

DECAY OF FIRE-CAUSED SNAGS IN OCALA SAND PINE

Kenneth W. Outcalt

U.S. Department of Agriculture, Forest Service. Southern Research Station. 320 Green Street, Athens, GA 30602

ABSTRACT

Sand pine (*Pinus clausa*) scrub is adapted to, and regenerated by, periodic stand-replacement wildfire, which consumes the understory and kills the overstory. The heat of the fire opens the serotinous cones of Ocala sand pine (*P. clausa* var. *clausa*), releasing quantities of seed that reestablish the overstory, while the understory regenerates by sprouting or from soil-stored seed. Resource managers attempt to mimic this process by clear cutting and direct seeding, which seems to work quite well. However, this method results in far fewer snags, which may have important functions in the sand pine scrub ecosystem. Because sand pine is a short-lived species with very little heartwood, it is believed that these snags would be a temporary feature of the system, and thus were not that critical. My study tests this assumption by documenting the life of snags following a stand-replacement fire in sand pine scrub on the Ocala National Forest, Florida. Three stands were burned, one by a prescribed burn in May 1993 and two by natural fire in August 1993. Prior to the fire, there were 520 Ocala sand pine/ha, 96 oaks/ha, and 137 snags/ha. The fire killed all of the sand pine and most of the oaks. Decay proceeded more slowly than expected in the resulting snags. After 2 years 69% retained most of the bark. 27% had lost all bark and most of the limbs, and only 4% had visible sapwood decay. The first snags fell between 12 and 18 months following the fire, but it took 5 years for 50% of the snags to fall. At the end of 7 years following the fire, 32% of the sand pine snags were still standing. Thus, the snags in sand pine scrub occur as part of the structure of the sand pine ecosystem for much longer than expected. Managers may need to consider more prescribed fire in wilderness areas to generate these snags.

keywords: coarse woody debris, ecosystem management, fire in ecosystem management, Florida, Ocala National Forest, *Pinus clausa*, sand pine, snags.

Citation: Outcalt, K.W. 2003. Decay of fire-caused snags in Ocala sand pine. Pages SO-54 in K.E.M. Galley, R.C. Klinger, and N.G. Sugihara (eds.). Proceedings of Fire Conference 2000: The First National Congress on Fire Ecology, Prevention, and Management. Miscellaneous Publication No. 13. Tall Timbers Research Station. Tallahassee. FL.

INTRODUCTION

Sand pine scrub grows on deep droughty infertile sands of marine and aeolian origin. Water and wind formed these features as sea levels fluctuated during past glacial and interglacial periods (Kurz 1942, Laessle 1958, Snedaker et al. 1972). Because of washing and sorting during transport and deposition, soil parent material was nearly pure quartz sand (Laessle 1958). This produced soils which are almost exclusively entisols and mostly Quartzipsammments (Myers 1990) typified by the Astatula, Lakeland, Paola, and St. Lucie soil series.

The Ocala variety of sand pine is native to scrubs on the central ridge of Florida and a strip of old dunes stretching from St. John's County south to the northern portion of Dade County (now Miami-Dade County) on the east coast and from near Cedar Key south to Naples on the west coast (Small 1921, Harper 1927, Myers 1990). Choctawhatchee sand pine (*P. clausa* var. *immuginata*) is the dominant tree in scrubs along the Gulf Coast, including off-shore islands, of northwest Florida from the Apalachicola River westward into Alabama. Interior scrub, the largest contiguous area of Ocala sand pine scrub, occupies about 101,000 ha on the Ocala National Forest (Brendemuehl 1990). This area has hot, humid summers, somewhat dry winters, and a long growing season averaging 300 days. Precipitation is abundant averaging 1300 mm per year (1960–1980) with a maximum in July and a minimum in May. Even though rainfall is plentiful, the area ex-

periences frequent drought periods, which can develop within 2 weeks of a heavy rainfall because of the low soil moisture-holding capacity.

Sand pine scrub is a unique community with a suite of species that occur nowhere else (Christman and Judd 1990). Ocala sand pine scrub has an overstory of even-aged sand pine with twisted and leaning trunks over an understory of evergreen shrubs (Myers 1990). Typical understory species include myrtle oak (*Quercus myrtifolia*), sand live oak (*Q. geminata*), Chapman's oak (*Q. chapmanii*), turkey oak (*Q. laevis*), rusty lyonia (*Lyonia ferruginea*), rosemary (*Ceratiola ericoides*), scrub palmetto (*Sabal etonia*), and saw palmetto (*Serenoa repens*) (Outcalt 1997). Because of the well-drained soils and competition from the sand pine overstory and understory shrubs, herbs and grasses are very sparse in mature scrub habitats. Typical species include beak rush (*Rhynchospora megalocarpa*), milk peas (*Galactia* spp.), and bluestems (*Andropogon* spp.). Lichens (*Cladonia* spp.) form extensive patches on the forest floor (Greenberg et al. 19950).

Species richness and diversity of herbaceous plants are significantly greater, however, in recently disturbed areas (Greenberg et al. 199517). Most of the endemic species thrive in this open scrub where sand pine is in the seedling stage. As with many ecosystems in the southeastern U.S., the primary disturbance creating these open conditions is fire. Because of its sparse ground cover and compacted litter layer, much of the time sand pine scrub is virtually fireproof. However, every 10 to 100 years, usually during the spring

(April or May), drought, high winds, and extreme conditions result in a catastrophic wildfire (Hough 1973). This fire kills the sand pine overstory and burns off the understory (Myers 1990). The heat from the fire opens the many serotinous cones contained in the crowns of the sand pine, which release the seed for establishment of the next stand (Cooper 1951). Herbaceous species, including many endemics, respond rapidly to the disturbance by invading, resprouting, or germinating from the soil seed bank (Johnson 1982, Hartnett and Richardson 1989). Without this high-intensity disturbance the sand pine scrub would succeed to xeric oak hammock (Laessle 1958, Veno 1976) and lose many plant and animal species requiring young, open scrub sites (Greenberg et al. 1994, 1995a,b).

Most of the sand pine scrub on the Ocala National Forest is currently managed for pulpwood production by clear-cutting followed by site preparation and direct seeding of sand pine. When wildfires do occur, most of the sand pine stems are removed in a salvage logging operation. Recent research indicates only minor differences in vegetation recovery among stands disturbed by clear-cutting and site preparation versus wildfire followed by salvage logging (Greenberg et al. 1995b). The impacts of removing wildfire-killed sand pine on scrub biodiversity remain unknown.

It is known from research elsewhere, that snags and the fallen logs they generate have important ecosystem functions. Snags are especially important for cavity-nesting birds, whose density in Florida ecosystems is positively correlated with density of snags (McComb et al. 1986). Snags also provide sites that birds use for perching, singing, foraging, and roosting (Caine and Marion 1991). Birds such as woodpeckers also forage on fallen logs (Horton and Mannan 1988). Fallen logs are important habitat in southern forests for mammals such as cotton mice (*Peromyscus gossypinus*) (McCay 2000). An array of different insects including species of cockroaches, termites, beetles, moths, and bees also use fallen logs (Hanula 1996).

The importance of snags and fallen logs is recognized by public land managers, who follow local guidelines and leave some snags on all harvested and salvaged sites. The large pulse of many snags, which formerly occurred following wildfire in sand pine scrub, however, has been largely eliminated. Because Ocala sand pine is a short-lived tree that rarely reaches diameters above 40 cm, it has been assumed that fire-killed trees would stand for only a short period of time. Additionally, since decay rates are quite rapid for woody material on the forest floor, it has also been assumed that fallen sand pine logs would rapidly disappear. The objective of this study was to test these assumptions by documenting the life of snags and fallen logs following stand-replacement fire in sand pine scrub.

METHODS

The study was established in 1993 in mature sand pine scrub on the Ocala National Forest in central Flor-

ida. Six randomly located 10 X 50-m plots were established in stand 1, a 12.2-ha area occupied by 40-year-old sand pine. Within these plots all trees and standing snags larger than 6 cm in diameter were mapped and tagged with aluminum tags attached with aluminum nails at 2 m above the ground. Diameters were recorded for all stems greater than 6 cm and height was measured on every tenth stem. The stand was then burned by prescribed fire on 11 May 1993 (Outcalt and Greenberg 1998). The day of the prescribed burn the temperature was 26 °C, the relative humidity was 50%, and the wind was from the southeast at 3 km/h. The Keetch/Byram drought index (Keetch and Byram 1968) was 450. After the fire, plots were resurveyed, with the condition and position of all tagged stems noted. A qualitative measure of fire intensity was collected based on the condition of the tree tags assigned to the following scale: 0 = no damage, 1 = tag tarnished, 2 = lower end of tag slightly melted, 3 = lower half of tag melted, 4 = 75% of the tag melted, 5 = tag completely melted, 6 = tag melted and nail melted, 7 = tag and nail burned completely off.

Stands 2 and 3 were located in the Juniper Wilderness in a 50-ha area of 50-year-old Ocala sand pine scrub burned by prescribed natural fire in September 1993. Six plots were established in each of these two stands immediately following the fire. Trees were measured and tagged as in stand 1. Tagged trees in all stands were resurveyed semiannually for the first 3 years and annually thereafter to follow tree fates and rates of decay. Snags were recorded as standing if the upright bole was 3 m or taller. The following scale was used to record decay level: Class 1 = greater than 70% of bark remaining on the bole; Class 2 = between 30% and 70% of the bole has lost its bark; Class 3 = greater than 70% of the bark is gone from the bole; Class 4 = sapwood decay is evident on the bole; Class 5 = sapwood on entire bole is soft, but bole retains its shape; Class 6 = sapwood on entire bole is soft, and bole is becoming flat; Class 7 = bole is a fragmented pile of decomposing wood.

RESULTS

Prior to treatment, the highest density of Ocala sand pine was recorded in stand 1, while the lowest density was in stand 3 (Table 1). Fewer but larger trees were in stands 2 and 3 with a mean diameter 2.5 cm greater than the trees in stand 1. Sand pine basal area followed the same pattern as density with the largest basal area in stand 1 and the smallest in stand 3. Diameter distributions also reflected the differences in age and stand structure. In stand 1 there was the typical even-aged bell-shaped diameter distribution (Figure 1). The older stands, 2 and 3, showed a more skewed diameter distribution with fewer trees in the smallest diameter class and more in the larger size classes. Scrub oaks, comprising turkey, sand live, and myrtle oaks, composed 10% to 25% of the total trees in the stands. These were small stems with a mean diameter

Table 1. Characteristics (mean ± 95% confidence interval) of overstory trees prior to prescribed fire in 1993 in Ocala sand pine scrub on the Ocala National Forest, Florida.

Characteristic	Stand		
	1	2	3
Ocala sand pine			
Density (no./ha)	670 ± 137	470 ± 78	367 ± 131
Diameter (cm)	17.5 ± 0.6	20.1 ± 0.9	20.3 ± 1.2
Basal area (m ² /ha)	16.8 ± 1.6	13.8 ± 4.0	10.0 ± 3.5
Height (m)	16.9 ± 0.8		
Oaks			
Density (no./ha)	77 ± 48	157 ± 64	53 ± 39
Diameter (cm)	6.6 ± 0.8	7.0 ± 0.6	8.4 ± 0.7
Height (m)	4.2 ± 0.4		

at least 10 cm less than the sand pine (Table 1). These oaks composed the midstory layer of the stands as shown by the much smaller average height.

The fires scorched most needles on the sand pine trees, but some **trees** along the edge retained green crowns. Two months following the fires, all pines in the stands had brown needles and were obviously dead. During the first year, tops and branches were lost from a few of the dead sand pines. Decay was rather slow, however, with just 4% of the sand pine snags losing most or all of their bark during the first year. The first stems fell over during the second season following the fire (Figure 2). Ocala sand pine stems continued to fall the following years but it took over 4 years before 50% of them were on the ground. After 7 years, about one-third of the stems remained standing. Midstory scrub oaks in the stands began falling sooner and the 50% loss figure was reached a year sooner, at 3 years. Nearly all of the oak stems had fallen after 7 years.

Diameter of sand pine stems had little effect on snag longevity, as the rate of loss was essentially the same for a 6-cm stem as it was for a 26-cm stem (Figure 3). The loss of Ocala sand pine snags was relatively constant, declining about 8.5% per year. Assuming the decay rates remain constant, all snags will likely have fallen by 11 years following the fires.

Although diameter did not affect rate of snag loss,

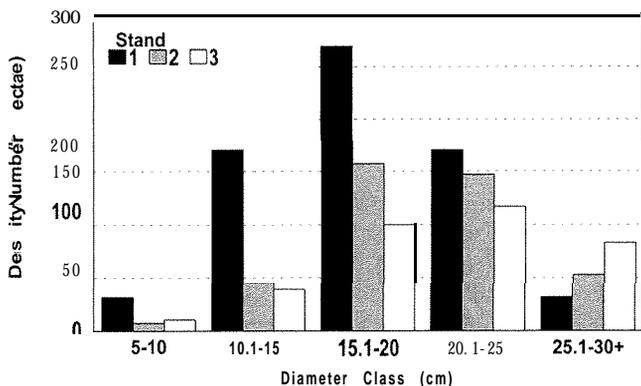


Fig. 1. Density of Ocala sand pine by diameter class, prior to prescribed fire in 1993, in sand pine scrub on the Ocala National Forest, Florida.

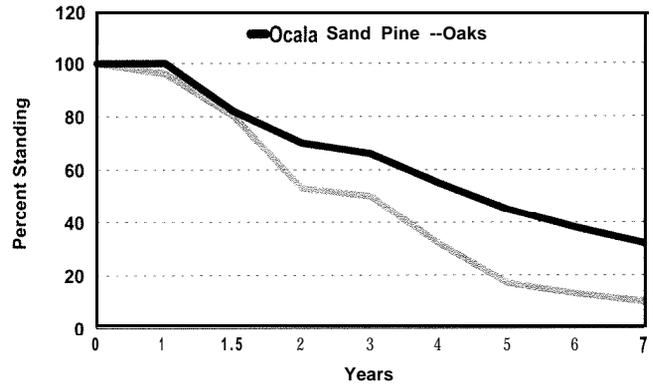


Fig. 2. Percentage of Ocala sand pine and scrub oak snags standing, following prescribed fire in 1993 in sand pine scrub on the Ocala National Forest, Florida.

longevity did seem related to fire intensity as shown by data from stand 1. Snags separated out into two general groups with those in the higher-intensity categories falling over more quickly than those less intensely burned (Figure 4). Those sand pine stems where fire was intense enough to melt 75% or more of the metal tag had a higher initial loss rate and declined to the 50% snag loss level by 3 years following the fires. The less intensely burned trees did not reach the 50% snag loss level until more than 5 years following the fire.

The progression of decay can be tracked by following the number of pine stems in **each category**. After 1.5 years, most of the pine snags still had much of their bark (Figure 5). Two years after the fires, there was a shift to more stems with some or most of the bark gone. This continued through years 3 and 4 along with an increase in the number of fallen stems. After 5 years, most of the stems had lost their bark and by 6 years, many had significant sapwood decay. Seven years following the fires there were no stems with the bark still on and nearly all had at least some sapwood decay. Few stems, however, had become completely soft and none had yet begun to lose shape. Scrub oak snags retained their bark longer than the sand pine with 66% retaining all bark 2 years following the fires. Sapwood decay was more rapid, however, once it be-

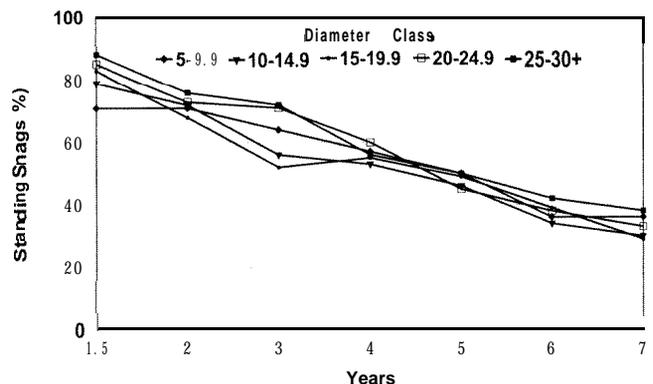


Fig. 3. Effect of diameter class on percentage of Ocala sand pine snags standing following prescribed fire in sand pine scrub on the Ocala National Forest, Florida.

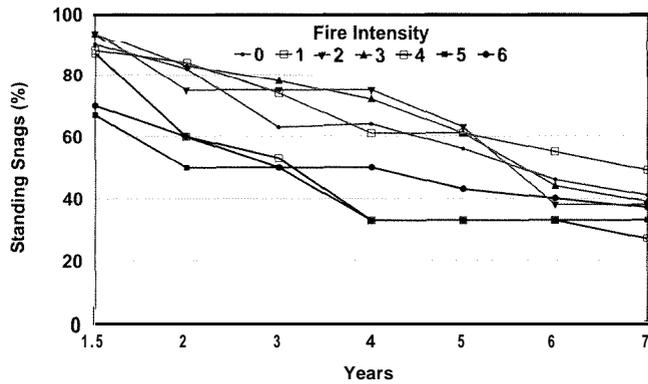


Fig. 4. Effect of fire intensity in stand 1 on percentage of Ocala sand pine snags standing over time following prescribed fire in 1993 in sand pine scrub on the Ocala National Forest, Florida.

gan with 20% of the oak stems losing shape and 10% were just fragmented piles of wood 7 years after the fires.

DISCUSSION

Because Ocala sand pine has little heartwood, it has been presumed it would decay quite rapidly and that standing snags would be a temporary structural component of burned stands. Once Ocala sand pine dies, the first stage of change is the loss of limbs and crowns, which began during the first 6 months following the fires. This is followed by the loss of bark from the bole, which began at 1.5 years and continued until nearly all stems had lost their bark at 5 years following the fires. It took 6 years, however, for most of the pine snags to develop significant sapwood decay. Because this sapwood decay proceeded more slowly than anticipated, snags lasted much longer than expected, with none falling until 1.5 years after the fires and 50% still standing after 4 years. Even after 7 years one-third of the snags were still standing, although many were broken and less than 6 m tall. Based on the rate of loss to date, it should take over 10 years for all of the snags to fall. This loss rate is only slightly faster than reported for fire-killed lodgepole pine (*Pinus contorta*) snags in Montana (Lyon 1977). It also followed a similar pattern to that found for the lodgepole pine snags that had few losses the first 2 years and then a steady decline thereafter.

The scrub oak snags were less durable than the pine: they began falling sooner and continued at a greater rate. Only a few were still standing after 7 years. In a study in the Southern Appalachians, Harmon (1982) also reported that oak snags decayed more rapidly than pine. Although loss rates were higher than for pines they were not nearly as rapid as those reported by Cain (1996) for herbicide-killed trees. His equation for similar-sized hardwoods (under 11 cm in diameter) predicts only 20% of the scrub oaks still standing after 2 years, while the actual amount was 52%. This could be due to a number of factors including cause of mortality, climate, or species differences. Conner et al. (1983) reported that herbicide-

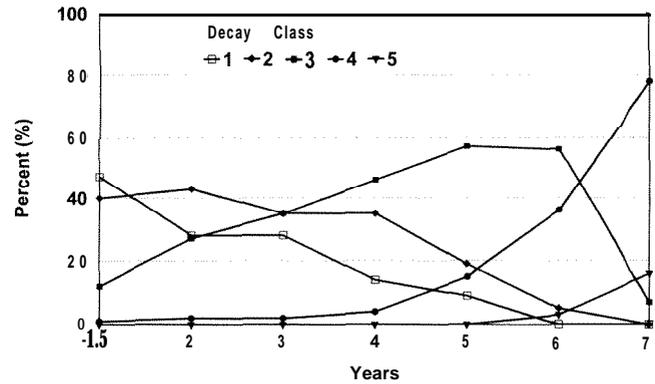


Fig. 5. Progression of decay in snags and fallen logs following prescribed fire in 1993 in sand pine scrub on the Ocala National Forest, Florida.

killed oaks decayed more rapidly than did girdled oak trees in an east Texas study. Thus, cause of death seems the most probable cause of the lower loss rate.

Raphael and Morrison (1987) found small-diameter snags of Jeffrey pine (*Pinus jeffreyi*), red fir (*Abies magnifica*), and white fir (*Abies concolor*) in California had a higher rate of loss than larger stems. Other studies have also reported smaller-diameter hardwood snags tend to fall more quickly than larger snags (Dickson et al. 1983, Cain 1996). However, tree diameter did not influence the rate of pine snag fall in my study. This is likely due to differences in species and diameter ranges. Western trees are much larger than sand pine and thus the study by Raphael and Morrison (1987) included snags with diameters exceeding 50 cm. Below 38 cm snags had an equal loss rate and it was only the larger snags which were more persistent. Thus, their data agree with my findings across the range of sand pine diameters (6 to 35 cm). There are likely species differences also, as lodgepole pine, a tree with similar ecology and physiological attributes to Ocala sand pine, showed no relationship between diameter and rate of falling (Raphael and Morrison 1987) even for the largest snags.

MANAGEMENT IMPLICATIONS

Although fire-killed snags in short-lived species like Ocala sand pine and lodgepole pine are not as durable as Douglas-fir (*Pseudotsuga menziesii*) snags, which can last for decades (Cline et al. 1980), they may be just as important in their respective ecosystems. Ocala sand pine snags are an important structural component for at least a decade following fires. It appears that cooler fires might increase the longevity of snags even further, as those burned less intensely stood longer in this study. Since the fire return interval is every 10 to 100 years, this means under natural fire regimes Ocala sand pine snags occupied a given area at least 10% of the time or on a landscape scale would occur on at least 10% of the area at any given time. In addition snags will continue to be important as coarse woody debris on the forest floor for some years after they fall as most have not yet reached the stage

where all sapwood is soft and the log is beginning to lose shape 7 years after death. These snags and fallen logs represent a significant habitat that species have evolved to exploit. Current management prescriptions call for leaving 4 to 6 snags per hectare based on needs of cavity-nesting birds (McComb et al. 1986). This is supplying snags, but it is a much different structure than would have occurred in natural regimes. Thus, managers may need to consider more prescribed fire in wilderness areas to generate the higher-density snag habitats. They also need to evaluate the function of the snags on areas burned by wildfire before they decide to salvage them for the revenue they can generate. These snags may have a much higher value to the ecosystem than previously believed.

ACKNOWLEDGMENTS

I thank the staff of the Ocala National Forest, U.S. Department of Agriculture, Forest Service for conducting the prescribed fires. Mike Allen suffered through the heat and tangled jungle of fallen stems and sprouting oaks to help collect the data. I am indebted to Patricia A. Outcalt for data summary, analyses, and figures for this paper.

LITERATURE CITED

- Brendemuehl, R.H. 1990. *Pinus clausa* (Chapm. ex Engelm.) Vasey ex Sarg. Sand pine. Pages 294–301 in *Silvics of North America: 1. Conifers*. Volume 1. Agriculture Handbook 654, U.S. Department of Agriculture, Forest Service, Washington, D.C.
- Cain, M.D. 1996. Hardwood snag fragmentation in a pine-oak forest of southeastern Arkansas. *American Midland Naturalist* 136:72–83.
- Caine, L.A., and W.R. Marion. 1991. Artificial addition of snags and nest boxes to slash pine plantations. *Journal of Field Ornithology* 62:97–106.
- Christman, S.P., and W.S. Judd. 1990. Notes on plants endemic to Florida scrub. *Florida Scientist* 53:52–73.
- Cline, S.P., A.B. Berg, and H.M. Wight. 1980. Snag characteristics and dynamics in Douglas-fir forests, western Oregon. *Journal of Wildlife Management* 44:773–786.
- Conner, R.N., J.C. Kroll, and D.L. Kulhavy. 1983. The potential of girdled and 2,4-D-injected southern red oaks as woodpecker nesting and foraging sites. *Southern Journal of Applied Forestry* 7: 125–128.
- Cooper, R.W. 1951. Release of sand pine seed after a fire. *Journal of Forestry* 49:33 1-332.
- Dickson, J.G., R.N. Conner, and J.H. Williamson. 1983. Snag retention increases bird use of a clear-cut. *Journal of Wildlife Management* 47:799–804.
- Greenberg, C.H., L.D. Harris, and D.G. Neary. 1995a. A comparison of bird communities in burned and salvage-logged, clear-cut, and forested Florida sand pine scrub. *Wilson Bulletin* 107:40–54.
- Greenberg, C.H., D.G. Neary, and L.D. Harris. 1994. Effect of high-intensity wildfire and silvicultural treatments on reptile communities in sand-pine scrub. *Conservation Biology* 8: 1047–1057.
- Greenberg, C.H., D.G. Neary, L.D. Harris, and S.P. Linda. 1995b. Vegetation recovery following high-intensity wildfire and silvicultural treatments in sand pine scrub. *American Midland Naturalist* 133: 149-1 63,
- Hanula, J.L. 1996. Relationship of wood-feeding insects and coarse woody debris. Pages 55–81 in J.W. McMinn and D.A. Crossley, Jr. (eds.). *Biodiversity and coarse woody debris in southern forests*. General Technical Report SE-94, U.S. Department of Agriculture, Forest Service, Southeastern Forest Experiment Station, Asheville, NC.
- Harmon, M.E. 1982. Decomposition of standing dead trees in the southern Appalachian Mountains. *Oecologia* 52:214–215.
- Harper, R.M. 1927. Natural resources of southern Florida. Pages 27-206 in Florida State Geological Survey eighteenth annual report. State Geological Survey, Tallahassee, FL.
- Hartnett, D.C., and D.R. Richardson. 1989. Population biology of *Bonamia grandiflora* (Convolvulaceae): effects of fire on plant and seed dynamics. *American Journal of Botany* 76: 361–369.
- Hintze, J.L. 1995. NCSS 6.0 statistical system for Windows. User's guide. Number Cruncher Statistical Systems, Kaysville, UT.
- Horton, S.P., and R.W. Mannan. 1988. Effects of prescribed fire on snags and cavity-nesting birds in southeastern Arizona pine forests. *Wildlife Society Bulletin* 16:37–44.
- Hough, W.A. 1973. Fuel and weather influence wildfires in sand pine forests. Research Paper SE-106, U.S. Department of Agriculture, Forest Service, Southeastern Forest Experiment Station, Asheville, NC.
- Johnson, S.F. 1982. Some demographic characteristics of the Florida rosemary *Ceratiola ericoides* Michx. *American Midland Naturalist* 108: 170-1 74.
- Keetch, J.J., and G.M. Byram. 1968. A drought index for forest fire control. Research Paper SE-38, U.S. Department of Agriculture, Forest Service, Southeastern Forest Experiment Station, Asheville, NC.
- Kurz, H. 1942. Florida dunes and scrub, vegetation and geology. Florida Geological Survey Bulletin No. 23:1–154.
- Laessle, A.M. 1958. The origin and successional relationship of sandhill vegetation and sand pine scrub. *Ecological Monographs* 28:361–387.
- Lyon, L.J. 1977. Attrition of lodgepole pine snags on the Sleeping Child burn, Montana. Research Note INT-219, U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station, Ogden, UT
- McCay, T.S. 2000. Use of woody debris by cotton mice (*Peromyscus gossypinus*) in a southeastern pine forest. *Journal of Mammalogy* 8 1:527–535.
- McComb, W.C., S.A. Bonney, R.M. Sheffield, and N.D. Cost. 1986. Snag resources in Florida—Are they sufficient for average populations of primary cavity-nesters? *Wildlife Society Bulletin* 14:40–48.
- Myers, R.L. 1990. Scrub and high pine. Pages 150–193 in R.L. Myers and J.J. Ewel (eds.). *Ecosystems of Florida*. University of Central Florida Press, Orlando.
- Outcalt, K.W. 1997. An old-growth definition for sand pine forests. General Technical Report SRS- 12, U.S. Department of Agriculture, Forest Service, Southern Research Station, Asheville, NC.
- Outcalt, K.W., and C.H. Greenberg. 1998. A stand-replacement prescribed burn in sand pine scrub. *Proceedings of the Tall Timbers Fire Ecology Conference* 20: 141–145.
- Raphael, M.G., and M.L. Morrison. 1987. Decay and dynamics of snags in the Sierra Nevada, California. *Forest Science* 33:774–783.
- Small, J.K. 1921. Old trails and new discoveries. A record of exploration in Florida in the spring of 1919. *Journal of the New York Botanical Garden* 22:25–40, 49-64.
- Snedaker, S.C., A.E. Lugo, H.K. Brooks, A.H. Horton, and D.A. Pool. 1972. Ecology of the Ocala National Forest. U.S. Department of Agriculture, Forest Service, Southern Region, Atlanta, GA.
- Veno, P.A. 1976. Successional relationships of five Florida plant communities. *Ecology* 57:498–508.