Small-Scale Disturbances In Longleaf Pine Forests

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ABSTRACT

Small-scale disturbances are neglected areas of study in longleaf pine forests. The vegetation of this habitat is species-rich and studies in other diverse forests and grasslands have demonstrated that small-scale disturbances are common and are often critical in maintaining a portion of the native flora. In longleaf pine forests, actions of gopher tortoises, pocket gophers, ants and other arthropods all expose patches of soil but only a handful of published studies explore the impact of these disturbances on the habitat.

In addition to animal-mediated disturbances, other types of small-scale patches are found in old-growth longleaf pine forests. Observations made on the Wade Tract Preserve, an old-growth stand, indicate that there are previously undescribed disturbances associated with large (>25 cm DBH) downed trees. Downed longleaf pines can result in more than one type of small-scale disturbance; these include: 1) eradicated areas of ground cover related to fire in heavy fuels near logs, 2) complex patches of intensely burned and unburned areas created by the interaction of fire and large branches of downed tree crowns, 3) unburned patches on the leeward sides of large logs and 4) tip-up mounds created by uprooted trees. These disturbances are almost non-existent in modern longleaf forests because they are populated by relatively small trees. Ongoing research indicates that disturbances associated with large logs may be critical to understanding patterns of establishment and spatial arrangement of both ground cover species and longleaf pine seedlings in old-growth forests.

INTRODUCTION

A large body of scientific literature demonstrates the ecological significance of small-scale disturbances, especially as they relate to aspects of plant community ecology including species richness, evenness and dominance, and spatial heterogeneity (cf. Sousa 1984, Pickett and White 1985). In addition, fire may affect disturbance pathways that in turn enhance diversity (Malanson 1987). Research on small-scale disturbances has been relatively extensive in some habitats, including grasslands (cf. Loucks et al. 1985, Platt 1975), temperate hardwood forests (cf. Runkel 1985) and tropical rain forests (cf. Denslow 1987). In grasslands, most research focuses on animals as agents of disturbance whereas in forests such studies concentrate on fallen trees.

Despite acknowledgment of the general importance of disturbances in determining the structure and function of many ecosystems, there is little published information on disturbance in longleaf pine-wiregrass forests (but see Kaczor and Hartnett 1990). If it can be established that agents of disturbance were part of the pre-European settlement old-growth landscape, then knowledge of them may significantly improve our understanding of the ecology of this forest. Kessler et al. (1992) note that a healthy forest is one that maintains not only species but also natural processes.

This paper considers the topic of small-scale disturbances in longleaf pine forests and reviews available literature. In addition, it presents observations on small-scale disturbances on the Wade Tract Preserve, an old-growth longleaf pine-wiregrass forest in southern Georgia. I present a brief discussion of the interaction of fire and small-scale disturbances, particularly those related to large, downed logs. Of special interest is the possible relationship between large downed trees and the establishment of juvenile longleaf pine.

WADE TRACT PRESERVE

The Wade Tract Preserve (WTP), a privately owned 80 ha old-growth longleaf pine-wiregrass stand in Thomas County, Georgia is managed by

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Tall Timbers Research Station. Soils include Faceville, Orangeburg and associated series; Wharton (1979) described the substrate as "low in organic content, ... and acidic with a heavy clay subsoil...". For much of this century, the site was burn almost annually in early spring. During the last decade, each half of the preserve has received prescribed fire during the lightning season (May-June in this part of the Coastal Plains) every other year. The ground cover has suffered minimal human disturbance; the site was never clear cut and no live trees have been harvested in recorded history, although standing dead trees were sometimes removed (salvaged). In addition, the native fauna appears to be intact, except for the local extirpation of some large mammals such as panther, bear and red wolf. Among the resident animal species, gopher tortoises, pocket gophers and a variety of ants (including harvester and fire ants) create soil disturbances. Folkerts et al. (1993) discusses additional soil disrupting arthropods for the region.

The WTP served as the focus for work by Platt et al. (1988) and Platt and Rathbun (1993) that quantifies the spatial relationship between juvenile and adult components of the longleaf pine population. A permanent grid system divides the site into 100 m x 100 m (1 ha) cells. Platt et al. (1988) provides additional information on the site.

The WTP is one of the few longleaf sites that currently exhibits a full range of old-growth conditions, including large downed logs. Logs began to accumulate in 1979 when the site became a preserve; dead and dying trees were no longer salvaged. Platt et al. (1988) noted that lightning and small wind storms kill a small number of old trees every year. There was a large pulse of adult mortality in 1985 when the forest was impacted by Hurricane Kate. Platt and Rathbun (1993) discuss the effect of the hurricane on the longleaf pine population; Engstrom and Evans (1990) outline the impact of this disturbance on cavity trees of red-cockaded woodpeckers.

In this paper, data are presented from 10 randomly chosen 1 ha cells on the WTP. The smallest disturbances, those created by pocket gophers and ants, were surveyed within a few weeks after prescribed fires, in an effort to maximize locating them. At the same time, previously unmarked gopher tortoise burrows were added to a long-term data base. Information on large downed logs was collected throughout the year.

DEFINITION OF SMALL-SCALE DISTURBANCE

Sousa (1984) defined a disturbance as "a discrete, punctuated killing, displacement, or damaging of one or more individuals (or colonies) that directly or indirectly creates an opportunity for new individuals (or colonies) to become established". Many authors distinguish between large- (coarse) and small- (fine) scale events. Sousa's definition is particularly appropriate for small-scale perturbations that occur in most terrestrial ecosystems. White and Pickett (1985) suggest consideration of small areas ranging from 1 cm^2 to 100 ha. This size range reflects that of individual plants or patches of vegetation killed as the result of animal activity, pathogenic infections, wind damage, lightning strikes, etc. Some sources of mortality, such as drought, are obviously large-scale (> 100 ha). Others, such as herbivory (grazing) and fire, may operate at multiple levels of scale.

Although fire is usually included in general lists of disturbances (cf. Sousa 1984, White and Pickett 1985), there is a debate over whether frequent, low-intensity fires that kill few, if any established individuals is a disturbance. Collins (1990) argues that it is. White and Pickett (1985) focus on additional aspects of community change and distinguish two alternative types of disturbance, "destructive events and environmental fluctuations". Most fire in longleaf pine forests results in short-term environmental fluctuations and these types of effects will not be covered in the current paper. However, there are conditions in this habitat that involve the action of fire in conjunction with one or more additional components that produce responses consistent with expectations for small-scale disturbances. Collins and Gibson (1990) noted that prairie fires often act in consort with other factors such as soil disturbances. Possible examples of multi-agent disturbances, where fire is one factor in the small-scale destruction of vegetation in longleaf pine forests, are discussed below.

SPATIAL SCALE

Spatial heterogeneity and biodiversity can be viewed at many scales. In review papers of region-wide ground cover diversity, Peet and Allard (1993) and Harcombe et al. (1993) provide documentation of the large-scale community complexity of longleaf pine habitats. Both papers consider the importance of soil type and hydrology in determining plant species composition. On a local scale, spatial patchiness of longleaf trees was noted by Schwartz (1907) and quantified for stems > 2 cm DBH by Platt et al. (1988). However to date, only scattered published information on small-scale disturbance exists for longleaf pine forest ground cover (see below).

SOIL DISRUPTION BY ANIMALS

The gopher tortoise (*Gopherus polyphemus*) is often noted as an agent of soil disturbance in longleaf pine forests (cf. Myers 1990). This land turtle constructs burrows and in doing so produces mounds (aprons) of soil in front of the excavated hole; existing vegetation is buried. Burrows can remain in use, with soil continuously disrupted, for many years. In their study on sandhill sites, Kaczor and Hartnett (1990) describe mounds each covering approximately 1 m^2. Smaller patches of bare soil are associated with other organisms, including the pocket gopher (*Geomys pinetus*), ants and scarab beetles (Kalisz and Stone 1984, Folkerts et al. 1993).

Although gopher tortoise mounds are abundant on the WTP, so are other types of animal disturbances; in places, they exceed 100 distinct patches per hectare (Table 1). Burrowing spiders, beetles and mice create some of these but each is less than 2 cm^2. Of potentially greater significance are three-types of larger disturbances: gopher tortoise, pocket gopher and ant mounds (Table 1). On the WTP, gopher tortoise mounds represent the largest area of small-scale disturbance related to animal activity. On average, 0.2% or more of each ha is disturbed by tortoises. The size of adult gopher tortoise mounds on the WTP is similar to that reported by Kaczor and Hartnett (1990). At any point in time, pocket gopher and ant disturbances contributed minor amounts to the overall area impacted by animals. However, Folkerts et al. (1993) point out that small substrate disruptions may have significance for soil aeration and introduction of organic matter into surface substrate.

In addition to creating patches of bare soil, animal activity may also alter levels of microsite soil nutrients. Differences in soil chemistry between

TABLE 1: Small-scale disturbances in the ground cover of an old-growth longleaf pine-wiregrass forest in Thomas County Georgia. Sample based on 10 randomly chosen 1 ha plots, censused in 1991.

Disturbance	$\bar{X}$ number/ha (+/- s.e.)	Range of Number/ha	Range of Estimated Area Covered/ha
Gopher Tortoise Mounds	10.2 (5.6)	0-21	0-21 m^2
Pocket Gopher Mounds	51.7 (32.0)	1-93	0.02-2.0 m^2
Ant Mounds[a]	3.4 (4.3)	0-10	0-0.4 m^2
Large Logs[b]	5.7 (3.9)	1-11	75-1,500 m^2
Stump Holes (many with no logs)	24.0 (8.9)	13-33	5.2-13.2 m^2
Stumps[c] (many with no logs)	17.8 (8.5)	9-39	?

[a] areas created by harvester and fire ants are pooled
[b] >25 cm dbh
[c] majority of area occupied by dead wood and not available for colonization

gopher tortoise mounds and undisturbed sites was documented by Kaczor and Hartnett (1990). On sandhill sites, they observed a general decrease in soil nutrients in mounds as compared to undisturbed soil (Table 2). Soil mixing by gopher tortoises did not enhance most microsite nutrients (Kaczor and Hartnett 1990). This contradicts decades-old suggestions that tortoises return leached nutrients to the surface (Harper 1914). Kaczor and Hartnett (1990) also documented a smaller amount of organic matter on mounds compared to undisturbed soil. This suggests that tortoises do not move large amounts of fecal material to the surface.

Although Kalisz and Stone (1984) included longleaf sites in their study of a scarab beetle (*Peltotrupes youngi*) and a pocket gopher (*Geomys pinetus*), they measured soil nutrients only on beetle disturbances in areas with sand pine (*Pinus clausa*). Gentry and Stiritz (1972) examined soil nutrients in disturbances created by ants that are often found in longleaf sites; unfortunately their sites were on old-field land. Though the data from these projects did not target longleaf sites, it does have limited use in the current discussion, indicating that beetles and ants may enhance nutrients in their disturbances (Table 2).

Golley and Gentry (1964) studied the southern harvester ant (*Pogonomyrmex badius*) in South Carolina. Although the study site was on deep sandy soils, appropriate for longleaf pine, it was old field land. Their data show a substantial increase in both number of plant species and individuals found on two-year old abandoned ant hills compared to one-year old ones. There is no way to extrapolate these results to intact longleaf pine ground cover but they do suggest that similar research in longleaf pine forests could be interesting.

There is the possibility that the ground cover in longleaf pine forests were once impacted by large mammals. Today, buffalo are not usually thought of as indigenous to the Southeast but they were present in the region until the eighteenth century. Bartram (1791) noted that the animal, "...once so very numerous, is not at this day to be seen in this part of the country...". There is no easy way to evaluate what impact this species had on native vegetation of the Southeast. However, observations in modern prairies suggest that they may have played a role, although perhaps a small one, in maintaining biodiversity in longleaf pine forests. Polley and Wallace (1986) demonstrated that buffalo wallows were a significant feature in Okla-

TABLE 2. Comparison of selected soil chemical characteristics on and off mounds created by animal soil disturbances. It should be noted that each organism was studied at a different site. > = reading from mound was greater than off mound; < = reading from mound was less than off mound; ns = readings were not significantly different; — = no data collected; OM = percent organic matter.

Agent of Disturbance	Soil Chemical Characteristics							
	pH	P	K	Ca	Mg	NH_4	NO_3	OM
Gopher Tortoise[a] (*Gopherus polyphemus*)	>	ns	>	<	<	<	ns	<
Harvester Ant[b] (*Pogonomyrmex badius*)	ns	>	ns	ns	—	—	—	—
Scarab Beetle[c] (*Peltotrupes youngi*)	—	>	—	ns/>[d]	ns/>[d]	—	—	—

[a] from Kaczor and Hartnett 1990, central Florida
[b] from Gentry and Stiritz 1972, South Carolina; old-fields sites
[c] from Kalisz and Stone 1984, central Florida
[d] Ca and Mg were measured together on two sites with outcomes of "ns" and ">"

homa grasslands. They determined that the disturbance created by the trampling and dust-bathing of bison (*Bison bison*) increased habitat diversity and influenced plant species composition. At times, NH_4, NO_3, P, Mg, and/or pH were altered inside the wallow as compared to undisturbed soil.

Although there is obviously a need for additional study on possible soil nutrient differences on and off animal-created disturbances, a more immediate standard of significance may be measures of how soil disturbances impact the plant community structure. There are only preliminary studies on this topic. Kaczor and Hartnett (1990) monitored seed germination on gopher tortoise burrow mounds in central Florida sandhills for one year. Generally, there was a lower coverage of forbs on abandoned mounds than on undisturbed plots. Less than half of the spring recruits (summed over all species) survived to late summer of the same year. Although individuals of *Pityopsis graminifolia* were smaller on mounds compared to undisturbed plots, the authors postulated that this was because a high proportion of stems of this clonal plant were vegetative recruits in undisturbed areas and true seedlings on tortoise mounds. Additional research is needed to determine if these soil disturbances are true safe havens for plant establishment.

Kaczor and Hartnett (1990) and Hermann (1990) suggest that vegetation on mounds associated with old and/or abandoned gopher tortoise burrows represent patches in the ground cover mosaic. On their sandhill sites, Kaczor and Hartnett (1990) found more plant species on old mounds than mounds associated with recently abandoned burrows or on undisturbed sites. They found four species exclusively on recently abandoned mounds but no species exclusively on old mounds. Hermann (1990) also noted no plant specialists for mounds in the WTP on less sandy soils.

Mounds of abandoned burrows with a clay component may take longer to return to a pre-disturbance state than those on deep sandy soils. WTP soils have a clay component and on that site Hermann (1990) noted a significant difference persisted in the amount of bare soil in undisturbed areas compared to mounds abandoned for more than a decade. This is in contrast to observations on mounds in sandy soil on the Conecuh National Forest in Alabama; here effects of disturbances may disappear in just a few years after burrow abandonment (C. Guyer, pers. comm.).

Casual observations on the WTP detected no vegetation recruitment patterns associated with pocket gopher disturbances. None of more than 100 longleaf seedlings survived more than 3 months after germinating on pocket gopher mounds. Although undocumented, it appears as though fire ant (*Solenopsis* sp.) mounds may be more likely to be associated with established clumps of grass than any other type of vegetation. It may be important to determine if fire ants construct mounds preferentially next to specific ground cover species and to distinguish mounds constructed by native versus exotic fire ants. Work by Tschinkel (1987) suggests that the recently introduced fire ant (*S. invicta*) is not likely to be present.

There are also reasons to explore possible interactions between fire and gopher tortoise mounds and perhaps trails created by the animals. Mounds associated with active gopher tortoise burrows may not normally provide safe sites for recolonization; the soil is periodically disturbed by tortoise activity (Hermann 1990). However, there appears to be a narrow ring, a few centimeters in width, on the outer vegetated edge of mounds that supports a different microsite climate. Casual observation indicates that these narrow rings of vegetation often have lower intensity or less frequent fire than surrounding vegetation, probably due to less and/or compacted fuel. The amount of such areas that have been surveyed to date are too small to draw definitive conclusions. There is some indication that this zone may provide relatively safe sites for longleaf pine establishment.

TREE FALL GAPS AND LARGE, OLD TREES

Tree falls and resulting canopy gaps have been studied in forests world-wide. Much of this research focuses on increased light and sometimes concurrent shifts in temperature and/or relative humidity, all related to the removal of a tree canopy over a patch of forest floor. These topics are noticeably absent in the longleaf pine literature, probably for two reasons. The most obvious one is that longleaf pine forests are remarkably open in canopy structure. The openness is the result of widely spaced trees with sparse crowns. Changes in light regimes following a tree fall in a longleaf pine forest appear to be insignificant compared to closed canopy hardwood stands. To date there is no documentation that changes in light regimes as the result of a longleaf pine canopy gap, in an already open forest, impact community diversity.

There is a less obvious but more significant reason that tree falls have not been studied in longleaf pine forests. Trees that make up the vast majority of modern longleaf forests usually are only a few decades old; this contrasts with old-growth stands in which individuals survive for centuries. There are many potential differences between the impact of a tree fall of an 80 year old longleaf pine compared to a 250 year old one. The relatively young trees are substantially smaller than trees dominating true old-growth. Wood characteristics are much different between young and centuries-old trees (reviewed in Wahlenberg 1946). Additional significance of the dearth of old trees is highlighted below.

In addition to the impact of opening a hole in the canopy, a fallen tree may also result in a soil disturbance. If the tree tips up, roots are dislodged and a relatively large bare patch of soil may be created. Schaetzl et al. (1989) reviewed ways in which these areas are significantly different from surrounding undisturbed habitat in a variety of forests. Tree uprooting has not been studied in longleaf pine forests. It is logical to assume that old-growth trees would differ from younger trees in the impact of this type of disturbance.

Another type of disturbance associated with large, fallen trees is the stump hole created by the decay and burning of the root system of standing dead or snapped off trees. Roots of dead, large longleaf burn and create underground tunnels. D.B. Means (pers. comm.) has long suggested, that these sites are important refuges for a range of small mammals, amphibians, reptiles and invertebrates. In other forest types, they may even serve as nest sites for bird species. Stump holes that result from large, old trees are expected to be structurally more complex and persist longer than those caused by smaller, younger individuals. Again, this difference is related to differences in initial size of the disturbance and to length of time each persists.

Logs of large, dead trees may be the most overlooked source of small-scale disturbance in old-growth longleaf forests. In other forest types, the logs of large trees are known to have a variety of important roles in community structure and function (cf. Masser et al. 1988). Among other things, they have been documented to alter nutrient cycling and seedling recruitment of both trees and understory species.

Preliminary data from 10 randomly chosen 1 ha plots on the WTP, indicate that from 1-15% of each hectare may be directly impacted by large downed logs (Table 1). Although individuals of most ground cover species have been eliminated from these sites, not all of the area is immediately available for recolonization. Some portion of these zones is currently covered by bark and/or decaying wood.

Long-term studies are necessary to determine the actual patterns of revegetation and consequently the significance of logs on ground cover composition and structure. However, there are preliminary data that suggest areas associated with large downed longleaf pine logs may play a critical role in ground cover dynamics and in longleaf pine establishment.

For example, *Cassia nictitans* (wild sensitive plant, a native ruderal), one year post-burn, had much higher stem densities in some log sites (11.4 +/- 5.8 s.e.) compared to nearby areas away from logs (2.6 +/- 1.9 s.e.). One m^2 areas were surveyed next to 10 burned logs. In some cases, these large logs burn for many days after the passage of the fire (Figure 1); above ground vegetation was killed and did not resprout; bare areas of soil were created and, at 25 cm above the soil surface, vegetation cover was less that 20% a year after burning.

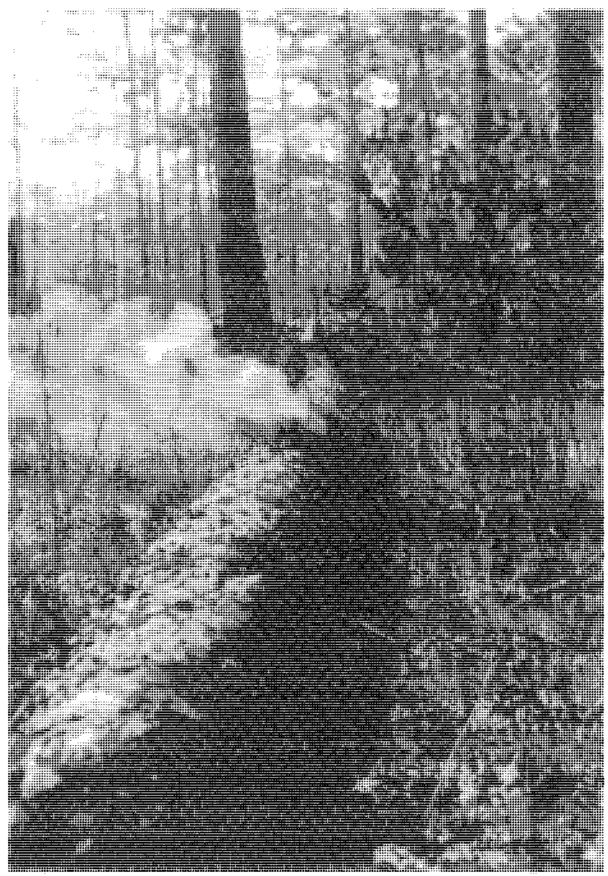

Figure 1: This log of a 200+ year old longleaf pine burned for more than 5 weeks after a June fire.

In 10 m^2 plots near but not including areas burned by a log, vegetation cover was greater than 75% a year after burning.

More significant to overall forest structure is preliminary evidence that burned areas associated with large logs, especially the crown region, are important sites for longleaf pine establishment (Figure 2). Three and a half years after germination and one year after a lightning-season fire, some longleaf juveniles near burned logs initiated height growth. No other juveniles, growing in any other type of microsite appeared to be leaving the grass stage. Of 214 longleaf juveniles surveyed in burned log areas, 29 had some height growth; most of these were between the large branches of the downed crown. Of 136 juveniles surveyed away from logs, none exhibited height growth. Although the numbers are small, the difference is significant (X^2 = 20.1, p=.02).

It is not clear what characteristics of the microsite of burned log areas are specifically advantageous and if this advantage to juvenile longleaf pine will persist and/or increase over time. In addition, soil type and/or ground cover vegetation density may influence this interaction with fire. On sandy soil the impact may be decreased. It is clear that small-scale disturbances associated with large downed logs, warrant continued study.

INTERACTIONS BETWEEN DISTURBANCE AND FIRE

Other authors have noted that small-scale disturbances in grasslands may interact with fire (reviewed by Collins and Gibson 1990). For example, the interaction of grazing and fire resulted in increased complexity of community structure (Collins 1987). When additional types of disturbances (such as small soil disruptions) are considered, structure may not be greatly affected by fire but fire can enhance the rate of recolonization (cf. Collins 1989).

Myers (1990) commented on the possible interaction of downed trees and fire in another Southeastern forest type, Florida scrub. He noted that old, fallen sand pine trees (*Pinus clausa*) can "...burn longer and hotter than the rest of the vegetation" and suggested that the resulting bare areas would be available for colonization.

Preliminary information from the WTP studies suggest that similar, multi-agent disturbances were once potentially common place in old-growth longleaf pine forests. Large numbers of animal-created soil disturbances covering relatively small areas may have been typical. At least during some time periods, large downed trees were probably also common and could have impacted much

Figure 2: A clump of established longleaf pine juveniles are associated with the burned out crown area of a 200+ year old tree on the Wade Tract Preserve.

larger areas than animal disturbances. Fire is acknowledged to have been frequent over the geographic range of longleaf pine (cf. Robbins and Myers 1992). Consequently the potential for complex, multi-agent disturbances in pre-settlement forests was very likely.

DISTURBANCE REGIMES IN OLD- AND SECOND-GROWTH FORESTS

Modern concepts of ecosystem management require that land stewards understand the structure and function of natural (ie. old-growth) forests so that they may better evaluate the impact of various management activities (cf. Swanson and Franklin 1992). In second-growth longleaf pine forests, if the native fauna remains intact and prescribed fire is applied appropriately, fire and animal-mediated soil disturbances are likely to interact in ways that approximate pre-settlement conditions. Conversely, the dearth of old, large longleaf pine trees in modern forests may almost completely eliminate related types of disturbances that once interacted with fire in pre-settlement forests. Review of information from the Wade Tract Preserve suggests that these disturbances may have impacted large areas, had important interactions with fire and been critical in the controlling, in part, the spacial structure old-growth forests.

CONCLUSIONS

The preliminary information outlined in this paper suggests that small-scale disturbances were important components of the pre-European settlement landscape of the Southeastern United States. To date, conservation efforts focused on rehabilitating second-growth stands have dealt almost exclusively with re-establishment of fire regimes. Unfortunately this may not be sufficient to re-create a full range of components of a natural landscape. Animal-created disturbances will be present in many second-growth sites but there is likely to be a dramatic shortage of large downed trees. Our lack of understanding of the impact of downed old-growth trees may limit current efforts at designing effective ecosystem management plans for this habitat.

If we are to understand the natural, old-growth state of longleaf pine forests, continued research is needed on many aspects of disturbance ecology. Swanson and Franklin (1992) discuss the benefits of understanding how old-growth forests function even when the goal of management is not to mimic naturalness. They note "... the strategy is to use knowledge of natural ecosystems to develop practices of sustainable ecosystem management...". The information presented above demonstrates that small-scale disturbances are prevalent in old-growth longleaf pine forests; there are indications that the patches that result from the disturbances play a role in determining spatial patterns in ground cover species and in the establishment phase of longleaf pine trees. We may not be able to effectively implement the concept of ecosystem management in longleaf pine forests until there is more extensive research available on the impact of small-scale disturbances.

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