# Silviculture that sustains: the nexus between silviculture, frequent prescribed fire, and conservation of biodiversity in longleaf pine forests of the southeastern United States[1]

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**Abstract:** The longleaf pine (*Pinus palustris* Mill.) forest ecosystems of the US southeastern Coastal Plain, among the most biologically diverse ecosystems in North America, originally covered over $24 \times 10^6$ ha but now occupy less than 5% of their original extent. The key factor for sustaining their high levels of diversity is the frequent application of prescribed fire uninterrupted in time and space. Pine fuels, critical to application of fire and regulated by canopy distribution, provide the nexus between silviculture and fire management in this system. Typical silvicultural approaches for this type were, in large part, developed to maximize the establishment and growth of regeneration as well as growth and yield of timber, with much less regard to how those practices might influence the ability to sustain prescribed burning regimes or the associated biodiversity. However, many landholdings in the region now include conservation of biodiversity as a primary objective with sustained timber yield as an important but secondary goal. This review synthesizes the literature related to controls of biodiversity for longleaf pine ecosystems, and silvicultural approaches are compared in their ability to sustain natural disturbance such as fire and how closely they mimic the variation, patterns, and processes of natural disturbance regimes while allowing for regeneration.

**Résumé :** Les écosystèmes forestiers de pin des marais (*Pinus palustris* Mill.) de la plaine côtière du sud-est des É.-U., qui sont parmi les écosystèmes les plus biologiquement diversifiés en Amérique du Nord, couvraient à l'origine plus de 24 millions d'hectares mais occupent maintenant moins de 5 % de leur étendue originale. Le facteur clé dans le maintien de leur degré élevé de diversité est l'application fréquente du brûlage dirigé ininterrompu dans le temps et dans l'espace. Les combustibles de pin, essentiels à l'utilisation du feu et régis par la distribution de la canopée, fournissent le lien entre la sylviculture et la gestion du feu dans ce système. Les approches sylvicoles typiques pour ce type de forêt ont été en grande partie développées pour favoriser l'établissement et la croissance de la régénération ainsi que la croissance et le rendement en matière ligneuse sans porter beaucoup d'attention à la façon dont ces pratiques pouvaient influencer la capacité de maintenir un régime de brûlage dirigé ou la biodiversité qui y est associée. Cependant, plusieurs propriétés dans cette région retiennent maintenant la conservation de la biodiversité comme premier objectif avec le rendement soutenu de matière ligneuse en tant que but important mais secondaire. Cet article dresse la synthèse de la littérature reliée au contrôle de la biodiversité dans les écosystèmes de pin des marais et compare les approches sylvicoles en fonction de leur capacité à maintenir les perturbations naturelles comme le feu et du degré de fidélité avec lequel elles reproduisent les variations, les comportements et les processus des régimes de perturbation naturelle tout en tenant compte de la régéneration.

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## Introduction

Sustainable silvicultural practices conserve biological diversity, water resources, soils, and landscapes to maintain ecological functions and ecosystem integrity (Wilkie et al. 2003). Longleaf pine (*Pinus palustris* Mill.) ecosystems of the southeastern Coastal Plain (USA) offer a unique model in which to apply the principles of sustainability to the stewardship of forest lands. Longleaf pine systems contain globally significant levels of biodiversity, are among the most threatened biomes, and are fire dependent (Landers et al. 1995). Moreover, the southeastern United States has also been the nation's leading forest products producer for many years (Wear 1996); however, globalization of the forest industry has placed additional pressure on the region to produce higher-quality forest products that are more resilient in global market fluctuations (Franklin and Johnson 2004).

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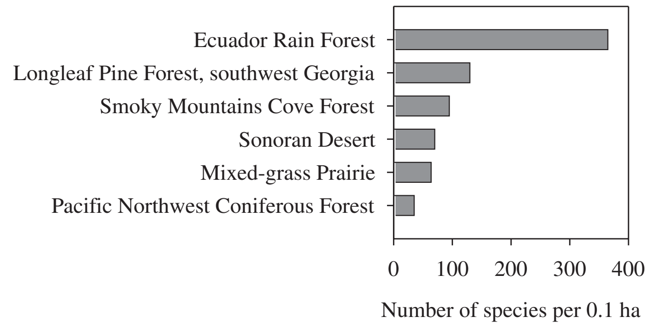
These market changes may favor longleaf pine forests that produce high-quality sawtimber and poles, and tend to be less susceptible to common insects and diseases (Wahlenburg 1946). In this context, we review the literature that addresses sustainable timber management of southern pine forests by identifying critical characteristics of the disturbance regime and then assessing the discrepancies between them and silvicultural approaches (Simberloff 1999; Palik et al. 2002).

Longleaf pine savannas and woodlands are among the most diverse communities in temperate North America, having high levels of species richness and large numbers of endemic flora and fauna (Walker and Peet 1984; Hardin and White 1989; Peet and Allard 1993; Fig. 1). Species richness is high at multiple scales; as many as 50 plant species can occur in a single square metre, while more than 1000 species can be found over a few thousand hectares (Peet and Allard 1993; Drew et al. 1998; Kirkman et al. 2001). In fact, nearly one-quarter of all plant species found in the US and Canada occur in longleaf pine landscapes (Clewell 1986; Stein et al. 2000). The biologically rich longleaf pine ecosystem was once the dominant cover type in the Coastal Plain but has become increasingly rare. At least 95% of the original extent of the longleaf pine forest ($24.3 \times 10^6$ ha; Outcalt 1996) has been converted to other land uses, degraded by fire suppression, or replaced by other types of forests (Landers et al. 1995; Outcalt 1996). This loss of habitat has resulted in concern for the persistence of many of the endemic flora and fauna associated with longleaf pine: nearly two-thirds of all species that are recognized as declining, threatened, or endangered in the southeastern US are associated with this ecosystem (Kirkman and Mitchell 2006).

Fire frequency is indisputably the most important factor for sustaining native southeastern US ecosystems (Heyward 1939; Wahlenburg 1946; Lemon 1949; Christensen 1981; Hiers et al. 2000; Kirkman et al. 2004). Longleaf pine communities burn frequently and have one of the highest fire return intervals of ecosystems globally (Christensen 1981). While the range of fire return intervals may vary from 1 to 10 years (Christensen 1981, 1988; Bridges and Orzell 1989; Abrahamson and Hartnett 1990; Ware et al. 1993; Glitzenstein et al. 1995), fires recurring every 1–3 years maintain a more open-canopy structure that is associated with higher species richness (Glitzenstein et al. 2003; Kirkman et al. 2004). While frequent fire is essential to maintaining biodiversity, many, if not most, remnant stands of longleaf pine have had some fire suppression or insufficient fire return intervals (Outcalt 1996; Kush et al. 1999). Therefore, one of the primary tasks for sustainable management of longleaf pine ecosystems is the maintenance of frequent fires, primarily through application of prescribed fire by managers in southeastern pine forests (Provencher et al. 2001).

Any management activity in longleaf pine stands that compromises frequent fire can also lower biodiversity (Leach and Givnish 1996; Liu et al. 2005). Silvicultural activities affect fire management by altering the distribution, type, and amount of fuels. The high fire frequency and low fire intensity necessary to sustain the longleaf pine plant community requires that fuels be continuously distributed in time and space. Since pine needles represent more than one-half the available fuels for maintaining fire (Ottmar 2002), silviculture necessarily impacts fire through its influences on the variation in fine fuel production by affecting tree crown distribution.

**Fig. 1.** Longleaf pine systems are among the most species-rich temperate ecosystems. Species-richness comparisons are derived from Barnes et al. (1983), Cunningham (1994), Halpern and Spies (1995), and Kirkman et al. (1998, 2001, 2004).




Disturbances to the overstory, both natural and those from timber harvest, influence the spatial variation in crown cover of pines (Platt et al. 1988; Palik and Pederson 1996; Palik et al. 2003), which in turn influences needle loading and fire behavior (Williamson and Black 1981). Longleaf pine needles provide ideal fine litter for frequent fire, both because of their high resin content and structure (Hendricks et al. 2002). Bunchgrass crowns act as perches for fallen needles, creating a well-ventilated fuel bed that dries easily (Myers 1990). This synergy among fine fuels, i.e., grasses and needles, is the salient feature of this system that allows for the very frequent fire regimes required to sustain the high levels of biodiversity characteristic of these systems. Thus, any silvicultural system that is oriented toward goals of sustaining native biodiversity and timber management must consider the nexus between management impacts on forest dynamics and the ability to sustain fire over space and time.

## Objectives

It is within this context that we examine how silviculture impacts fire management and, thus, conservation of biodiversity. In this review, we present how management in longleaf pine stands might provide a model for natural disturbance-based silviculture that satisfies both timber and conservation needs. We specifically discuss even-aged versus uneven-aged timber management approaches, as well as competing models for uneven-aged management, with respect to their ability to sustain native biodiversity through facilitating fuel bed continuity and frequent fires.

## Nexus between forest canopy and fire management

Historically, in extensive longleaf pine-dominated areas of the Coastal Plain, the landscape was more or less continuous with some interruptions by moist bottomland sites (Wahlenburg 1946). Early accounts of longleaf pine forests describe an open, parklike appearance with a monotypic pine overstory and a grass-dominated herbaceous understory (Schwarz 1907). The forests were multi-aged with even-aged cohorts regenerating in small patches formed by the largest openings in the forest. This forest structure is found in today's landscape only in the presence of frequent fire.

In the absence of fire, a dense, closed midstory develops under the open pine canopy. The constituents of this midstory vary; on xeric and mesic sites broad-leaved hardwoods such as oaks (*Quercus* spp.) tend to dominate, while in hydric flatwood sites the midstory is composed of shrubs such as gallberry (*Ilex* spp.) and saw palmetto (*Serenoa repens*). Off-site species such as sand pine (*Pinus clausa* [Chapm. ex Engelm.]) can also form a closed midstory. A dense midstory alters the fire regime such that fires become less frequent and more severe. The diversity of flora and fauna rapidly decline as midstory cover increases (Means and Grow 1985).

Fire ecology and the ecological consequences of fires to flora and fauna have been the subject of many reviews (Christensen 1988; Noss 1988; Myers 1990; Stout and Marion 1993; Ware et al. 1993); however, as of yet no review has explored the connections that exist between overstory management, the ability to maintain fire continuously over space and through time, and the consequences of various silvicultural alternatives for sustaining biodiversity.

The longleaf pine overstory, and by extension any silvicultural management of that forest, not only influences how pine fuels are distributed through time and space, but also can influence stand dynamics in ways that significantly affect prescribed burning. Understory communities of longleaf pine savannas often have a high density of oaks and other hardwood species present in advance regeneration, but they tend to be kept in low stature because of frequent fire (Jacqmain et al. 1999). Competition from overstory pines slows midstory growth and enhances the ability of fire to keep them from developing into a closed midstory (McGuire et al. 2001). Top kill of hardwood stems by prescribed fire is a function of their size (Glitzenstein et al. 1995). The pine overstory helps in maintaining control of hardwoods not only by slowing growth between fire events, but increasing fire intensity with increased pine fuel loads (Williamson and Black 1981). Complete removal of pines releases midstory hardwoods, dramatically increasing their growth rates while concomitantly decreasing the pine fuels available to control hardwoods by fire (McGuire et al. 2001).

Hardwood and shrub dominance after pine overstory removal can also be exacerbated by disturbance of understory grasses when many overstory stems are removed following harvest. The loss of grass cover from logging damage disrupts fuel continuity, creating patches of lowered fire frequency. Midstory hardwoods are released in these areas and produce broad-leaved litter that suppresses grasses. Because of both chemical and structural features, broad-leaved litter burns less readily and with less intensity than the pine and grass fuels (Williamson and Black 1981). This decreases the frequency and intensity of future fires and creates a positive feedback cycle favoring fire-intolerant species that produce less flammable fuels over that of fire-dependent understory species. Thus, the potential impact of timber harvesting is multifaceted, with direct effects such as lowering fine fuel production and competition and indirect effects such as the disruption of fuel continuity by logging equipment.

While the connection between pine overstory and maintaining frequent fire is clear, much of the literature on longleaf pine management has focused more narrowly on longleaf pine silviculture itself or accelerating establishment and early growth of seedlings (Boyer and Peterson 1983). Release of hardwood or shrub competition by harvesting overstory pines could be controlled by herbicides or mechanical removal (Boyer 1988). However, this approach is problematic when managing for biodiversity, especially since the species-rich understory plant communities can be negatively impacted by disturbance from intensive mechanical site preparation and chemical treatments (Hedman et al. 2000; Provencher et al. 2000).

## Silvical and natural history traits

Understanding silviculture approaches requires an appreciation of the silvical and natural history traits of longleaf pine and its associates. First and foremost, longleaf pine reproduces episodically every 5–10 years with regional synchrony (Boyer and Peterson 1983). This regional masting may be an adaptation to reduce seed predation through predator satiation (Janzen 1970). In a heavy seed crop year, 85%–95% of trees bear cones, while less than 65% bear cones in light seed years (Wahlenburg 1946). The number of cones per tree also follows similar trends. In a good year, more than half of trees bear 50 cones or more, while in a poor year, they can have <5% with more than 50 cones (Wahlenburg 1946). Longleaf pine seeds are wind dispersed generally from October through November, with the seeds falling at a time when few other species are fruiting. The seeds have a soft coat and are high in calories and nutrients; hence, they suffer high predation rates (Boyer 1964). Longleaf pine seeds are the largest of all the southern pines and germinate within a week of falling, given optimal conditions of temperature and moisture.

Longleaf pine seeds require bare mineral soil to establish, but considerable amounts of bare ground can persist several years after a fire in frequently burned longleaf pine grasslands (Wahlenburg 1946). Since litter can stunt seedling growth (Facelli and Pickett 1991) and increase fire intensity, (Williamson and Black 1981) preparation of the fuel bed in advance of seedfall is critical. While burning before seedfall to prepare the seedbed has been the focus of much discussion (Croker and Boyer 1975), the reductions in fuel loadings by burning before the seed rain could be just as important for subsequent seedling establishment. Newly established longleaf pine seedlings are fire sensitive. If fuel is removed prior to germination and new fuels are allowed to accumulate for only a short time (i.e., 1.5–2.5 years) before the next fire, those seedlings that established in open microsites will grow large enough to increase their probability of survival after a fire (Grace and Platt 1995). If fuels have built up before seedfall, then fires will result in greater mortality, with only the largest seedlings surviving.

Seedling survival tends to increase with distance from adults (Grace and Platt 1995). Seedlings in close proximity to adults grow slower because of competition for light (Battaglia et al. 2003) and are more vulnerable to subsequent fires because of increased needle fall and higher fire intensity (Grace and Platt 1995; Palik et al. 1997, 2003; McGuire et al. 2001). Thus, greater seedling establishment is promoted in more open portions of the savanna, because these areas tend to have less adult competition and lower fire intensity.

Longleaf pine attributes, such as their grass stage, shade intolerance, and wide edaphic tolerance, are all important characteristics to consider when developing a sustainable silvicultural regime. During the grass stage, seedlings show little height growth, because most resources are being allocated to root system development, diameter growth, and bud production. This stage can last from 2 to more than 10 years depending on growth rate (Wahlenburg 1946). Grass-stage seedlings can be overtopped by vegetation and remain stunted, particularly in the absence of overstory competition and fuels; however, on xeric sites, deciduous oaks often facilitate establishment (Wahlenburg 1946). The sensitivity of seedlings to competition and the more rapid early growth of longleaf pine seedlings in full sunlight have resulted in a focus on even-aged approaches for regeneration, often with intensive mechanical or chemical site preparation to control competitors (Boyer and Peterson 1983). The presence of the grass stage has also contributed to the perception that longleaf pine is a slow-growing species (Boyer and Peterson 1983), but on upland sites in the southeastern Coastal Plain, longleaf pine can equal or exceed growth rates of other southern pines over several decades (Shoulders 1985).

## Stand structure and biodiversity of southeastern pine forests

### Variation in canopy structure

The high diversity of plant communities in the southeastern Coastal Plain are only sustained in frequently burned, open-canopy woodlands and savannas (Walker and Peet 1984; Kirkman et al. 2001). The open-canopy structure allows for two vegetative strata to develop: an overstory canopy dominated by pine and an understory dominated by grasses but rich in species (Mitchell et al. 1999). While these open canopies allow considerable light to reach understory community, they vary in density and light attenuation from as much as >80% of full sun to as little as 20%–30% (Battaglia et al. 2003). In this range of light conditions, understory plants are able to sustain high levels of diversity (Kirkman et al. 2001), productivity (Mitchell et al. 1999), and function such as $N_2$ fixation (K. Hiers, unpublished data). In the absence of fire, fire-sensitive shrubs and trees invade the midstory, leading to a decline in understory vigor and biodiversity (Provencher et al. 2001).

The open-canopy structure of longleaf pine woodlands is not only important to maintain plant diversity but also influences the faunal communities. From a biodiversity perspective, this is no more evident than in the response of Gopher tortoises (*Gopherus polyphemus*). Gopher tortoises are abundant in frequently burned longleaf pine woodlands (Guyer and Hermann 1997; Means 2005). Not only are gopher tortoises a species of concern, but they are a keystone species providing critical habitat for more than 300 species of vertebrates and invertebrates, some of which are also rare and endangered (e.g., gopher frog, *Rana capito*) and require gopher tortoise burrows to sustain their populations (Guyer and Hermann 1997; Means 2005). Conversion to closed-canopy plantations of other southern pine species results in loss of the gopher tortoises and associated species (Aresco and Guyer 1999). Uniform structure of dense pine plantations, sparse groundcover, and few snags are detrimental to other herpetofaunal species, such as the flatwoods salamander (*Ambystoma cingulatum*; Means et al. 1996), and typically these plantations support the lowest numbers of bird species (Repenning and Labisky 1985; Thill and Koerth 2005).

Open-canopy grasslands are critical for many ground-nesting species such as Bachman's sparrow (*Aimophila aestivalis*), a species listed as a Federal Species of Concern because of loss of habitat. The spacing of individual trees and clumps of trees is important for bird species that forage in open spaces within forests, such as flycatchers (e.g., eastern kingbird (*Tyrannus tyrannus*)), common nighthawk (*Chordeiles minor*), and loggerhead shrike (*Lanius ludovicianus*). In wetter areas, very open woodlands interspersed with savannas are important habitats for sandhill cranes (*Grus canadensis)*.

### Variation in vigor and age

Longleaf pine canopies can be quite varied in age structure if allowed to develop over time (Fig. 2). Regeneration develops in patches under the more open-canopied areas in these woodlands (Platt et al. 1988; Palik et al. 1997). Openings often result from the coalescing of disturbances at the scale of single trees due largely to lightning and (or) windthrow (Palik and Pederson 1996; Myers and Van Lear 1998) or from larger disturbances such as hurricanes or downbursts (Palik et al. 2002). These dense patches of regeneration are eventually thinned because of competition and fire, and ultimately reach dominant positions in the overstory.

Longleaf pine overstory can achieve ages up to 500 years with maximum age limited by lightning and windthrow (Platt et al. 1988). The variation that appears in the canopy architecture of older trees is especially important for bird species, such as red-cockaded woodpeckers (*Picoides borealis*; e.g., amount of heartwood and fungal infection) and bald eagle (*Haliaeetus leucocephalus*; e.g., large limbs high in the canopy). Perhaps more than any other animal species, red-cockaded woodpeckers require relatively old, living pine trees. Although some cavities have been made in trees as young as 30–40 years, most cavity trees typically vary from 60 to 200 years for longleaf pine and have occurred in trees as old as 450+ years (Landers and Boyer 1999). Red-cockaded woodpeckers also prefer old trees for foraging (Engstrom and Sanders 1997; Zwicker and Walters 1999). Twenty-five species of animals have been documented to use active or inactive and enlarged red-cockaded woodpecker cavities (Baker 1971). The ability of the woodpecker to excavate cavities in living pine trees makes it a keystone species. Old trees tend to support primary (e.g., woodpeckers) and secondary cavity nesters (e.g., wood duck (*Aix sponsa*)) in greater numbers because cavities may be more easily excavated in decayed locations. Forests containing old trees with red-cockaded woodpecker cavities and many snags are also excellent habitats for southeastern American kestrels (*Falco sparverius paulus*; Gault et al. 2004).

Over time, natural disturbances not only create variation in live trees but also add structural diversity to the forest through coarse woody debris in the form of standing dead and downed logs (Fig. 3). Tip-up mounds and stump holes provide refugia for several bird species, including northern

**Fig. 2.** Longleaf pine regeneration develops in less dense portions of an open canopy structure, while overstory trees can achieve ages of >500 years. *Photo by J. Ariail,* Joseph W. Jones Ecological Research Center.

bobwhite (*Colinus virginianus*), Carolina wrens (*Thryothorus ludovicianus*), and Bachman's sparrow (Means 2005; R.T. Engstrom, personal observation). Snags are highly important to the diverse community of animals in longleaf pine forests. Forty-five species of birds have been documented to use snags in the southeastern United States (Hamel 1992), but frogs, snakes, and lizards have also been observed (Goin and Goin 1951; Franz 1995; Boughton et al. 2000). Groups of evening bats (*Nycticeus humeralis*) have been observed in groups of up to 20 individuals beneath the sloughing bark of pine snags (Baker 1974). In an experimental study in loblolly pine (*Pinus taeda* L.) forests, Lohr et al. (2002) found that removal of downed logs and snags from study plots resulted in reduced bird species richness and avian abundance and fewer territories of woodpeckers, Carolina wrens, and great crested flycatchers (*Myiarchus crinitus*) but did not affect the nonbreeding bird community. While little published information is available that describes how snags are recruited and documents their persistence in frequently burned longleaf pine systems, monitoring plots at Eglin Air Force base in Florida and several old-growth forests in the Red Hills of northern Florida and south Georgia suggest that forests with old-growth characteristics can have approximately 4 snags/ha (K. Hiers, unpublished data). Younger forests tend to have about half that density, most likely because of lower persistence rather than increased recruitment, although this is an area that is in need of scientific attention.

## Silvicultural approaches

Experience and research have shown that longleaf pine can be managed using any typical silvicultural system, whether even-aged or uneven-aged, as long as the species' ecological characteristics are taken into account (Guldin 2004). In patterning silvicultural manipulations after natural disturbances, the even-aged systems represent the largest scale and intensity of disturbances (e.g., tornados, hurricanes, or stand-replacing fires) while the uneven-aged approaches represent the small-scale, less intense disturbances (e.g., local insect or lightning-caused mortality). In addition to effects on residual stand structure and the level of site disturbance, the different cutting methods also represent a gradient in overstory retention and, therefore, a gradient in the distribution of fine fuels, which allow managers to manipulate fire regimes.

### Even-aged management

Early silvicultural research focused on even-aged approaches to management of longleaf pine. Clearcutting, the most common form of silviculture in southern pines, was problematic with longleaf pine because of mortality of advanced regeneration in cleared forests, low seed dispersal distance, and difficulty in successful planting of bare-rooted seedlings (Boyer and Peterson 1983). More recently, however, research using larger seedlings grown in low-density nursery beds and container-grown seedlings allowed for consistent success in planting longleaf pine (Boyer 1988; Brissette 1990; Barnett 2002*a*, 2002*b*; Barnett et al. 2002). Direct seeding of open or cleared areas has also been used successfully in some instances, but only when seed coatings are employed to reduce seed predation by birds and rodents (Nolte and Barnett 2000). Cutting the overstory in ways to initiate even-aged stands and accelerating early growth of seedlings was thought to be necessary because of the shade-intolerant nature of longleaf pine, the slow growth of grass-stage seedlings, and the susceptibility of seedlings to competition. With the removal of the overstory and the subsequent reduction in fine fuel production and release of broad-leaved species from competition, fire alone is often insufficient to suppress competing vegetation. Mechanical or chemical site preparation and release treatments are often recommended as necessary to successfully regenerate longleaf pine in clearcuts (McGuire et al. 2001).

**Fig. 3.** Dead trees, both standing snags and downed logs, diversify forest structure and provide significant habitat for a variety of faunal species. *Photo by J. Ariail,* Joseph W. Jones Ecological Research Center.

Seed tree and shelterwood systems have also been used as even-aged natural regeneration approaches, although seed tree cuts have been limited in their success (Boyer and Peterson 1983). Seed tree cuts with 20–25 seed trees/ha retain insufficient overstory with respect to fuels distribution and competition to suppress hardwoods, which rapidly dominate the site, requiring chemical or mechanical site preparation before seedfall. Seed tree approaches also suffer from insufficient propagules because of lightning- and wind-driven tree mortality, if an extended period passes before a sufficient seed crop is produced (Boyer and Peterson 1983). To overcome inherent difficulties of seed tree and clear-cutting, considerable work has been applied to shelterwood approaches (Boyer 1993). The shelterwood system calls for a preparatory cut that leaves a pine basal area of 13.8–16.1 $m^2 \cdot ha^{-1}$ in dominant and codominant trees. Either a seed cut follows or the seed cut is the first in a two-cut system that leaves 7 $m^2 \cdot ha^{-1}$ of the best trees. The seed cut is done 5 years in advance of the final harvest, during which all adults are removed to release established grass-stage seedlings. This technique produces three times the amount of seeds over the seed tree approach and maintains greater overstory fuel and overstory competition to help maintain fire and grassland pine structure (Boyer 1979). This approach can also be modified to a reserve shelterwood approach (also called irregular shelterwood) in which adult trees are retained indefinitely and new cohorts are allowed to grow toward the canopy, providing opportunities to rapidly develop a more varied age structure with two age classes (Franklin et al. 1997; Palik et al. 2002). Both the seed tree and shelterwood systems result in an even-aged stand or a forest with only two cohorts. This can have a negative impact on other forest characteristics important to species previously discussed.

## Uneven-aged management

### *Group selection*

Group selection or gap-based overstory approaches to uneven-aged management flow conceptually from even-aged management and represent a moderate level of overstory disturbance. In this approach, gaps are created through the selection of groups of trees for removal from the stand, creating gaps in the canopy that release sufficient resources to encourage seedling establishment and release (Brockway and Outcalt 1998). The gap-oriented approach to uneven-aged management of longleaf pine stems from observations that regenerating seedlings are often found in the center of openings in the forest matrix (Schwarz 1907), with the tallest seedlings and saplings found furthest from adults, and a decline in height with closer proximity to adults. The recommended size of gaps varies but has been suggested to be as large as 2 ha (Brockway et al. 2005). Brockway and Outcalt (1998) report that competitive exclusion of longleaf pine seedlings by the overstory exists because of interactions between belowground competition and fire, thus requiring a minimum gap diameter of 30 m (~0.3 ha). James et al. (2004) suggest that gap size should vary from 0.2 to 0.5 ha for trees 20 m in height and can be considered a “mini-group selection” management approach.

The recommended basis for the selection of groups of trees for gap-based silviculture has generally been based on area control. In many cases, silvicultural recommendations have been to develop “balanced” stands with the goal that the stand be composed of different cohorts of trees occupying equal areas. For instance, if cohorts were regenerated every 10 years (cutting return interval) and carried on for 100 years, approximately 10% of the stand would be regenerated each cutting cycle, but if cohorts were maintained for 200 years, 5% of the area would be regenerated at each entry (Smith et al. 1997).

An alternative to an area-based control scheme is to use a structural control approach to tree selection such as the BDq method to create gaps (Guldin 2004). Under this scheme, the target number of trees of various sizes that need to be removed to meet the desired structural goal can be selected adjacent to each other rather than dispersed throughout the stand, thereby creating gaps in the canopy.

Though group selection is often applied using gaps of relatively uniform shape, size, and distribution, that application is more a convenience than a requirement (Smith et al. 1997). In fact, sizing and arranging gaps according to the natural variation in stand conditions will provide more ecological benefits than a uniform approach. In addition, the creation of gaps can easily high grade quality trees, older individuals, and seed trees when all trees in a specified area are removed for gap creation, unless care is taken in locating the harvested areas (Guldin 2004). An alternative is to retain some of the best trees in the gap (group selection with reserves), thereby creating a structure similar to a small-scale seed tree or shelterwood, with the residual trees providing fuel and seed within the gap (Guldin 2004). This technique also mimics natural disturbances where gaps are often occupied by individual trees that survive the disturbance (Palik and Pederson 1996), a structure which helps to maintain fuel continuity. The creation of gaps with retention grades toward a variable overstory retention approach (Lindenmayer and Franklin 2003).

Though gaps or group selection can be an effective approach to manage longleaf pine regeneration, they both can lead to potential problems with fire regimes. When gaps are cut with few or no residual trees retained within the gaps, the result can be considerable variation in fuels across the stand and a disruption in fuel bed continuity. All gap-based approaches concentrate residual stocking in the forest matrix. Fine fuel loads are much higher in the forest matrix than in the gaps except at the edges (Brockway and Outcalt 1998). In addition, understory hardwoods are released in the gaps and produce litter of lower flammability that lengthens fire return intervals in the gaps (Williamson and Black 1981; McGuire et al. 2001; Kirkman et al. 2004). Insufficient fire return interval within gaps also may allow hardwoods to compete with grasses and further decrease the fine fuel loadings that help sustain high fire frequency. When multiple trees are removed in the gaps, damage to bunchgrasses through the harvesting process can occur (McGuire et al. 2001). Prescribed burning then becomes more difficult: if managers decide to burn based on the fuel loadings of the forest matrix outside the gaps, then the fire intensity can be insufficient to carry fire into the gaps. If conditions are selected to adequately carry fire into gaps, the pine overstory in the matrix can be put at risk because of extreme fire intensity, costing future growth and potentially causing overstory mortality.

### *Single-tree selection approaches*

The silvicultural approach that results in the smallest scale of canopy disturbance is the single-tree selection method. The most frequently discussed single-tree selection method in the literature for southern pines is the BDq approach (Farrar 1996; Guldin 2004). In this approach, trees are selected for removal such that a reverse-J shaped diameter distribution, representative of a multi-aged forest, is retained (Farrar and Boyer 1991; Farrar 1996). With the BDq approach, a target residual basal area ($B$) and maximum diameter ($D$) are specified a priori, while the distribution of trees across diameter classes is determined by the diminution quotient ($q$), a value that reflects the ratio of the number of trees in diameter class $a$ to the number in diameter class $a + 1$ (Smith et al. 1997). Of the three factors, selecting an appropriate basal area is said to be the most critical to success of the method (Guldin 2004).

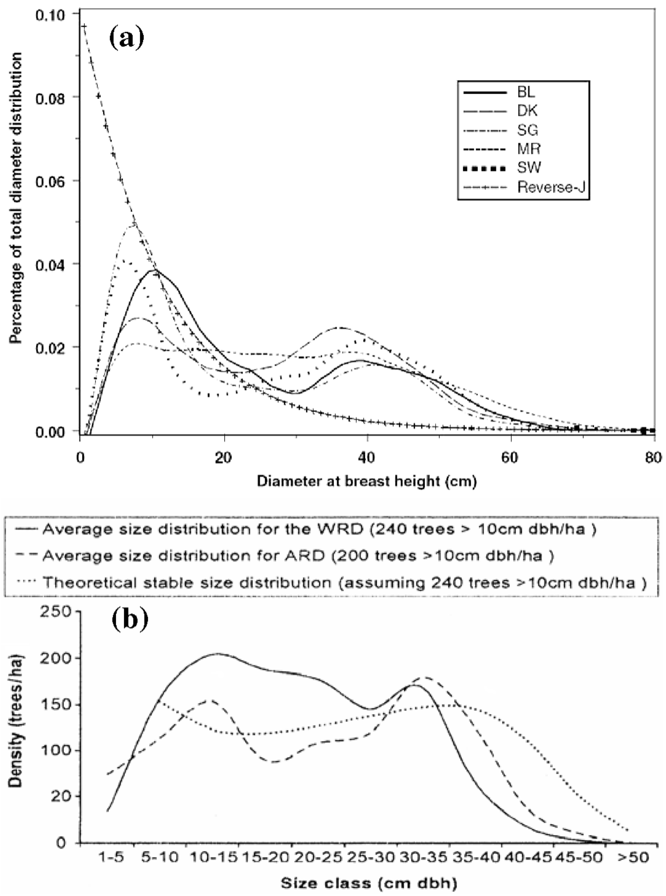
While the BDq approach can be conceptually linked to patterns observed in natural disturbances, silvicultural application often varies in substantive ways from patterns found in landscapes structured by natural disturbances. Specification of a target residual basal area is not necessarily in conflict with a disturbance-based approach to uneven-aged management. That is, a forester can easily determine and justify a target residual basal area and then, using inventory data, calculate the number of trees or size of canopy gaps needed to reach this target at a given harvest entry. However, natural disturbances rarely result in uniform residual basal area throughout a stand or forest (Palik and Pederson 1996). Guidelines developed to sustain biodiversity as well as maintain the flow of timber products should therefore account for variation in diameter distribution and average basal area within and between stands.

In contrast, selection of maximum tree diameters and $q$ has the potential to move stands structurally in directions having little or no natural analogy. The theoretical goal of the $q$ quotient, which ranges from >1 to 2, is to create balanced multi-aged stands that will sustain timber yield; that is, stands with uniform ratios between successive diameter distributions across the full range of diameters. Several conceptual difficulties arise with this approach. First, the system equates diameter with age, such that larger trees are assumed to be older. Longleaf pine can be suppressed in growth for a number of decades then released and grow rapidly decoupling size and age (Gilliam and Platt 1999). Second, there is little evidence that balanced multi-aged stands occur with any regularity in natural pine woodlands (O’Hara 1996; Moser et al. 2002). Nor are there any data that connect maximum diameter limits to trees lost through natural disturbances. These difficulties arise because the focus in the BDq method is to have a structurally regulated forest to provide sustainable timber yield, and other desirable characteristics of the forest such as wildlife habitat, aesthetics, and biodiversity are thought to follow as a result and generally are not high-priority objectives.

In contrast, a single-tree selection approach practiced by Stoddard, Sr. and Neel in the Red Hills region of north Florida and south Georgia takes a variable overstory retention approach (Lindenmayer and Franklin 2003). This method has resulted in the maintenance of biodiversity and conservation values in the region while simultaneously producing substantial revenues from timber harvests (Engstrom et al. 1996). The Stoddard–Neel approach (SNA) explicitly states that no one value of the ecosystem is maximized at the expense of other amenities (Palik et al. 2002). It is this difference in guiding philosophy that differentiates the SNA from other uneven-aged approaches more than the specifics of timber marking or harvesting. The SNA relies on marking guidelines that restrict cutting to a portion of the growth, maintains variation in the density and diameter distribution of the forest, encourages regeneration establishment and release, and maintains structural diversity in the canopy (Fig. 4). The selection criteria provide guidance for trees that are harvested but, more importantly, focus on the trees that are retained within the stand. Some of the philosophical differences and their practical outcome in application will be covered here, while a more detailed treatment can be found in Mitchell et al. (2000).

The SNA recognizes the central role that forest aesthetics

**Fig. 4**. Diameter distribution of longleaf pine stands under 50 years of a Stoddard–Neel single-tree selection approach (*a*) have similar diameter distributions as a demographic model recently published by Moser et al. (2002) (From Moser et al. 2002, reproduced with permission of Forestry, Vol. 75, p. 446, © 2002 Institute of Charted Foresters.) and (*b*) differs significantly from the traditional, inverse J-shaped diameter distribution. (From James et al. 2004, reproduced with permission of Hancock House Publishers Ltd., pp. 60–69, © 2002 Hancock House Publishers Ltd.)




has in its management activities. Management of the timber sustains the pine–grassland view of an open-canopy forest with multi-aged pine cohorts, a grass-dominated understory rich in species, and with sight obstructed only by occasional patches of regeneration or by wetland forests that are embedded within the longleaf pine landscape. A by-product of the focus on aesthetics is that the structure of the forest is a surrogate measure for the effectiveness of frequent burning, the maintenance of a diverse understory, and the presence of valuable wildlife habitat. After a property reaches the desired condition of a stand with full stocking, multiple age classes, and the presence of some old trees, it is managed by harvest and natural disturbance at smaller spatial scales, with forest structure relatively stable over larger spatial scales (Moser et al. 2002). For some private landowners, the aesthetic value and wildlife amenities are often the motivation that allows them to forego the shorter-term income that can be derived from liquidating the timber base. While the importance of aesthetics was well recognized by early conservationizts like Leopold (1949) and Stoddard (1931), it is often ignored in the contemporary silviculture community and the scientific community concerned with land management.

While aesthetics guide the SNA, the silvicultural foundation of this approach relies on cutting only a percentage of growth in each subsequent harvest. The timber base of a property is viewed as an endowment: the standing crop, analogous to the principal in an annuity, grows through time such that it is never intentionally reduced, and only a portion of the growth is removed at any time. This conservative approach leads to the maintenance or an increase of stocking over time. Although valuable timber is harvested under the SNA, ecological considerations are paramount in determining which trees are harvested or retained (Mitchell et al. 2000). Extraction of adult trees is done with care to enhance the ecosystem by enhancing the age structure of pine, a gradual conversion from off-site pines to longleaf pine on upland sites, and removal of undesirable hardwoods to encourage grass and pine fuels to sustain frequent, controlled burns. Trees are also harvested when removal has little effect on sustainability such as the removal of trees of low vigor or economic defect in stands of fully stocked, multi-aged longleaf pine stands. This approach not only requires that each stand and property be viewed based on its unique condition and setting in the landscape, but that each tree is individually evaluated for removal or retention. The SNA also promotes a long-term sustainable view of forest management rather than a short-term, economically driven model for forestry, with most results realized over many years from cumulative effects rather than from one or two discrete cutting cycles or management actions.

In selecting trees for harvest, longleaf pine is preferentially retained over other pine species. However, as site moisture increases, slash (*Pinus elliottii* Engelm.) or loblolly pine becomes more abundant and eventually the dominant tree species (Christensen 1988). Therefore, in wetter sites, the canopy retention criterion must be adjusted to account for changes in species dominance.

The selection of trees for harvest under the SNA also requires that some extremely marketable trees be retained if they have significant value to the long-term health of the forests (Mitchell et al. 2000). For example, under the SNA, large, old stems are often retained in the stand, even though they are frequently the most economically valuable and may have reduced growth rates. Older live trees are favored for retention over younger trees because of their value for red-cockaded woodpecker habitat and as a source of coarse woody debris (Conner et al. 1994). The presence of dead and dying trees is a structural feature of a healthy pine–grassland ecosystem (Chapman 1932); thus, one of the goals of tree selection in the SNA is to retain some decadence. This represents a fundamental departure from more traditional silviculture, which is oriented to minimize losses due to decadence. When compared with the BDq method, SNA uses ecological factors to preferentially retain large old trees, rather than applying selection rules based on diameter that result in the systematic removal of older larger trees. Some undesirable trees (those that display some sort of defect such as forked or crooked stems), while preferentially removed, are retained in small numbers, since they might provide niches for certain wildlife. Trees are retained regardless of their condition, however, when their foliage is critical as a fuel supply for fire management.

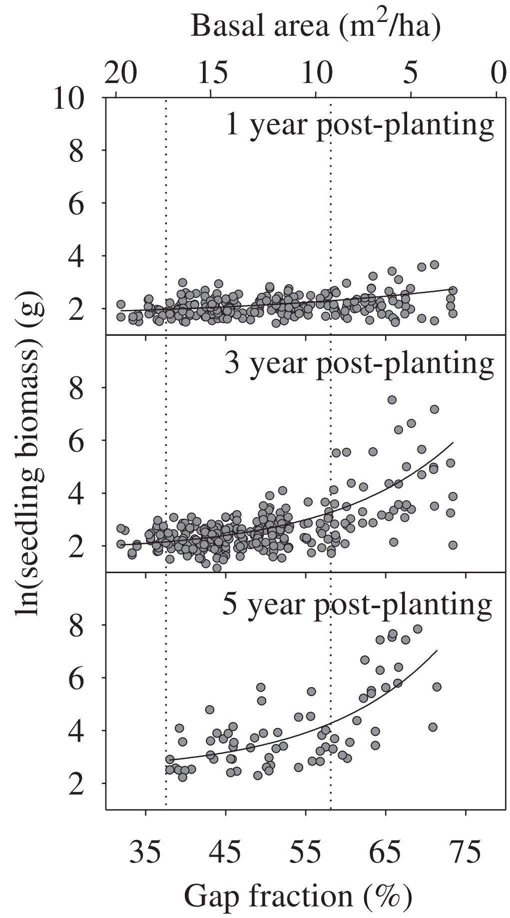
Tree harvest is also guided by the goal of maintaining heterogeneity in pine density throughout the stand, ranging from areas with a nearly closed canopy to patches with widely scattered trees. Therefore, in practice the SNA can result in the use of group selection, as different stand conditions are encountered, similar to the practices promoted by Graham and Jain (2005) and James et al. (2004). Cutting can be done to release seedlings present in the grass stage or enhance openings in the forest to encourage the establishment of regeneration, but gap size and total gap area are restricted to maintain the canopy cover needed to provide adequate fuels. Although longleaf pines are considered shade-intolerant trees, seedlings develop well in gaps as small as 0.1 ha; thus, cutting need not frequently exceed 0.25 ha for the purpose of encouraging regeneration (McGuire et al. 2001).

The SNA also incorporates time into regeneration considerations. Cutting individual trees during one cutting cycle starts the process of regeneration that continues through several cutting cycles, gradually enlarging openings and releasing seedlings (Fig. 5). Grass-stage seedlings, once established, can survive for 10–15 years until released through harvest operations or natural causes of mortality. Not only does variation in stand age structure influence recruitment of regeneration, but it also influences the abundance of trees with the kind of resin flow and sapwood to heartwood ratios that are favored by the red-cockaded woodpecker (Ross et al. 1997).

The SNA focuses on minimizing damage from logging operations (Palik et al. 2002). This is done through training or selection of logging crews familiar with low-impact techniques, with a clear understanding of what techniques are acceptable before timber is sold. Harvests are designed to utilize previously disturbed areas for logging decks and skidding trails if possible and done at times that minimize damage to the understory and soil, such as when soils are dry. Subsequent harvests are scheduled every 7–10 years to allow the understory sufficient time for recovery. In addition to timber harvests, soil disturbance associated with other management such as fire breaks, roads, or wildlife food plots are also placed in previously disturbed sites. Collectively, management is geared toward reducing damage associated with silviculture and then allowing sufficient time between harvests to recover from any damage. Fire is applied as soon as fuels can carry fire and then reapplied frequently to aid in the restoration process following harvests.

Landowner objectives in this region are becoming broader and more complex, oftentimes including conservation of biodiversity as well as sustained yield of timber. Public lands owned by the US Forest Service, Department of Defense, and US Fish and Wildlife Service — all with multiple-use objectives — have been gradually moving from silviculture that was largely developed with a focus on wood production to systems that restore, enhance, or maintain biodiversity while providing income from timber. In addition, state-owned lands are often managed with a goal to decrease operational costs. By working with a natural

**Fig. 5.** Longleaf pine regeneration can be thought of as a three-stage process. In the first stage, pine canopy density is too great to allow for pine seedling establishment but, because of competition and fire intensity, helps control hardwood density (gap fraction of <35%). In the second stage, pine overstory density is sufficiently open to allow for grass-stage seedling establishment but not sufficient for those seedlings to establish height growth (35%–60% gap fraction). In the third stage, seedlings are released and grow rapidly (gap fraction >60%) (From Kirkman and Mitchell 2006, reproduced with permission of Appl. Veg. Sci., p. 65, © 2006 Opulus Press.).




disturbance model, using fire as the primary vegetation management practice and natural regeneration, costs are significantly reduced when contrasted with systems that require intensive site preparation with chemicals or mechanical means and artificial regeneration. The high-quality wood that is produced, the more even flow of timber receipts (compared with even-aged management at a stand scale), the increase in value of land and timber, and the flexibility in marketing timber also work to make this attractive to a segment of private lands with profitable net income as their economic goal (B. McCall, Larson and McGowin, Inc., personal communication). Instruments such as conservation easements provide additional economic value to conservation approaches. Furthermore, if ecological services such as C sequestration, water production and protection, and endangered species banking become viable enterprises, the economic performance of conservation practices may be adopted over a larger land base. However, landowners that use economic decision models such as return on asset, internal rate of return, or present net value may be less interested in this type of management because of the long time frames, the high cost of money, the lack of increase in return associated with stands moving from pulpwood to other higher-value timber products, and the restrictions of timber recovered (i.e., only a percentage of growth is harvested in SNA). While the land base that has conservation as a primary goal and timber income as a secondary goal is smaller in area, recent surveys suggest that a growing number of private landowners own lands for reasons other than maximizing economic return from timber (Wicker 2006). These lands and public properties represent a significant and growing reservoir of the regional biodiversity. Silviculture that varies with objectives will be important in sustaining that diversity.

## Conclusions

For silviculture to maintain conservation value while sustaining timber yields, it must encompass (*i*) variation of age structure including young regenerating seedlings and older adults, (*ii*) variation in vigor from live trees to decaying stems, and (*iii*) variation in density typical of landscapes dominated by natural disturbance. While older trees and disturbance processes like fire are critical to sustainable forestry, sufficient recovery periods after disturbance should also be recognized as salient features of any ecological forestry system. To sustainably produce timber resources in the context of longleaf pine conservation, silvicultural approaches must redirect attention from a singular, timber-oriented focus on regeneration dynamics and wood production to the broader issue of maintaining ecosystem function such as the ability to sustain frequent fire. Variable overstory retention silviculture, whether gap-based with residual trees or individual tree-based, successfully places wood production and regeneration in that context of fuels management, thus enhancing biodiversity.

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