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# Modeling silviculture after natural disturbance to sustain biodiversity in the longleaf pine (*Pinus palustris*) ecosystem: balancing complexity and implementation

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## Abstract

Modeling silviculture after natural disturbance to maintain biodiversity is a popular concept, yet its application remains elusive. We discuss difficulties inherent to this idea, and suggest approaches to facilitate implementation, using longleaf pine (*Pinus palustris*) as an example. Natural disturbance regimes are spatially and temporally variable. Variability leads to a range of structural outcomes, or results in different pathways leading to similar structures. In longleaf pine, lightning, hurricanes, surface fires, and windthrow all lead to similar structures, but at different rates. Consequently, a manager can select among various natural disturbance patterns when searching for an appropriate silvicultural model. This facilitates management by providing flexibility to meet a range of objectives. The outcomes of natural disturbances are inherently different from those of silviculture, for example, harvesting always removes boles. It is instructive to think of silvicultural disturbances along a gradient in structural outcomes, reflecting degree of disparity with natural disturbance. In longleaf pine this might involve managing for two-cohort structure, instead of multi-cohort structure characteristic of old growth stands. While two-cohort structure is a simplification over the old growth condition, it is an improvement over single-cohort management. Reducing structural disparity between managed and unmanaged forests is key to sustaining biodiversity because of linkages that exist between structural elements, forest biota, and ecosystem processes. Finally, interactions of frequency, severity, intensity, seasonality, and spatial pattern define a disturbance regime. These components may not have equal weight in affecting biodiversity. Some are easier to emulate with silviculture than are others. For instance, ecologists consider growing-season fire more reflective of the natural fire regime in longleaf pine and critical for maintenance of biodiversity. However, dormant season fire is easier to use and recent work with native plants suggests that seasonality of fire may be less critical to maintenance of species richness, as one component of biodiversity, than is generally believed. Science can advance the goal of modeling silviculture after natural disturbances by better illustrating cause and effect relationships among components of disturbance regimes and the structure and function of ecosystems. Wide application requires approaches that are adaptable to different operational situations and landowner objectives. A key point for managers to remember is that strict adherence to a silvicultural regime that closely parallels a natural disturbance regime may not always be necessary to maintain biodiversity. We outline examples of silvicultural systems for longleaf pine that demonstrates these ideas. © 2002 Elsevier Science B.V. All rights reserved.

*Keywords:* Natural disturbance; Silviculture; Longleaf pine; Biodiversity; Prescribed fire

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## 1. Introduction

Studies of forest ecosystems illustrate the important role of natural disturbance in regulating ecosystem properties, including biodiversity (Glitzenstein et al., 1986; Franklin et al., 1987; Busing and White, 1997). We define biodiversity broadly to include the variety and spatial patterns of physical structures, processes, species, and genotypes in a forest. Species and genetic diversity often are dependent on structural and process diversity (Franklin, 1988). Natural disturbance influences these interrelationships in numerous ways. For instance, canopy disturbances alter microclimate and resource availability (Mladenoff, 1987; Palik et al., 1997), favoring different suites of organisms than those occurring in a closed forest (Ehrenfeld, 1980; Collins et al., 1985). Surface fires affect soil resource availability and microclimate and, ultimately, plant and soil fauna communities (Wilbur and Christensen, 1983; Walker and Peet, 1983). There are many other examples. Our point is that natural disturbances create variety and heterogeneity of structures and processes in a forest, which, in turn, influence the variety and diversity of species found in that forest.

It follows that maintenance of species and genetic diversity in managed forests may reflect the degree that silvicultural disturbances create the same variety and spatial heterogeneity of structures and processes as natural disturbances. There is ever increasing attention paid to this idea of modeling silvicultural disturbances after natural disturbances to maintain biodiversity (Seymour and Hunter, 1992; Franklin et al., 1997). This attention reflects concern over the role of traditional forest management in loss of biodiversity (deMaynadier and Hunter, 1995). Recent ecological research offers innovative silvicultural approaches designed to sustain biodiversity while managing for timber (e.g. Coates and Burton, 1997). Unfortunately, it is not always transparent how these ecological perspectives deal with real-world constraints of managing forests for profit. In other words, the lack of clear guidelines for implementation of natural disturbance-based silvicultural models hinders adoption of the approach.

We suggest that difficulty in implementation stems from three characteristics of natural disturbances. First, there often are several types of natural disturbances affecting a particular type of ecosystem, resulting in different structural outcomes or in different pathways leading to similar structure. A manager may find it difficult to duplicate this same variety with silviculture. Second, the outcomes of natural disturbance are inherently different from silvicultural disturbance. Acceptance of some differences is key to developing silvicultural approaches that balance trade-offs among different objectives. Lastly, natural disturbance regimes reflect interactions of multiple components including type, intensity, severity, frequency, seasonality, and spatial pattern. Some components have greater impact on biodiversity than others, and some are easier to emulate with silviculture, suggesting that a manager need not always adhere to a strict natural disturbance-based model. In the following pages, we discuss these three characteristics in more detail, illustrating our ideas using longleaf pine (*Pinus palustris* Mill.) ecosystems in the southeastern United States. Our objective in this discussion is to call attention to the constraints that make emulation of natural disturbance with silviculture difficult. More importantly, we suggest approaches that help to overcome this difficulty and reduce the complexity of meeting both biodiversity and timber management goals using natural disturbance-based silviculture.

## 2. Natural disturbances vary over space and time

Often, several different types of natural disturbance affect a given forest ecosystem. In terms of rates of change or degree of alteration of forest structure, the outcomes of these disturbances may differ. The question for a manager who is trying to model silviculture after natural disturbance is what is the appropriate model to follow.

The structural outcomes of different types of disturbance can vary markedly. For instance, canopy disturbances in conifer forests of the coastal Pacific Northwest include large-scale, stand-replacing fire, wind disturbance that opens small gaps, and low to moderate intensity fires that kill patches of trees (Spies and Turner, 1999). A manager can view this variation as an impediment to designing silvicultural practices that emulate nature, because of difficulty in choosing the appropriate model, or they can view variation as an opportunity to be creative silviculturally. Variation in types of natural disturbance suggests that there are several legitimate natural models on which to base silvicultural disturbance, all leading to different structural outcomes. This choice gives managers great opportunity to meet different objectives by varying the characteristics of their silvicultural practices over space or time.

Another approach for dealing with variability in types of disturbances is to look for commonalities in their structural outcomes. For instance, does individual tree windthrow and larger patch blowdown create canopy gaps of similar size, only at different rates? The idea here is that structural characteristics such as gap size directly affect functional characteristics of a forest, such as soil resource availability or faunal habitat. Nature may reach similar stand structures following alternative pathways, all of which lead to similar outcomes in terms of effects on biodiversity. The concept that function follows form suggests that the particular pathways followed by silvicultural disturbance may be less important than the resultant structural outcomes.

As an example, consider longleaf pine ecosystems in the southeastern United States. The characteristic stand structure of mature and old growth longleaf pine woodlands includes multiple cohorts of trees, with regeneration occurring in canopy gaps (Platt et al., 1988a). The minimum gap size for unimpeded growth of longleaf pine regeneration, based on research into the effects of overstory structure on competition, is approximately 0.14 ha (Palik et al., 1997). Maximum opening size may range up to several hectares, but most gaps are smaller.

From a silvicultural standpoint, it is instructive to consider how different natural disturbances create gaps in the longleaf pine canopy. There are several characteristic types of canopy disturbance that affect longleaf pine. These range from individual tree windthrow and lightning strikes, to group lightning strikes and crown fires that kill patches of trees, to large-scale blowdowns from hurricanes (Platt and Rathbun, 1993; Palik and Pederson, 1996). All of these disturbances create gaps of the size required for successful longleaf pine regeneration, but they do not occur with the same frequency or intensity (Table 1). Consequently, they create gaps at different rates. Hurricanes form large gaps in seconds, whereas it may take centuries for single-tree windthrow events or lightning strikes to expand gaps to the minimum size required for regeneration of longleaf pine (Table 1).

In this example, the pathways leading to a representative stand structure vary naturally depending on disturbance type. By analogy, different patterns of regeneration harvesting, such as single-tree removal or large patch cuts, may be equally valid ways to create stand structures that are representative of natural forest structure (Fig. 1). The key requirement for longleaf pine is that each type of silvicultural disturbance ultimately creates gaps greater than 0.14 ha in size, so that competitive environments conducive to growth of longleaf pine regeneration occur in the stand.

## 3. Differences in outcomes of natural disturbance and silviculture

Despite a silviculturist's best efforts, it is not possible to imitate a natural disturbance regime with silviculture. By design, the latter results in a number of changes that have no natural equivalents, especially in terms of the magnitude of change. The most obvious differences involve removal of trees and impacts to the forest floor and understory plant communities. For example, most natural canopy disturbances leave the bulk of aboveground biomass of a tree on site, unlike

Table 1
Characteristic canopy disturbances of longleaf pine woodlands

| Disturbance | Rate of large gap formation (>0.14 ha) | Return frequency or rate of occurrence in a given forest landscape | Reference |
|---|---|---|---|
| Hurricane | Instantaneous | Decades | Platt and Rathbun (1993) |
| Group lightning strike or gap-creating fire | Moderate: weeks to months | 1 gap × 1000 $ha^{-1}$ × 5 per year | Palik et al. (1997) |
| Individual tree windthrow or lightning strike | Slow: up to 250 years | 0.4% mortality of overstory trees per year | Palik et al. (1997) |

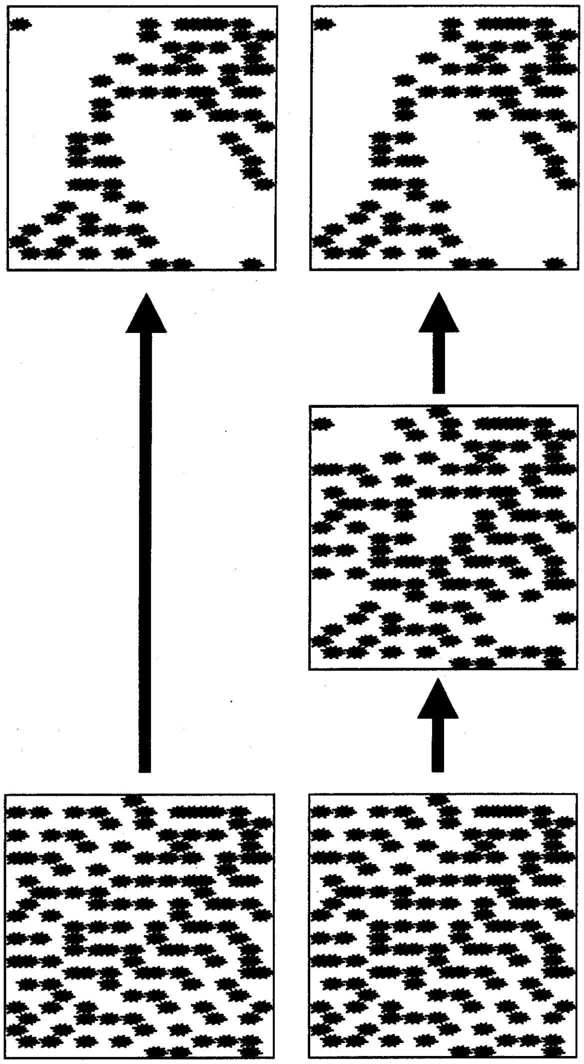

Fig. 1. Stylized representation of alternative pathways to reach a stand structure characterized by large canopy openings. In the left pathway, a single disturbance, such as a hurricane or patch cut, opens the gaps rapidly. In the right pathway, the large gaps form gradually over time, through the coalescing of several smaller openings caused by small disturbances, such as individual tree windthrow or single-tree selection.

commercial thinning and regeneration harvests. Soil compaction, while perhaps occurring naturally under large tree-falls, can be widespread after harvesting (Grigal, 2000). Some types of natural disturbance, like windthrow, disrupt soil and the forest floor, in turn affecting understory plant communities. The spatial pattern of disruption within a stand after natural disturbance is more localized and patchy compared to the disruption that occurs with equipment traffic during harvesting.

While the disparities between natural disturbance and silviculture can never be fully overcome, the differences between the two are a function of specific aspects of the silvicultural disturbance regime, including its intensity, frequency, and spatial pattern. We anticipate that the more these elements of silviculture resemble the characteristics of the natural disturbance regime, the narrower will be the gap in disparities of outcomes.

Ultimately, the degree of difference between natural and silvicultural disturbance depends on management objectives. Natural disturbance is not constrained by any objective and, conversely, it is unlikely that the objective of silviculture in a commercial forest is restricted to mimicking nature to sustain biodiversity. Still, it is important to understand the degree of difference in structural outcomes of natural and silvicultural disturbance, because this reflects where along a gradient of trade-offs between biodiversity and timber values a silvicultural action could take a forest (Palik and Engstrom, 1999). The gradient might range from monospecific plantations to unmanaged old growth forests, with every conceivable variation on disturbance intensity and structure, and dependent biodiversity, in between. By placing the current or potential structural condition of a forest on this gradient, it is possible to judge the degree of disparity between the intensively managed and unmanaged conditions. The appropriate silvicultural actions can be undertaken to reduce the disparity.

In the longleaf pine region, the historical forest management regime is replacement of native woodlands with short-rotation plantations of other native species including slash pine (*Pinus elliottii* Engelm.) and loblolly pine (*P. taeda* L.). This type of management provides little opportunity for development of structural complexity, as generated by natural disturbances. The plantations are a stark contrast to structurally complex, multi-cohort mature and old growth longleaf pine woodlands. Within these endpoints are many structural variations including, for instance, two-cohort stands where regeneration harvests leave some of the overstory intact. Structurally, the two-cohort stand is a simplification over the multi-cohort condition, yet it is more complex than plantations of loblolly or slash pines or even longleaf pine. Presumably, the two-cohort stand is more conducive to maintain functional and organismal diversity in patterns similar to the old growth condition, although the extent that this holds true is unknown.

We do know that the residual overstory in two-cohort longleaf pine stands inhibits the development of regeneration through resource competition (Boyer, 1993; Palik et al., 1997). The same impact is apparent in other types of forests, such as Douglas-fir (Birch and Johnson, 1992; Acker et al., 1998). In most forests, loss of growth, with gains in structural complexity, is an inherent consequence of balancing multiple management goals within the same stand. One solution to these constraints on growth of timber, or maintenance of biodiversity, is to partition the landscape into areas where stands have greater or lesser disparity with the ideal condition, similar to the landscape triad approach (Hunter and Calhoun, 1996). In such a landscape, the objective for stands with the greatest disparity from the natural condition, like plantations, is to maximize fiber production. Conversely, conservation of biodiversity is the highest priority in forest reserves.

Creative incorporation of overstory retention into stands managed for timber is another approach for minimizing growth loss and providing for biodiversity. Our research on longleaf pine suggests that at a given level of low overstory retention, for example, 6–10 m$^2$/ha, clumping of residuals in large patches, rather than dispersing them across the site, minimizes growth inhibition (Palik et al., 1997). This is a consequence of a negative hyperbolic relationship between abundance of overstory competitors and growth of regeneration (Fig. 2). Because of this relationship, seedling growth increases only at low overstory basal area, below ca. 8 m$^2$/ha. With dispersed residuals, basal areas for most competitive neighborhoods in a stand exceed this level. Conversely, with clumped residuals, a greater proportion of the stand has a basal area below the competitive breakpoint of 8 m$^2$/ha. This results in better performance of regeneration across a greater proportion of the stand. Still, dispersed residuals may provide important ecological benefits not obtained with clumped residuals. Flexibility in spatial patterns of retention within a stand may be an important consideration, including both dispersed and clumped retention, when a goal of siliviculture includes maintenance of a broad range of ecological characteristics (Franklin et al., 1997).

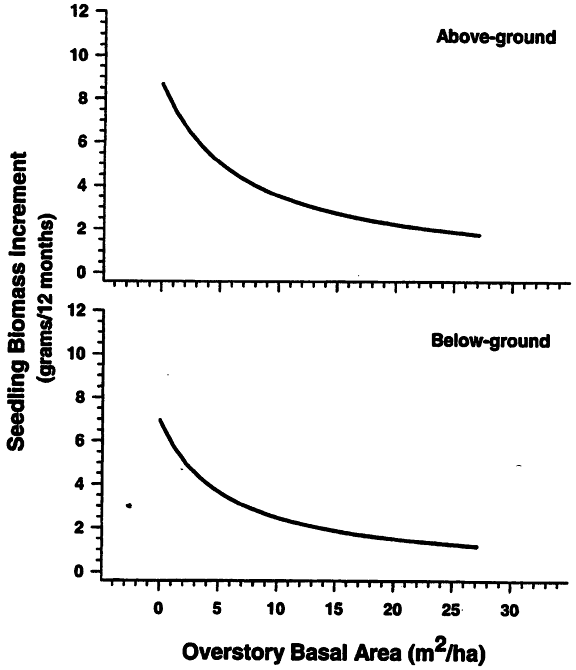

Fig. 2. Longleaf pine seedling biomass increment as a function of overstory basal area (trees with diameter at 1.4 m > 10 cm).

## 4. The multiple components of a disturbance regime

Natural disturbance regimes involve complex interactions among multiple components, including types of disturbance, their intensity, severity, frequency, spatial pattern, and seasonality. Changes in any of these components could alter ecosystem characteristics, including various components of biodiversity.

The same suite of components defines silvicultural disturbance regimes, with similar potential for change in any one component to affect changes in ecosystem characteristics. What is not clear is whether all components, or specifics of a component, have equal effect on biodiversity. Indeed, some deviation from the natural disturbance regime may be acceptable, if this results in minimal alteration of biodiversity.

Understanding the relationships between disturbance components and biodiversity helps to define the consequences of the disparity gap we discussed in the last section. Further, it fosters implementation of natural disturbance-based silvicultural approaches if certain deviations ease implementation, while causing minimal changes in biodiversity.

Contrasting the importance of fire season and fire frequency in longleaf pine ecosystems illustrates this concept. Pre-European fire regimes in longleaf pine systems are thought to consist of frequent (2–10 years) surface fires occurring during the lightning-season (Ware et al., 1993). Historically, managers alter this fire regime primarily by burning in the late winter rather than summer (Robbins and Myers, 1992). Often, this is done to increase northern bobwhite quail (*Colinus virginianus* Corey) production and because there is greater opportunity to burn in the dormant season. Researchers believe that many species native to longleaf pine ecosystems evolved under, and are adapted to, frequent lightning-season fire (Platt et al., 1988b; Brewer and Platt 1994a,b). Consequently, altering season of burn or frequency should have important consequences for maintaining native species richness in longleaf pine ecosystems, an important component of biodiversity.

In the case of native plants, we do know that fire in different seasons causes dramatic changes in the level, synchrony, and timing of flowering for some species (Platt et al., 1988b). For instance, wiregrass (*Aristida beyrichiana* Trin and Rupr.) and golden aster (*Pityopsis graminifolia* [Michx.] Nutt.) flower prolifically in response to lightning-season fires (Platt et al., 1988b, Brewer and Platt, 1994b). Such short-term changes in plant reproduction following fires in different seasons may drive patterns of species distribution and abundance and thus may affect population persistence.

Additional work on the compositional dynamics and reproductive biology of other native plants in longleaf pine ecosystems suggests that the emphasis on a single season of burn (i.e. lightning-season fire) is much less critical than fire frequency. One long-term study demonstrates little change in overall species diversity, distribution, or abundance with changes in season of burn (Streng et al., 1993). In another study, season of burn had no effect on reproduction and population persistence of the fire-dependent federally endangered species, *Schwalbea americana* L., whereas frequent fire was critical (Kirkman et al., 1998). A recent study on flower production of native legumes found that fires in different seasons benefited species differently (Hiers et al., 2001). Two species increased flower production with lightning-season fire, three species had highest flower production with dormant season fires, while seven species showed no response in flower production to season of fire.

These results suggest that the relationship between lightning-season fire and reproductive success of plants such as wiregrass cannot be extrapolated to all species in longleaf pine system. Moreover, the legume research (Hiers et al., 2001) implies that lightning-season fires have not exerted strong selection pressure on species within longleaf pine ecosystems in general, or plants have adapted to a wider range of fire seasons than previously considered.

Implementation of a managed fire regime that includes both lightning-season and dormant season fire is more likely to result in use of fire by managers of longleaf pine, because dormant season fire is easier to apply than lightning-season fire. Moreover, variation in fire season may result in conservation of a wider range of indigenous, fire-adapted plants. More generally, an understanding of the influence of individual components of a disturbance regime, fire season in our example, in influencing biodiversity facilitates implementation of natural disturbance-based silviculture by giving managers greater flexibility to pursue multiple objectives at different places or times.

## 5. Conclusions and application

Patterning silviculture after natural disturbance is a great challenge. The difficulty stems from the variability and complexity of a natural disturbance regime. This variability makes identification of a single model for silvicultural disturbance difficult and perhaps inappropriate. Even when the disturbance model is clear, its complexity renders it virtually impossible to duplicate. In reality, it may not be possible, or even necessary, to consistently emulate all components of the natural disturbance, like seasonality of burning.

The task of emulating natural disturbances with silviculture is especially challenging when one considers the socio-economic constraints inherent to forest management. For instance, silviculture, unlike natural disturbance, relies on human understanding. Currently, the indicators of ecological sustainability are not well defined (Simberloff, 1999). Moreover, relatively few foresters possess the knowledge required to incorporate biodiversity goals into timber management. This situation should improve with time, yet it is still problematic that most timber sales in the United States take place without the benefit of ecological inventories, trained foresters, or even a management plan (Birch, 1996; Mills et al., 1996). Another distinction is that silviculture, when part of commercial forest management, must keep operational costs low and profit margins in mind. Unlike natural disturbance, silviculture faces operational constraints, such as moving equipment between residual trees, or over downed logs, or around small wetlands. These constraints not only add to management costs, they may simply be impossible to overcome on the ground with existing equipment or levels of training. An equally compelling challenge is the growing recognition that biodiversity goals must be incorporated into commercial forest management to sustain productivity and meet the interests of concerned constituencies.

These dual challenges point to the need for approaches that balance biodiversity and timber management goals. The balance may shift towards one goal or the other at different times or different locations, depending on objectives. In all cases, the ultimate objective is to facilitate implementation of natural disturbance-based silviculture without ignoring the economic goals of commercial timber management or the interests of stakeholders concerned about biodiversity. Ultimately, stakeholders on both sides of the issue require the best scientific information available to form their opinions and guide their decisions.

To help meet this information need, we outline examples of longleaf pine silvicultural systems that use some of the principals we discuss. Our intent in presenting these examples is to illustrate how managers might better meet biodiversity objectives, while pursuing a wide range of timber management goals.

Our first example is based on an old growth stand managed for biodiversity and longleaf pine "heartwood" sawtimber (Fig. 3 top). Timber is salvaged only from lightning struck and blown-down trees. Due to the high-value of heartwood timber, the value of wood harvested from this stand is three to four times that cut

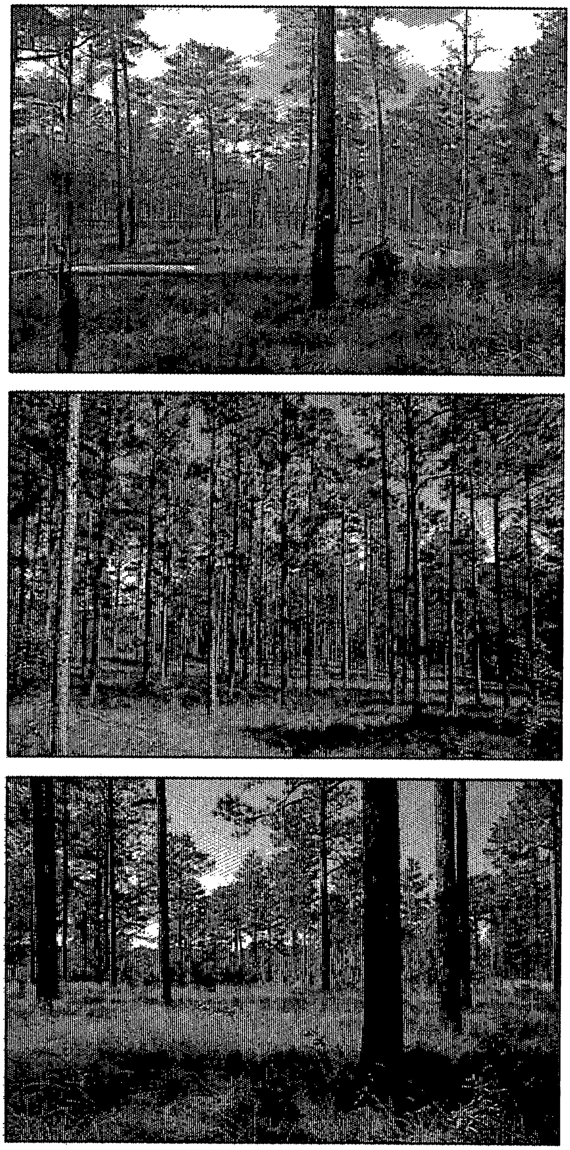

Fig. 3. Examples of different longleaf pine stand structures and silvicultural approaches. The top photo is an old growth stand managed by removing lightning-killed pines. Management goals for this stand focus primarily on maintaining structural biodiversity, but include harvesting some high-value "heartwood" sawtimber. The middle stand is managed using single-tree selection to create large gaps needed for sustained growth of longleaf pine regeneration. The objective of management in this stand is primarily to maintain structural diversity, but with greater opportunities for timber removal than in the previous example. The bottom photo shows a two-cohort stand, managed by leaving behind some of the overstory during a regeneration harvest. The objective for this stand is to maximize opportunities for timber removal, while still maintaining significant amounts of structural diversity.

from younger stands, where the trees contain little heartwood (personal communication with property manager). This approach allows natural disturbance events to select trees for harvest. While few stands in the southeastern United States are managed this way, because of the lack of old growth forest, it nevertheless represents one end of the spectrum for using natural disturbance as a guide for developing a silvicultural approach.

Our second example (Fig. 3 middle) is a longleaf pine stand managed using single-tree selection (Engstrom et al., 1996). With this approach, the standing crop of timber is viewed similarly to an annuity that is never liquidated, but a portion or all of the growth in standing crop is harvested after threshold stocking targets are met. Trees are selected in ways that increase the health and value of the stand through time by removing defective, diseased, or low vigor trees. In addition to improving overall stand health and value, goals for marking include maintaining continuous forest cover and fuels for frequent burning. Enlarging existing gaps encourages regeneration. Due to spatial variation in stand density, cutting just one or two trees can sometimes enlarge gaps sufficiently to encourage development of longleaf pine seedlings (McGuire, 1999).

Our last example (Fig. 3 bottom) is an irregular shelterwood with variable retention (following Franklin et al., 1997). Beginning with a well-stocked mature stand, e.g. 60–80 years old, the manager reduces basal area down to a stand-level average of $\sim$6–10 $m^2$/ha. Within the stand, the residual trees are left in spatial patterns that range from large clumps to dispersed individuals. With this spatial structure, some individual competitive neighborhoods contain high basal area of overstory trees, while others contain no trees that inhibit survival or growth of regeneration. The ultimate goal of this harvest is to create a two-cohort structure, by providing environments favorable for new longleaf pine regeneration in portions of the stand, while retaining structural diversity in the overstory.

Assuming a rotation age of 60–80 years, the target of the next regeneration harvest is removal of the older cohort and portions of the younger cohort, again removing only enough of the overstory to reduce residual basal area to $\sim$6–12 $m^2$/ha. Alternative approaches include: (i) carrying the older cohort through a second rotation by targeting only the younger cohort in the regeneration harvest; or (ii) moving the stand towards multi-cohort structure by leaving portions of both the initial cohorts intact.

Prescribed surface fire is an important intermediate treatment in all of our examples. A stand should be under-burned every 1–3 years. Seasonality of burning can vary to meet different objectives. Lightning-season fire should be used in conjunction with regeneration harvests to provide mineral seedbeds in anticipation of good longleaf pine seed years (Croker and Boyer, 1984). These fires may also provide maximum control of hardwood competition (Glitzenstein and Platt, 1995). Dormant season fire may be used in some years to enhance breeding success of northern bobwhite quail.

Simberloff (1999) suggests that any proposed silvicultural system designed to maintain biodiversity and produce timber should be treated as an hypothesis, due to the limited number of empirical studies to support or refute the approach. Our examples with longleaf pine ecosystems are not different, but we provide a start with some of our own research (Palik et al., 1997), as do others in different regions (e.g. Franklin et al., 1997). The challenge now is for the broader research community to work with forest managers to implement and monitor a wide range of silvicultural alternatives designed to be profitable, practical, and yet effective at protecting biological diversity.

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