Piedmont of South Carolina;
2. monitor snag dynamics (e.g. recruitment and decay) in these stands over an extended period; and
3. determine the distribution of wildlife cavities in relation to snag characteristics and dynamics.

2. Materials and methods

2.1. Study area

We conducted the study on the Clemson University Experimental Forest (CUEF), in the upper Piedmont of South Carolina, between December 1982 and January 1990. The 7024 ha tract largely consisted of severely eroded agricultural old-fields when acquired by the university in 1934, but currently is dominated by regenerated forest typical of those silviculturally managed in the southeastern Piedmont, including loblolly pine plantation, mixed pine-hardwood, upland hardwood, and cove hardwood. Shortleaf pine (*Pinus echinata*), sweetgum (*Liquidambar styraciflua*), upland oaks (*Quercus* spp.), and hickories (*Carya* spp.) dominate in the mixed pine-hardwood and upland hardwood types. Cove hardwood stands are comprised mainly of yellow poplar (*Liriodendron tulipifera*) and mesophytic oaks. Hardwood stands, mostly in steeper drainages, that were not converted for agriculture had been high-graded by the 1930s. Since, these hardwood stands have naturally regenerated. Existing pine plantations primarily are the result of clearcutting of regenerated old-field sites and subsequent replanting into pine. Some trees were left standing, but active maintenance of residual snags or large-diameter trees historically was not a management objective on the CUEF.

Elevations range from 214 to 305 m (National Oceanic and Atmospheric Administration, 1974), and the terrain is slightly rolling-to-hilly. Average rainfall on the CUEF ranges from 122 to 140 cm annually, while the average annual temperature is ≈15.6°C, with a mean high of ca. 25.6°C in July and a mean low of 6.7°C in January (National Oceanic and Atmospheric Administration, 1974).

2.2. Field methods

We randomly established five 0.1 ha plots (20 m×50 m) in four stands each of the following 10 stand types: pine plantation 1–9 years old, pine plantation 20–40 years old, pine plantation >40 years old, pine-hardwood 20–30 years old, pine-hardwood 31–50 years old, pine-hardwood >50 years old, cove hardwood 40–60 years old, cove hardwood >60 years old, upland hardwood 40–60 years old, and upland hardwood >60 years old. We permanently marked each plot and oriented the long axis at a right angle to ridges and streams.

We counted snags and cavities in all plots during winter months. We defined snags as standing dead trees ≥10.2 cm diameter breast height (DBH) and ≥1.8 m tall (Thomas et al., 1979). We measured DBH with a diameter tape and total height with a hypsometer. Snags were numbered at breast height with paint and at stump height with an aluminum tag. We recorded the following information for each snag: species, DBH, height, stage of decomposition, number of wildlife cavities, and year of tree death if senescence began after initiation of the study. We defined stage of decomposition as:

1. a snag with bark and limbs intact;
2. a declining snag with loose and sloughing bark, and most limbs broken; and
3. a snag with decayed and sloughing bark and a broken top (Carmichael and Guynn, 1983).

We defined a cavity as any completely excavated opening in a tree's bole or limbs that could provide shelter for wildlife. Feeding areas, cavity starts, and natural crevices were not counted as cavities. We used 10×40 binoculars to aid in the visual inspection of snags and excavated openings from several different angles. The number of cavities were recounted on each snag during subsequent years of the study. We did not document nesting use of individual cavities by excavating birds or presence of any secondary cavity users. Instead, we tallied completed cavities as an index of the suitability of a given snag for excavation and subsequent use by primary and secondary cavity nesters.

We measured snags present in previous years for changes in height, stage of decomposition, and number of cavities. If a previously recorded snag could not be found, the ground was searched for the marked stem to verify that the snag had fallen and the year of snag loss was recorded. For snags that were located during the study, we addressed relationships between the year since tree death (YSD) and snag height, stage of snag decay, and number of cavities present. An index of wildlife use of each snag was determined by counting the number of cavities present and calculating the total number of cavity years. We defined a cavity year as one cavity present for 1 year (i.e. a snag that contained two cavities for a period of three years yielded six cavity years).

2.3. Statistics

During the study, 55 plots were destroyed by forest operations and five other plots were excluded from the analysis for logistical reasons. For each of the remaining 140 plots (see Table 1 for distribution of samples among types), we quantified trends in snag density, size, recruitment, loss, decay, and cavity occurrence by stand type, age, and species. Snags were tallied into the recruitment class if they were not present the previous year, and snags were classified as lost if they fell or disappeared. Recruitment and loss rates were expressed as snags/ha/year. Net recruitment (i.e. snag recruitment minus snag loss rates) also was calculated. Relative recruitment and loss rates, which are recruitment and loss rates divided by snag density, were included to account for the effects of varying snag densities. We used Student's *t*-tests to evaluate differences between recruitment and loss rates within each of the four stand types. We determined differences in snag recruitment and loss rates, snag density, DBH, and height among stand types and among stand type–age class combinations using a completely randomized, one-way analysis of variance (ANOVA; SAS Institute, 1989). When the assumption of homogeneity of variance was not met, we transformed the data using the $\log_e(Y+1)$ transformation (Steel and Torrie, 1980). However, we report only untransformed means and standard errors. When the ANOVA yielded a

Table 1
Mean diameter breast height (DBH), height, and density of snags by stand type on the CUEF (1982-1990). Standard errors are in parentheses below means

Stand type (N)	Mean DBH (cm)	Mean height (m)	Mean density (snags/ha)	Recruitment rate (snags/ha/year)	Loss rate
Upland hardwood (30)	20.3AB [a]	9.5	35.6A [a]	5.6	6.6AB [a]
	(0.4)	(1.5)	(4.9)	(0.7)	(1.0)
Cove hardwood (29)	20.3AB [a]	9.8	31.9A [a]	6.5	6.7A [a]
	(0.4)	(2.2)	(3.7)	(0.9)	(0.7)
Pine-hardwood (44)	18.7B [a]	9.8	28.0AB [a]	6.4	7.0AB [a]
	(0.2)	(1.2)	(2.4)	(0.9)	(0.9)
Pine plantation (37)	22.1A [a]	10.4	20.2B [a]	4.7	4.7B [a]
	(0.5)	(2.2)	(2.3)	(0.6)	(0.6)
Overall mean	20.3	9.9	28.4	5.8	6.2

[a] Columnar means followed by the same letter were not significantly different ($p \leq 0.05$) according to Tukey's HSD.

significant F-statistic, we used Tukey's honestly significant difference (HSD) to identify significant differences among means. We calculated Pearson product moment correlation coefficients to determine relationships between YSD (i.e. year of snag recruitment) and mean height, stage of decay, number of cavities, percent of snags with cavities, and percent of snags standing. Correlation coefficients also were computed for relationships between snag DBH and number of cavities, snag height, stage of decay, recruitment rate, and loss rate. We performed a χ-square test to determine if the percent of original trees standing each year after tree death was independent of diameter class (10.2–15.2, 15.3–20.3, 20.4–25.4, 25.5–30.5, and >30.5 cm). Statistical significance was accepted at α=0.05 for all tests.

3. Results

The average snag DBH and height across all stand types and years was 20.3 cm and 9.9 m, respectively (Table 1). The only significant difference in mean snag DBH by stand type was between pine plantation ($\bar{x}$=22.1 cm) and pine-hardwood ($\bar{x}$=18.7 cm), and there were no significant differences in mean snag height by stand type (Table 1). Snag height increased with snag DBH (r=0.71; p=0.0003), but there was no significant relationship between stage of snag decay or number of cavities/snag and snag DBH.

Mean snag density was 28.4 snags/ha across stand types and years. Upland hardwood and cove hardwood stand types had significantly higher snag densities than pine plantation (Table 1). Snag densities also varied significantly among stand type–age class combinations (Table 2). Cove hardwood (40–60 years old), pine-hardwood (31–50 years old), and upland hardwood (>60 years old) had significantly higher snag densities than 1–9-year-old pine plantation. Snag densities within stand types generally decreased with increasing stand age class or were highest in intermediate age classes (Table 2).

Loss rates, but not recruitment rates, differed significantly among stand types (Table 1). Cove hardwood had higher ($p \leq 0.05$) loss rates than pine plantation. Mean loss rates were equal to or exceeded recruitment rates within every stand type, but the differences were not significant (Table 1). The average net snag recruitment rate over all stand types was −0.43 snags/ha/year. Both recruitment and loss rates differed significantly among stand type–age class combinations (Table 2). Pine-hardwood (31–50 years old) had the highest recruitment ($\bar{x}$=10.0 snags/ha/year) and loss rates ($\bar{x}$=12.0 snags/ha/year). Pine plantation (1–9 years old) had the lowest recruitment rate ($\bar{x}$=1.79 snags/ha/year) and >40-year-old pine plantation had the lowest loss rate ($\bar{x}$=1.59 snags/ha/year). Snag recruitment rates generally were highest in the intermediate-aged stand classes. Higher recruitment and loss rates occurred within stand type–age class combinations with high snag densities. Relative recruitment rates, which account for varying snag densities in the age classes, showed similar patterns. The highest relative recruitment rates occurred in

Table 2
Mean snag density, recruitment rate, and loss rate by stand type–age class combinations on the CUEF (1982–1990). Standard errors are in parentheses below means

Stand type	Stand age (*N*)	Mean density (snags/ha)	Recruitment rate (snags/ha/year)	Loss rate	Relative recruitment	Relative loss
Cove	40–60 (14)	36.7A [a] (6.4)	8.3 A[a] (1.6)	6.63AB [a] (1.0)	0.23	0.18
Hardwood	>60 (15)	27.4AB [a] (3.9)	4.95AB [a] (0.8)	6.95AB [a] (0.9)	0.18	0.25
Pine	20–30 (19)	28.3AB [a] (4.4)	6.24AB [a] (1.2)	5.87AB [a] (1.0)	0.22	0.21
Hardwood	31–50 (10)	33.0A [a] (3.7)	10.0A [a] (2.6)	12.0A [a] (2.7)	0.30	0.36
	>50 (15)	24.2AB [a] (3.4)	4.29AB [a] (0.8)	5.24AB [a] (0.8)	0.18	0.22
Pine	1–9 (8)	12.0B [a] (2.8)	1.79 (0.6)	3.93BC [a] (0.5)	0.15	0.33
Plantation	20–40 (20)	25.8AB [a] (3.2)	6.50A [a] (1.0)	6.43AB [a] (1.0)	0.25	0.25
	>40 (9)	15.1AB [a] (4.1)	3.65AB [a] (0.7)	1.59C [a] (0.4)	0.24	0.11
Upland	40–60 (15)	35.9AB [a] (8.5)	5.43AB [a] (1.1)	6.29AB [a] (1.5)	0.15	0.18
Hardwood	>60 (15)	35.2A [a] (5.2)	5.71A [a] (0.8)	6.95AB [a] (1.2)	0.16	0.20

[a] Columnar means followed by the same letter were not significantly different ($p \leq 0.05$) according to Tukey's HSD.

pine-hardwood (31–50 years old), pine plantation ≥20 years old, and cove hardwood (40–60 years old). Conversely, the lowest relative recruitment was in older pine-hardwood and cove hardwood, both age classes of upland hardwood, and young pine plantation. The greatest relative snag loss rate was in 31–50-year-old pine-hardwood and 1–9-year-old pine plantation and the lowest relative loss occurred in pine plantation over 40 years old. Snag recruitment and loss rates were higher within smaller DBH classes and the 12.7 cm DBH class had the highest recruitment and loss rates (Fig. 1). DBH was negatively correlated with recruitment rate ($r=-0.85$; $p=0.0001$) and with loss rate ($r=-0.80$; $p=0.0001$).

Twenty snag species or species groups were observed on the CUEF (Table 3). Red oak and shortleaf pine snags were most common with 8.77 and 7.36 snags/ha, respectively. Several hardwood species, such as blackgum (*Nyssa sylvatica*) and eastern redbud (*Cercis canadensis*) were uncommon as snags (Table 3). The five most common snag species/species groups comprised 77–94% of all snags in each stand type (Table 4). Red oak snags were most common in

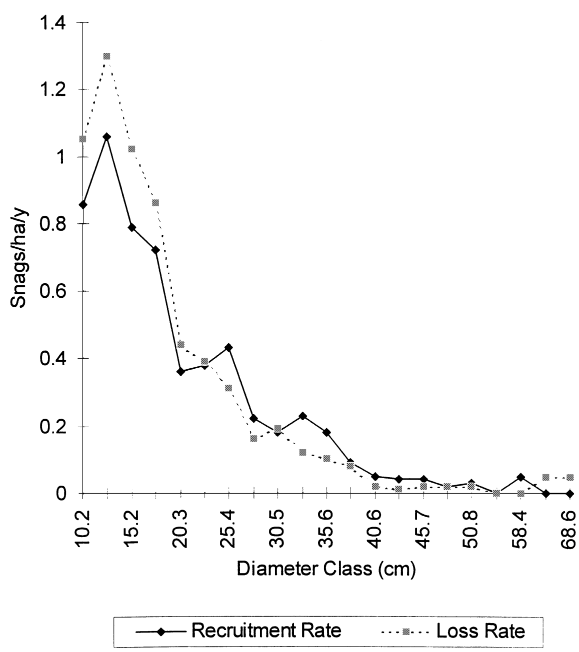

Fig. 1. Snag recruitment and loss rates by diameter class (cm) on the CUEF (1982–1990).

Table 3
Snag density, recruitment and cavities by species on the CUEF (1982–1990)

Snag species	Snags/ha (*N* [a])	Net snag recruitment [b] (snags/ha/year)	Cavities per snag [c]	Cavity years [c]
Red oak (*Quercus* spp.)	8.77 (838)	0	0.05	56
Shortleaf pine (*Pinus echinata*)	7.36 (743)	−0.27	0.18	193
White oak (*Q.* spp.)	3.79 (357)	−0.23	0.08	23
Loblolly pine (*P. taeda*)	3.59 (413)	0.22	0.10	47
Yellow poplar (*Liriodendron tulipifera*)	1.86 (121)	0	0.08	11
Red maple (*Acer rubrum*)	0.76 (16)	0		
Black walnut (*Juglans nigra*)	0.76 (16)	0		
Black cherry (*Prunus serotina*)	0.73 (54)	0.02		
Sourwood (*Oxydendrum arboreum*)	0.64 (65)	−0.12	0.04	3
Sweetgum (*Liquidambar styraciflua*)	0.63 (27)	0	0.05	2
Hickory (*Carya* spp.)	0.46 (41)	−0.06		
Eastern redcedar (*Juniperus virginiana*)	0.42 (35)	0.02	0.38	3
Ash (*Fraxinus* spp.)	0.38 (8)	0		
Virginia pine (*P. virginiana*)	0.25 (7)	−0.03	0.13	1
Dogwood (*Cornus* spp.)	0.23 (15)	0.02		
Black locust (*Robinia pseudoacacia*)	0.21 (6)	0.04	1.33	8
Elm (*Ulmus* spp.)	0.19 (4)	−0.05		
Mulberry (*Morus* spp.)	0.19 (6)	0.03		
Eastern redbud (*Cercis canadensis*)	0.10 (2)	0		
Blackgum (*Nyssa sylvatica*)	0.07 (2)	0		
	Σ=31.39	Σ=−0.41	$\bar{x}$=0.1 [d]	Σ=347

[a] Number of snag years.
[b] Recruitment rate minus loss rate.
[c] Values are included only for the ten species in which cavities occurred.
[d] Mean weighted according to number of snags present for each species with cavities present.

Table 4
Percent snag composition by stand type for the five most common snag species on the CUEF (1982–1990)

Snag species	Stand type			
	cove hardwood	pine hardwood	pine plantation	upland hardwood
	(percent)			
Red oaks	25	30	8	55
White oaks	19	8	7	13
Shortleaf pine	16	38	18	26
Loblolly pine	0	14	60	0
Yellow poplar	17	0	0	0

upland hardwood (55%) and cove hardwood (25%) stand types, while shortleaf pine was the most common snag species in the pine-hardwood type (38%). Loblolly pine (*Pinus taeda*) occurred as a snag species only in pine plantations and pine-hardwood types and comprised 60% of snags in pine plantations. Yellow poplar was present only in cove hardwood stands and comprised 17% of the snags within those stands.

Most of the snag species present on CUEF exhibited negative or zero net recruitment rates (Table 3). Shortleaf pine and white oak snags had the highest negative net recruitment, but loblolly pine, another common snag species, had the highest positive net change in recruitment. Several other snag species/species groups, such as red oaks and yellow poplar, were replaced at an equal rate by new recruits. Overall net snag recruitment/ha was -0.41, which is similar to the value obtained from Table 1 by averaging across the four stand types.

Analyses using YSD revealed clear chronological patterns in snag height, stage of decay, and number of cavities/snag (Table 5). The mean height of snags decreased with YSD, especially for noncavity snags, and mean stage of decay increased with YSD. Snags used for cavity excavation were generally taller and in a more advanced stage of decay than snags without cavities. The percent of snags containing cavities and the number of cavities/snag increased with snag age (r=0.80; p=0.05, and r=0.78; p=0.07, respectively). Relationships between YSD and snag height, snag decay, and numbers of cavities/snag were similar for the four predominate tree species on the CUEF (Table 6). Snag height decreased, stage of decay increased, and number of cavities/snag generally increased with YSD. Although 100% of white oak snags fell by 5 YSD, white oaks appeared to change at slower rates than the other three species/species groups (Table 6). Shortleaf pine had relatively higher numbers of cavities/snag soon after tree death than did the other species; but it, along with loblolly pine, exhibited a marked increase in numbers of cavities/snag between five and six YSD.

Across all stand types, cavities were excavated in 10 snag species/species groups with an overall mean of 0.1 cavities/snag (Table 3). Shortleaf pine was the only species to have both a large number of snags and a higher than average number of cavities/snag. Other softwood species, including virginia pine (*Pinus virginiana*), eastern redcedar (*Juniperus virginiana*), and loblolly pine, had equal to or above average numbers of cavities/snag. Shortleaf pine accounted for 56% of the cavity years observed, followed by red oaks (16%), loblolly pine (14%), and white oaks (7%). Black locust (*Robinia psuedoacacia*) was an uncommon snag contributor (i.e. 0.21 snags/ha), but the few snags of this species that were present contained an average of 1.33 cavities.

In all stand types, 21–38% of all snags fell before they were two years old, and over 50% fell by age three (Table 7). Approximately 4% of all snags remained standing six YSD. The percent of snags standing was highly correlated with YSD in all stand types (Table 7). Snags in upland hardwood had the greatest longevity with 21% standing five years after recruitment. The percent of snags standing also was significantly correlated with YSD for the five most common snag species (Table 7). Hardwood snags (e.g. yellow poplar and white oaks) apparently decayed more slowly than pine snags, but by six years after tree death at least 95% of all snags had fallen. Across all stand types, percent of snags standing each YSD was independent of diameter class (χ=16.8; p=0.67). Tests for independence between diameter class and snag longevity also were nonsignificant for each of the four stand types (cove hardwood, p=0.89; pine-hardwood, p=0.84; pine plantation, p=0.99; upland hardwood, p=0.81). The percent of the original snags standing in each diameter class decreased between four and six YSD, but the patterns of decline were consistent between diameter classes (Fig. 2). However, the smallest diameter class (10.2–15.2 cm) had the smallest percentage of snags standing each YSD.

4. Discussion

Mean snag density (28.4 snags/ha) on the CUEF over all stand types and years was greater than densities reported by Harlow and Guynn (1983), McComb et al. (1986), and Land et al. (1989) in other physiographic regions of the southeastern United States. Lightning-struck and beetle-killed trees rarely are salvaged on the CUEF, especially in hilly areas that are less accessible. Ice storms, a common cause of tree mortality, are more frequent in the Piedmont than in most other regions of the Southeast (USDA Forest Service, 1969). Pine plantations on the CUEF and in other regions generally have fewer snags than other stand types (McComb et al., 1986; McMinn and Hardt, 1996). Forested landscapes in other areas of the Southeast, especially areas of high timber production, most likely have more land in pine plantation than the CUEF, and therefore a lower average snag density.

Table 5
Height, stage of decay, and number of cavities by years since snag tree death on the CUEF (1982–1990)

Year since tree death (N [b])	Height (m)		Stage of decay [a]		Cavity/snag	Snags with cavities(%)
	cavities	noncavities	cavities	noncavities		
1 (573)	8.5	13.1	1.8	1.4	0.03	0.01
2 (395)	12.2	11.9	2.0	1.7	0.02	0.01
3 (237)	11.6	10.1	2.3	2.5	0.06	0.03
4 (141)	10.7	8.5	2.5	2.2	0.10	0.07
5 (72)	6.7	7.3	2.5	2.3	0.13	0.08
6 (20)	7.3	5.2	2.7	2.5	0.60	0.35
r [c]	−0.54	−1.00 [d]	0.97 [d]	0.83 [d]	0.78	0.80 [d]

[a] Decay stage: 1) a snag with bark and limbs intact; 2) a snag with loose sloughing bark and most limbs broken; and 3) a snag with decayed and sloughing sapwood.
[b] Number of snags.
[c] Pearson product moment coefficient of correlation between year since snag tree death and snag height, stage of decay, cavities/snag, and % of snags with cavities.
[d] Significant correlation, $p \leq 0.05$.

Table 6
Snag density, height, stage of decay, and number of cavities/snag by years since snag tree death and predominant species on the CUEF (1982–1990)

Species	Year since tree death	Number of snags	Height (m)	Stage of decay [a]	Cav./snag
Red oak	1	172	13.1	1.4	0.01
	2	125	11.5	1.7	0.02
	3	58	9.5	2.2	0.02
	4	40	8.5	2.3	0.05
	5	24	5.8	2.5	0.04
	6	4	4.2	2.8	0.25
	r [b]		−0.99 [c]	0.98 [c]	0.75
White oak	1	47	11.1	1.6	0.02
	2	31	9.2	2.0	0.00
	3	24	7.8	2.3	0.00
	4	13	8.2	2.2	0.23
	5	9	8.2	2.1	0.11
	6	0	.	.	.
	r [b]		−0.80	0.70	0.65
Shortleaf pine	1	144	13.8	1.2	0.13
	2	92	13.5	1.5	0.21
	3	61	11.3	1.9	0.08
	4	34	9.2	2.2	0.12
	5	19	8.0	2.3	0.05
	6	7	7.2	2.4	0.43
	r [b]		−0.98 [c]	0.97 [c]	0.41
Loblolly pine	1	122	14.5	1.3	0.01
	2	78	13.0	1.6	0.01
	3	45	12.1	1.8	0.16
	4	24	8.6	2.2	0.13
	5	6	6.9	2.2	0.00
	6	5	5.6	2.6	0.80
	r [b]		−0.98 [c]	0.98 [c]	0.67

[a] Decay stage: 1) a snag with bark and limbs intact; 2) a snag with loose sloughing bark and most limbs broken; and 3) a snag with decayed and sloughing sapwood.
[b] Pearson product moment coefficient of correlation between year since snag tree death and snag height, stage of decay, and cavities/snag.
[c] Significant correlation, $p \leq 0.05$.

Table 7
Snag longevity (percent of snags standing) by stand type and species on the CUEF (1982–1990)

Stand type and species	Years since tree death						
	1	2	3	4	5	6	r [a]
	(percent)						
Cove hardwood	100	73	47	28	13	2	−0.99
Upland hardwood	100	79	45	31	21	4	−0.98
Pine-hardwood	100	62	34	21	10	4	−0.95
Pine plantation	100	68	44	22	9	4	−0.97
Loblolly pine	100	64	37	20	5	4	−0.96
Red oaks	100	73	34	23	14	2	−0.96
Shortleaf pine	100	64	42	24	13	5	−0.97
Yellow poplar	100	75	57	36	14	4	−1.00
White oaks	100	66	51	28	19	0	−0.99

[a] Pearson product moment coefficient of correlation between % of snags standing and year since tree death. All correlations were statistically significant ($p \leq 0.05$).

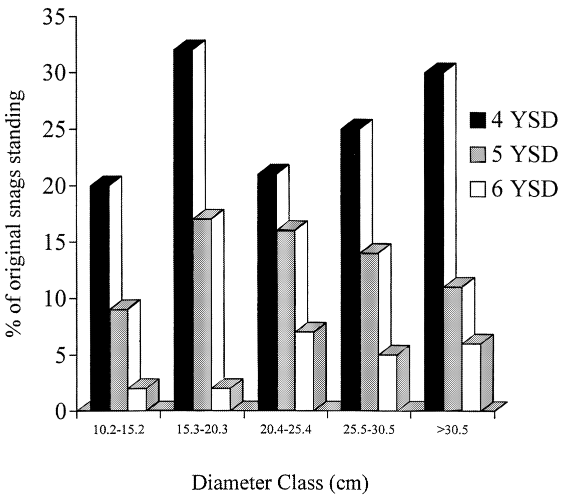

Fig. 2. Percent of the original snags in each of five diameter classes (10.2–15.2, 15.3–20.3, 20.4–25.4, 25.5–30.5, and >30.5 cm) standing 4, 5, and 6 years since death (YSD) of the tree.

Snag densities probably were higher in cove and upland hardwood stands because these stands were less intensively managed than pine areas. Harlow and Guynn (1983) documented greater snag densities in hardwood-dominated stands and attributed the findings to the difficult removal of dead and living trees from these densely stocked and wet areas. On the CUEF, pine-hardwood stands have the highest number of small snags and pine plantations contain the fewest (Sabin, 1991). In young pine plantations, most snags were large, mature stems left during previous harvest operations. Conversely, pine-hardwood normally is a transition stand type with competition between individual trees possibly resulting in the death of many small, suppressed stems (i.e. stem exclusion; Oliver and Larson, 1996) and a lower mean snag DBH. After canopy closure, more shade-tolerant hardwood species may begin to overtop less tolerant conifers.

We did not find consistent relationships, especially in pine plantations, between recruitment and loss rates. The only trees large enough to form snags in 1–9-year-old pine plantation were remnants of previous stands. Therefore, recruitment rates were low and relative loss rates remained high as the remnant snags continued to disappear. Again, we attributed the high recruitment and loss rates in 31–50-year-old pine-hardwood stands to competitive interactions during stem exclusion. Ohmann et al. (1994) reported highest snag recruitment in stands with closed canopies. Most likely, midstory and subdominant trees become suppressed and die between 30 and 40 years after stand initiation.

Higher densities of large snags typically have been documented in older stands (McComb et al., 1986; Rosenberg et al., 1988; Ohmann et al., 1994). Conversely, we documented decreasing snag densities with increasing stand ages, especially between intermediate and older-aged stands. Regenerating stands may have higher densities of small snags as a result of density-dependent tree mortality (Cline et al., 1980;

McMinn and Hardt, 1996). High densities of small diameter trees in young and intermediate-aged stands cause some stems to be overtopped or suppressed, and as the stands age, the tree canopy begins opening and mortality rate slows, resulting in lower snag densities (Cline et al., 1980). Many of the stands on the CUEF are unmanaged and may exhibit a negative association between snag density and stand age for the same reasons. On the CUEF, small diameter snags were most common in all stand types and highest snag turnover occurred in the smallest DBH classes.

The overall net recruitment rate (−0.4 snags/ha/year) was conspicuous. This trend likely was due to stand characteristics and management practices specific to the CUEF. Prior to the study, many stands were densely stocked, causing high tree mortality rates. As these stands aged, rates of tree death declined resulting in a reduced number of new snags present on the site. All of the upland and cove hardwood stands monitored during the study were >40 years old. Pine plantations, comprised mainly of loblolly pines, exhibited near zero net recruitment rates, whereas all stands with a hardwood component had negative net recruitment. Loblolly pine had the highest net recruitment rate, but two other prevalent species/species groups, shortleaf pine and white oak, had the lowest net change. Most pine plantations were in the 20–40-year-old range and were characterized by high density-dependent tree mortality compared to older hardwood stands.

We determined that most snags fell by six YSD on the CUEF. Over one half of all snags fell within the first three years after tree death. Accelerated senescence of snags on the CUEF may be due to warm, humid conditions in the region relative to most other areas in North America. Cain (1996) conducted a study in southeastern Arkansas and also determined that snags commonly fall within five years after tree mortality. Snag losses on the CUEF occurred consistently across all diameter classes, which contrasts with Cain's finding that deterioration rates were highest in the smallest diameter snags. Cain (1996) injected trees with herbicides, investigated only hardwood snags, and included ≤11.0 cm as the smallest diameter class, whereas we studied naturally-induced snags of all species and excluded any snags <10.2 cm DBH. These experimental differences may account for the differences in deterioration rates for various diameter classes in the two studies. On the CUEF, snags in upland hardwoods exhibited greater longevity than snags in other stand types, and yellow poplar and white oak snags disappeared at moderately slower rates than other common species. Conversely, in the southern Appalachians, oak snags have been documented to be rapid decayers when compared to pine snags, and white oaks deteriorate faster than red oaks (Harmon, 1982).

Snag characteristics (e.g. DBH, height, species, age), rather than densities, may be the most important factor determining wildlife use and cavity excavation in a given area. We recorded more cavities in taller, older and more decayed snags. Over one-third of the six-year-old snags contained cavities, but because most snags fell within six years after recruitment, potential cavity snags may be quite rare. Cain (1996) also determined that the percentage of snags containing cavities increased with time since tree mortality. The dramatic increase in the mean number of cavities at six YSD most likely is related to the degree of decay (Runde and Capen, 1987; Connor et al., 1994). Apparently this length of time is required for snags to decay sufficiently for cavity excavation. Moreover, the high incidence of softwood use, especially shortleaf pine, by cavity excavators probably was due to the relative ease of excavation.

Snags which continually break off and decrease in height decline in their suitability as nest sites (Evans and Connor, 1979). Many bird species require specific snag diameters and heights to excavate nesting cavities (Rosenberg et al., 1988). We documented no significant decline in height of snags containing cavities, but six-year-old noncavity snags were one-half the height of one-year-old noncavity snags. On the CUEF, the incidence of cavities generally increased with snag DBH, and snag diameter and height were positively correlated (Sabin, 1991). The number of cavities/snag increased markedly in snags with diameters greater than 33.0 cm (Sabin, 1991). However, snags >30.5 cm DBH fell as quickly as snags in smaller diameter classes. Although some stand types and type–age class combinations had higher snag densities than others, those stands did not necessarily contain suitable snag resources. High densities of small snags do not provide the nest sites required by cavity-nesting birds (Evans and Connor, 1979).

5. Conclusion

Understanding the chronological patterns of snag development and change requires long-term monitoring of forested habitats. On the CUEF, some snags persisted for at least six years and most cavities did not appear until this time. Shorter studies would have been unable to pinpoint the length of snag persistence or the time required for snags to become suitable for cavity excavation. We advise that future studies of snag dynamics in the Southeast be at least seven years in length. Furthermore, the complex patterns of snag dynamics on the CUEF underscore the need for regional data in order to establish local management guidelines.

Approximately 8.5 million ha of southern forests are comprised of pine plantations (USDA Forest Service, 1988), much of which are managed on short rotations (<25 years). We determined that snag densities were low in young, intensively managed pine stands on the CUEF. Between stand ages 20 and 40, snag densities doubled in pine stands, but snag density declined in older pine plantations as tree density declined and the forest canopy opened. Therefore, we recommend retention or designation of older, larger diameter trees ($\geq$33.0 cm) that can be converted to snags to promote suitable habitat for cavity-nesting species, especially in young pine plantations and older stands with low tree mortality. Retention of softwood species may be most beneficial due to its apparent preference by cavity excavators. Residual, live trees could be killed asynchronously to provide snags throughout early development of the stand. In older stands, especially sparsely-stocked mature pine plantations, snags could be created by girdling, injecting, or inoculating large-diameter, live stems (Connor, 1978; Cain, 1996). On the CUEF, most snags no longer are standing six YSD, and cavities generally are not excavated until six YSD. Therefore, it appears that standing snags suitable for cavity excavation exist for only one or two years. To enhance wildlife habitat, we advise that steps be taken to create snags on one- or two-year cycles.

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