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The Longleaf Pine Ecosystem

Ecology, Silviculture, and Restoration

With 92 Illustrations

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Chapter 4

Longleaf Pine Regeneration Ecology and Methods

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Introduction

Regenerating longleaf pine (*Pinus palustris*) is key to its long-term sustainable production of forest resources and its perpetuation as the dominant tree species in a variety of important ecosystems ranging from xeric to mesic to hydric site conditions. Early regeneration problems and the subsequent efforts to overcome these are significant features of the continuing longleaf pine saga. This chapter discusses recent restoration relevant to longleaf pine regeneration, disturbance dynamics including fire as an ecological process and describes the uniqueness of longleaf pine's regeneration environment. Fundamental information concerning reproductive biology (including genetics, flowering, pollination, fertilization, cone production, and seed dispersal) and seedling development (including germination, shoot growth, rooting, sprouting, competition, initiation of height growth, effects of fire, and seedling morality) is then presented. Various aspects of natural regeneration and artificial regeneration are discussed and the even-aged (i.e., clearcutting, seed-tree and shelterwood) and uneven-aged (i.e., group selection and single-tree selection) forest reproduction methods are introduced. We conclude by highlighting recent work that calls for application of silviculture techniques that more closely mimic natural disturbance regimes.

Ecological Relationships

Indispensable Nature of Regeneration

Successful reproduction is essential to perpetuate any population of organisms. Indeed, if an existing generation is unable to produce a succeeding generation, then the existing generation can appropriately be considered an ecological and evolutionary "dead end" for that population and perhaps the entire species. Despite the extended longevity of many tree species, some approaching 500 years, all individual organisms eventually die. If none of the offspring survive to the age of reproductive maturity, then the entire species will eventually perish. If the species is a dominant organism, then entire ecosystems will be degraded or lost, potentially threatening the survival of associated plant and animal species.

While species extinction and ecosystem loss may seem like rare events in the shorter term of human experience, from the longer-term

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FIGURE 1. Naturally regenerated even-aged second-growth longleaf pine forest on mesic uplands. Photo courtesy of the Forestry Images Organization.

perspective of geologic time, such events have not been uncommon. The survival of species and sustainability of ecosystems cannot always be assumed, even under the best circumstances. And when new species and/or cultures encounter native ecosystems, new pressures can stress the indigenous organisms and threaten ecological sustainability. Such has been the case in the southern United States, where the Age of Discovery and the Industrial Revolution brought substantial change to native longleaf pine forests (Frost this volume). Effective means of regenerating longleaf pine are important for continuation of this species and the long-term sustainability of longleaf pine forest ecosystems.

Declining Trend

Longleaf pine ecosystems were once among the most extensive in North America, occupying about 37 million ha prior to European settlement (Frost 1993, Landers et al. 1995). While the initial impact of immigrants during the eighteenth and nineteenth centuries was generally modest, as populations grew and logging activity expanded during the late nineteenth and early twentieth centuries, most native longleaf pine forests were harvested. The land was often converted to agricultural, residential and urban uses or planted with plantations of other easier-to-establish, faster growing trees such as slash pine (*Pinus elliottii*) and loblolly pine (*Pinus taeda*) (Croker 1987, Outcalt 2000). Although many second-growth longleaf pine forests naturally regenerated following this initial harvest (Fig. 1), recovery was impaired by irregular seed production, with good seed years occurring at intervals of five or more years (Boyer 1990a). Where longleaf pine seedlings did survive logging, they were often consumed by feral hogs (*Sus scrofa*), causing many areas of potential longleaf pine forest to be lost (Schwarz 1907, Croker 1987, Simberloff 1993, McGuire 2001). As the southern landscape became increasingly domesticated, the modified structure of expansive agricultural areas and linear

transportation corridors fragmented previously contiguous habitat, thereby impeding the movement of natural surface fires across these lands (Walker 1999). During the twentieth century, organized programs of fire suppression and policies of fire exclusion from the forest further interrupted natural fire regimes (Croker 1987). Since the absence of frequent surface fires impedes the natural regeneration of longleaf pine and allows invasion of longleaf pine sites by hardwoods and more aggressive southern pines, interruption of natural fire regimes is believed to be the most ecologically significant cause for its continuing decline (Wright and Bailey 1982, Landers et al. 1990, Pyne 1997, Gilliam and Platt 1999). Longleaf pine forests have undergone a steady decrease to 8 million ha in 1935 (Wahlenberg 1946), 2 million ha by 1975, 1.5 million ha in 1985 (Kelly and Bechtold 1990) and less than 1.2 million ha currently (Outcalt and Sheffield 1996). Occupying less than 3% of their original range (Ware et al. 1993), longleaf pine ecosystems are now recognized as being at high risk (Noss et al. 1995, Kush 2002). Unfortunately, area reductions continue for stands in every diameter class below 41 cm (Kelly and Bechtold, 1990), an indication that most remaining longleaf pine forests are aging without replacement.

Ecological Restoration

Extending along the Gulf and Atlantic Coastal Plains from Texas to Virginia and inland to the Piedmont and mountains in Alabama and Georgia, longleaf pine forests, woodlands, and savannas may occupy a wide variety of sites, ranging from wet poorly drained flatwoods to mesic uplands, xeric sandhills, and rocky mountain ridges (Boyer 1990a; Stout and Marion 1993). Distinguished by a generally open, parklike stand structure (Schwarz 1907; Wahlenberg 1946), naturally regenerated longleaf pine forests are typically an uneven-aged mosaic of even-aged patches distributed across the landscape, which vary in size, structure, composition, and density (Platt and Rathbun 1993; Brockway and Outcalt 1998) and contain numerous embedded special habitats such as stream bottoms, wetlands, and seeps (Hilton 1999). The natural variability of these ecosystems makes them excellent habitat for a variety of game animals and numerous nongame and rare wildlife species (Kantola and Humphrey 1990; Engstrom 1993; Guyer and Bailey 1993; Crofton 2001; Engstrom et al. 2001; Brockway and Lewis 2003; Means this volume).

The complex natural patterns and processes unique to longleaf pine forests create extraordinarily high levels of biological diversity in these ecosystems, with the great number of plant species per unit area qualifying these as among the most species-rich terrestrial ecosystems outside the tropics. As many as 140 vascular plant species have been observed in a 1000 m^2 area and equally impressive counts of more than 40 species per m^2 have been recorded (Peet and Allard 1993), a large number of which are restricted to or found principally in longleaf pine habitats. Habitat reduction resulting from decline of longleaf pine ecosystems has caused the increased rarity of 191 vascular plant taxa (Hardin and White 1989, Walker 1993) and several vertebrate species. Concern over loss of this unique ecosystem (Means and Grow 1985; Noss et al. 1995) has led to many efforts focused on effectively restoring longleaf pine ecosystems (Walker and Boyer 1993; Walker 1995; Kush 1996, 1998, 1999, 2001; Johnson and Gjerstad 1998, 1999; Brockway et al. 1998; Seamon 1998; Outcalt et al. 1999; Brockway and Outcalt 2000; Provencher et al. 2001a,b; Mulligan et al. 2002). Since longleaf pine still occurs in isolated fragments over most of its natural range, it is reasonable to conclude that restoration of these ecosystems is possible (Landers et al. 1995). Effective methods for regenerating longleaf pine will no doubt play a key role in ecological restoration efforts.

Disturbance Dynamics and Fire as an Ecological Process

Longleaf pine ecosystems exist in an environment influenced by large-scale catastrophic disturbance, such as damaging tropical storms. Lightning is an important agent in individual tree morality and creation of small-scale

disturbance in longleaf pine forests (Komarek 1968; Taylor 1974). The structure, pattern, and diversity of longleaf pine ecosystems are maintained by a combination of site factors and periodic disturbance events, including lightning strikes, tree mortality, and animal interactions at local scales and tropical storms, soils, and hydrologic regimes at broader scales. Disturbances across site gradients provide large living trees, snags, coarse woody debris, forest canopy gaps, and hardwood thickets that support numerous plant and animal species adapted to these disturbance-prone, yet largely stable ecosystems.

Longleaf pine is closely associated with wiregrass (*Aristida* spp.) in the eastern part and bluestem grasses (*Andropogon* spp. and *Schizachyrium* spp.) in the western portion of its range. The understories of longleaf pine forests are typically dominated by herbaceous plants because these bunchgrasses facilitate the ignition and spread of frequent surface fires (Landers 1991). In these ecosystems, longleaf pine and bunchgrasses function together as keystone species that facilitate but are resistant to fire (Platt et al. 1988; Noss 1989). They also exhibit substantial longevity and demonstrate nutrient and water retention to a degree that reinforces their site dominance and minimizes change in the plant community following disturbance (Landers et al. 1995). As a key ecological process and disturbance agent, the benefits of periodic fire include (1) maintaining the physiognomic character of longleaf pine ecosystems through excluding invasive plants that are ill-adapted to fire, (2) preparing a seedbed favorable for the establishment of longleaf pine seedlings, (3) reducing the density of understory vegetation thus providing microsites for a variety of herbaceous plants, (4) releasing nutrients immobilized in accumulated phytomass for recycling to the infertile soil and subsequently more rapid uptake by plants, (5) improving forage for grazing, (6) enhancing wildlife habitat, (7) controlling harmful insects and pathogens, and (8) reducing fuel levels and wildfire hazard (McKee 1982; Wade and Lewis 1987; Boyer 1990b; Wade and Lundsford 1990; Dickmann 1993; Brennan and Hermann 1994; Brockway and Lewis 1997).

Regeneration Environment

Difficulties encountered during early attempts to regenerate longleaf pine impeded its recovery and contributed to its historical decline (Croker 1987). Erratic seed production, poor seedling survival, and slow early growth of seedlings discouraged forestland managers from investing in longleaf pine. Management policies based on these initial observations further contributed to the decrease of longleaf pine forests, as harvested stands were deliberately converted to other southern pine species rather than being regenerated with longleaf pine. Fortunately, later research illuminated the ecological mechanisms and identified silvicultural methods for effectively regenerating longleaf pine by natural and artificial means (Boyer and White 1990; Barnett et al. 1990; Kush 2002) and the earlier policies of forest type conversion have now been largely reversed.

The unique structural and process dynamics characteristic of longleaf pine forests provide both challenges to and opportunities for applying science and adapting technology to efficiently obtain regeneration. Foremost, all longleaf pine forests are obligatorily pyrophytic ecosystems. Therefore, all regeneration techniques employed must be compatible with periodic surface fires. Longleaf pine forests are disturbance-prone and naturally regenerate in a variety of configurations ranging from relatively small circular or elliptical canopy gaps and attenuated strings to larger areas of partially blown down or almost completely blown down overstory trees (Croker and Boyer 1975; Palik and Pedersen 1996; Brockway and Outcalt 1998). As a tree species that is intolerant of competition, whether for light, moisture, or nutrients (Boyer 1990a), its seedlings become established and flourish as opportunists responding to resource availability. Although longleaf pine displays many traits consistent with an intolerant, early seral species, its seedlings often persist in the forest understory for prolonged periods similar to those of more tolerant, late-seral species. Suppressed longleaf pine seedlings will not respond with improved growth until released from competition with overstory trees and

long-suppressed individuals are, through time, increasingly prone to mortality. Whether a specific longleaf pine seedling survives to eventually become a dominant member of the forest canopy may depend as much on stochastic events (i.e., drought severity and duration, fire intensity and season, disturbance that results in timely release from competition) as it does on the competitive vigor (i.e., genetic attributes) of the individual. Whether by artificial or natural methods, by even-aged or uneven-aged silvicultural techniques, not only is efficiently regenerating longleaf pine feasible, it is also imperative for achieving ecological restoration and ecosystem sustainability goals.

Reproductive Biology

Genetics

Longleaf pine is a tree species of considerable genetic diversity, with variation among individuals typically greater than that among stands or geographically different seed sources (Snyder et al. 1977; Lynch 1980). Although genetic variation among populations is thought to be a result of the diversity of environments in which longleaf pine occurs throughout its native range (Boyer 1990a), measures of genetic diversity appear unrelated to climate variables (Schmidtling and Hipkins 1998). While the pattern of genetic variation for longleaf pine is similar to that of other southern pines (Schmidtling 1999), its unique pattern of allozyme variation is indicative of a very different history during the recent Ice Age (Schmidtling et al. 2000). Unlike other pines, longleaf pine appears to have migrated eastward across the southeastern United States from a single refuge in southern Texas and/or northeastern Mexico after the Pleistocene (Schmidtling and Hipkins 1998). The progressive decrease in allozyme diversity from western to eastern longleaf pine populations represents a loss in genetic variability from stochastic events during migration.

Longleaf pine may form a natural hybrid with loblolly pine, referred to as "Sonderegger pine" (*Pinus sondereggeri*). Since flowering of these two species frequently overlaps, there is no phenological barrier to natural crossing (Boyer 1990a). Hybridization between longleaf pine and slash pine is far less likely because of differences between their dormancy and heat requirements for flowering (Boyer 1981); however, artificial crossing can be easily achieved. Hybrids between longleaf pine and shortleaf pine (*Pinus echinata*) have not been observed in nature but have been artificially produced (Snyder et al. 1977).

With a pattern of genetic variation similar to that in other southern pines, longleaf pine is suitable for genetic improvement. However, the effort expended on this species is easily dwarfed by the immense resources devoted to loblolly pine and slash pine improvement programs (Schmidtling 1999). Traditional tree improvement approaches, which select "plus" trees in the forest based on size and form, have not proven to be suitable for longleaf pine. Variation in the "grass" stage of longleaf pine makes it impossible to determine the true age of a tree and thus its true growth potential. Therefore, tree improvement programs for longleaf pine have shifted their emphasis to a progeny test approach, with the duration of the grass stage and resistance to brown-spot fungus (*Mycosphaerella dearnessii*) the most important inherited traits of interest. When focusing efforts on accelerating the early height growth of longleaf pine, one of the greatest dangers is the possibility of incorporating loblolly pine genes that will result in a hybrid that begins growing earlier but has poor form and increased susceptibility to fusiform rust fungus (*Cronartium quercuum* f. sp. *fusiforme*). There is no ecotypic differentiation in longleaf pine based on site conditions and no important difference in survival or growth between eastern and western populations, as occurs with loblolly pine (Schmidtling 1999).

Flowering, Pollination, and Fertilization

Longleaf pine is monoecious, with male strobili (catkins) predominating in the lower crown and female strobili (conelets) occurring most frequently in the upper crown of the same tree (Schopmeyer 1974). Development of catkins

FIGURE 2. Elongated catkins, subtending a terminal bud, shown after their pollen has been shed. Photo courtesy of the Forestry Images Organization.

(Fig. 2) and conelets (Fig. 3) is initiated during the growing season before buds emerge, with catkins beginning to form during July and conelets being formed during a short period in August (Boyer 1990a). First appearing at the base of vegetative buds between mid-November and early December, purple catkins remain dormant for several weeks before resuming development between late December and early February (Boyer 1981). Conelet buds appear in January or February and conelets, upon emerging from the bud, are red until pollinated, after which they fade to yellowish green. The development rates of both catkins and conelets are almost entirely dependent on ambient temperature (Boyer 1990a).

The number of flowers produced appears related to weather conditions during the year of initiation. Catkin production is favored by abundant rainfall throughout the growing season, while conelet production is promoted by a wet spring and early summer followed by a dry period in late summer (Shoulders 1967). Because of the differential conditions that favor each sex, large crops of male and female flowers do not necessarily coincide (Boyer 1990a). Heavy annual losses of longleaf pine conelets can usually be expected, with observed losses ranging from 65% to 100% (Boyer 1974a; McLemore 1977; White et al. 1977). Insects, weather extremes, and insufficient pollen appear to be the primary causes for these losses, which primarily occur during spring pollination or the following summer.

Peak pollen shed and conelet receptivity typically vary from late February in the southern portion of the native range to early April in more northern areas (Boyer 1990a). Although pollen shedding and receptivity coincide on individual trees, there appears to be very little synchrony among trees in a longleaf pine forest, with some trees being consistently early and others being consistently late and overall dates highly influenced by air temperatures before and during the flowering period. Pollen shedding typically occurs during a period of 5 to 21 days, with an average of 13 days (Boyer 1981). Year-to-year variation in the time of pollen shedding appears to be related to accumulation of degree-day heat sums, with all temperatures greater than 10°C after January 1 promoting development of the male strobili (Boyer and Woods 1973; Boyer 1973, 1978).

While pollination takes place in late winter or spring, fertilization does not occur until the following spring. Conelets grow rapidly after fertilization, increasing in length from 2.5 cm to 18 cm by May or June (Boyer 1990a). Cones reach maturity between mid-September and mid-October of their second year and range in length from 10 cm to 25 cm. Although cone color changes from green to brown as they ripen, cones may be ripe before changing color (Schopmeyer 1974).

Cone Production and Seed Dispersal

Longleaf pine cone crops are highly variable from year to year (Fig. 4), with 1860 cones/ha

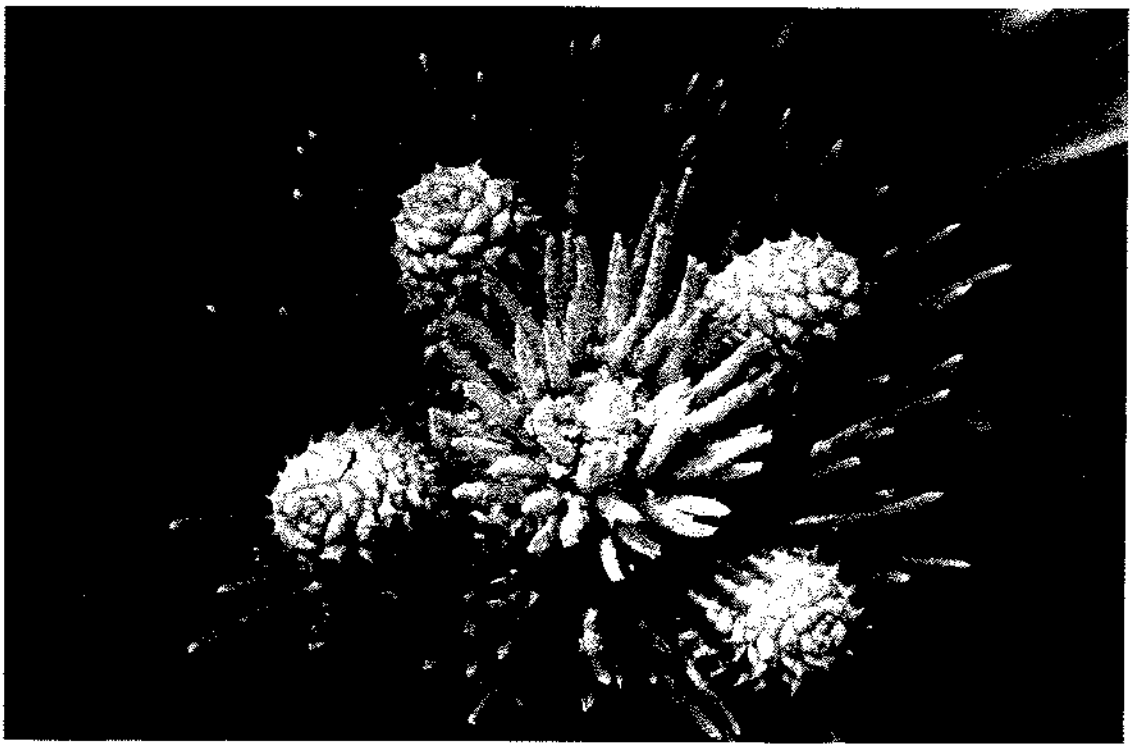

FIGURE 3. Conelets, located peripherally to terminal buds, are most often observed in the upper crown. Photo courtesy of the Forestry Images Organization.

(e.g., 30 cones/tree and 62 seed trees/ha) normally required for successful natural regeneration (Boyer 1996). While cone production may be influenced by the density of airborne pollen during flowering, low cone crop frequencies appear to be more a result of flower losses rather than a failure to produce flowers (Boyer 1974a, 1987a). Since 1986, cone crops on coastal plain sites from Louisiana to North Carolina have increased to an average of 36 cones/tree from an earlier average of only 14 (Boyer 1998). This increase in cone production appears to be a result of both an increase in flower production and an increase in the fraction of flowers surviving to become mature cones. Cone production of individual trees is influenced foremost by genetics and secondarily by tree size, crown class, stand density, and site quality. The greatest cone production occurs on dominant, open-grown longleaf pines having large crowns (Croker and Boyer 1975). Trees of 38–48 cm diameter at breast height produce on average 65 cones/year compared with 15 cones/year from trees in the 25–33 cm diameter at breast height size class (Boyer 1990a). The number of viable seeds per cone varies with the seed crop for a specific year, ranging from 50 seeds/cone in good years to 35 seeds/cone during average years to 15 seeds/cone in poor years (Croker 1973).

Peak seed production is observed in longleaf pine forests having stand densities between 6.9 and 9.2 m^2/ha, when principally comprised of dominant and codominant trees of cone-bearing size (Boyer 1979). Such stands produce seed crops adequate for natural regeneration once every 4 to 5 years on average (Croker and Boyer 1975). When forests of substantially greater density are thinned to this level, increased cone production resulting from decreased intraspecific competition does not occur for three growing seasons (Croker 1952). Release following conelet initiation

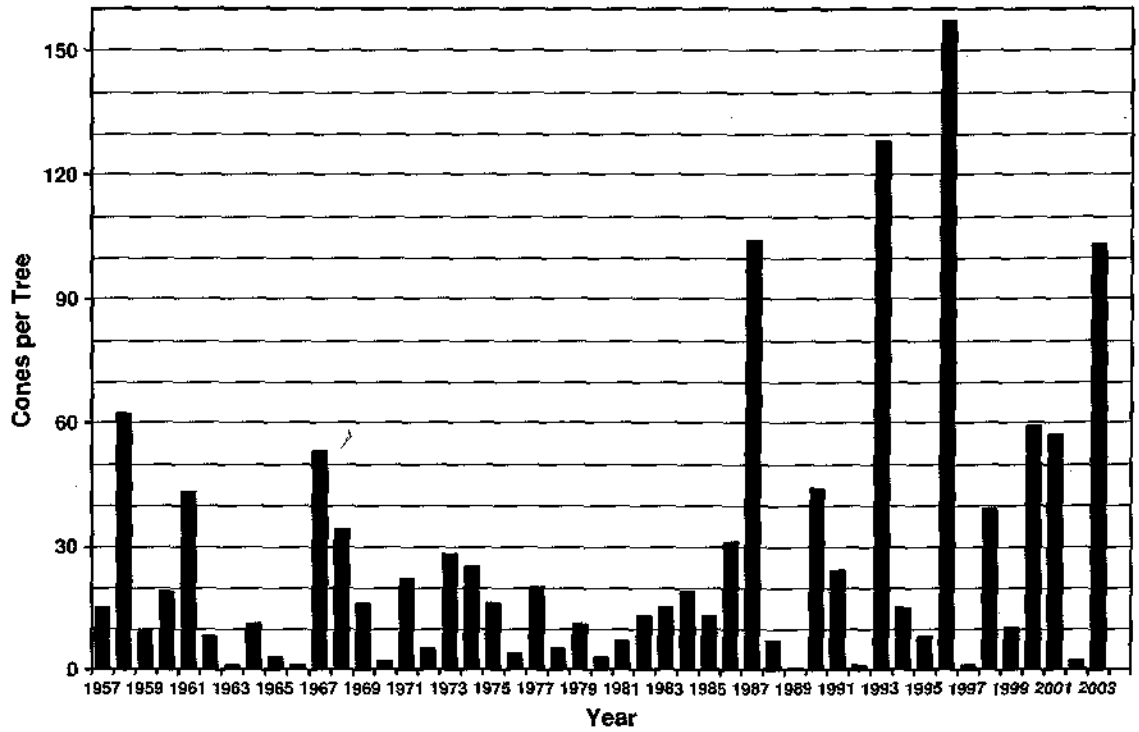

FIGURE 4. Example of high temporal variability for longleaf pine seed production: Cone crops at the Escambia Experimental Forest, southern Alabama, 1957–2003.

benefits the crop only by reducing moisture stress during dry periods (Boyer 1990a). Seeds are dispersed by wind during a 2- to 3-week period between late October and late November, depending on weather conditions. Longleaf pine seeds are the largest of the southern pines and their dispersal distance is limited, with 71% of sound seeds falling within 20 meters of the base of a parent tree (Croker and Boyer 1975).

Seedling Development

Germination and Shoot Growth

Longleaf pine seeds typically germinate (Fig. 5) within a week of contacting the ground (Boyer 1990a). While rapid germination may be an adaptation to reduce the risk of exposure to seed predators, newly germinated seedlings are also vulnerable to mortality from animals, pathogens, and adverse weather conditions (Croker and Boyer 1975). Although germination and establishment require that seeds contact mineral soil, the large seed and wing can impede penetration through dense grass or accumulated litter on the forest floor. Root systems of premature germinants fail to reach mineral soil and readily die from desiccation. The risk of regeneration failure can be significantly reduced by using mechanical treatment and/or prescribed fire to prepare a suitable seedbed before seedfall. Germination begins with emergence of the radicle and an almost simultaneous elongation of the cotyledons (Allen 1958). Hypocotyl elongation begins soon after radicle emergence but is limited. Growth of the cotyledons lifts the seedcoat from the ground. Limited hypocotyl growth causes the cotyledons of new germinants to remain at or near the ground line. Newly germinated seedlings are relatively inconspicuous with their small primary needles. Although secondary needles appear within 2 months, the epicotyl reaches a length of only 0.38 cm

FIGURE 5. Newly germinated longleaf pine seedlings emerging from thin forest litter (foreground) and among cones fallen from the parent trees. Photo courtesy of the Forestry Images Organization.

and, during the next 8 weeks, does not elongate as in other pines. This stemless condition is one of the unique characteristics of longleaf pine, commonly referred to as the "grass stage" (Fig. 6). Depending on ambient conditions, longleaf pine seedlings may remain in this stage for 2 to as long as 15 years, during which they are most susceptible to their major disease, brown-spot needle blight (Boyer 1990a).

Roots and Sprouts

While in the grass stage, longleaf pine seedlings devote much of their energy to root production. Following germination, the radicle forms a taproot that develops very rapidly. Growth rates may be as high as 50 cm in 15 days following germination in sandy soils under greenhouse conditions (Wahlenberg 1946). More typical rates are 0.8 cm/day during the first 60 days (Allen 1958). Taproot development is inversely related to moisture conditions, with greater root elongation occurring in drier soils. The general root structure of natural seedlings is unaffected by soil conditions, but these seedlings have slower root growth than those measured in greenhouse tests. The root system of a typical 1-year-old seedling consists of a taproot 60–70 cm long and a number of strong laterals 50–60 cm long in the upper soil layers with numerous attached feeder tips (Wahlenberg 1946). Laterals extend outward, and though they often change direction due to obstructions, they remain at a uniform depth from origin to tip (Heyward 1933). On wetter flatwoods sites, root systems have the same general architecture, but root distribution is restricted mostly to surface horizons, above the spodic layer that occurs in soils typical of these

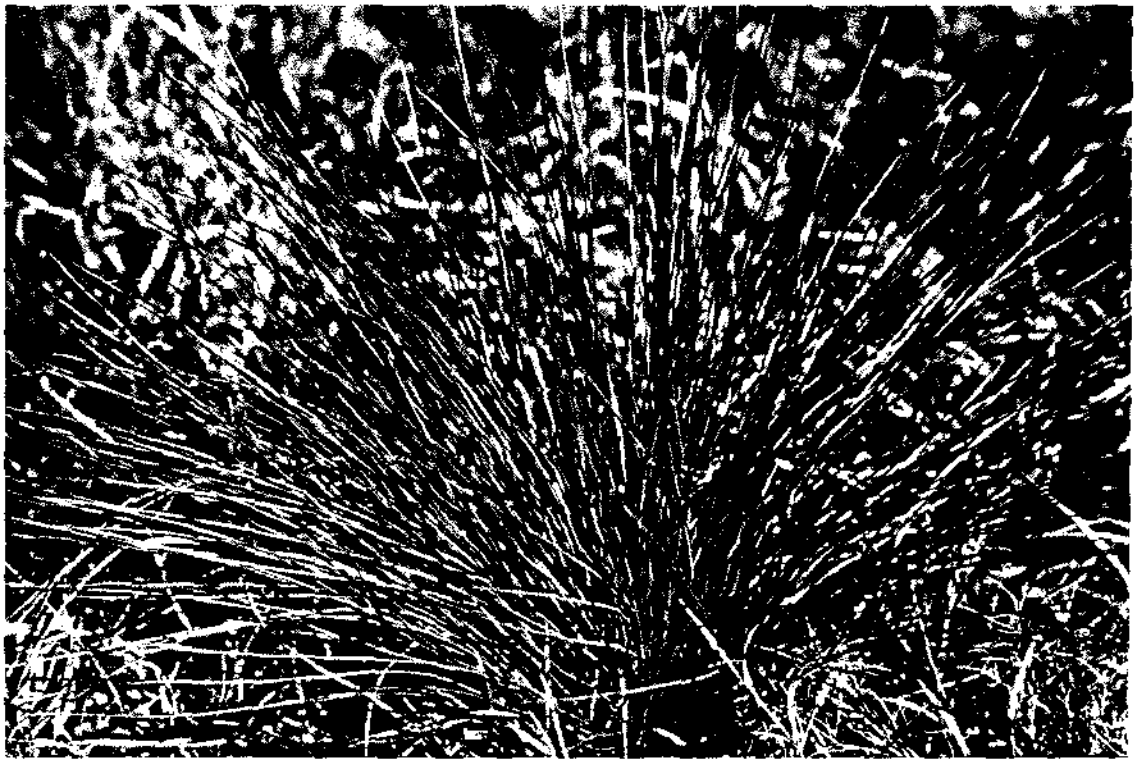

FIGURE 6. Longleaf pine seedling in the grass stage. Photo courtesy of the Forestry Images Organization.

areas. Even in well-drained sands, 90% of all lateral roots are found in the upper 30 cm of the soil.

Longleaf pine seedlings can sprout from the root collar if the top is killed. Under natural conditions, sprouts often result following top kill from fire. This sprouting ability diminishes rapidly once seedlings emerge from the grass stage and begin stem elongation. As many as 40% of the grass-stage seedlings that were cut off at the groundline have been found to have living sprouts 1 year later (Farrar 1975). Only 14% of the seedlings, that had initiated height growth but were less than 1.37 m tall, produced sprouts when cut at the groundline. None of the trees more than 1.37 m tall produced sprouts after cutting. Three years after cutting, 30% of the grass-stage seedlings still had surviving sprouts, but these were growing very slowly. Although fewer of the seedlings that had begun height growth sprouted, those sprouts were much larger 3 years after treatment. Sprouts from smaller seedlings are rather weak and often die following subsequent fires.

Competition

Longleaf pine seedlings are intolerant of interspecific and intraspecific competition (Harrington, this volume). Seedling growth rates improve as the distance from adult pines increases, with the suppressive effect from stands of overstory trees adjacent to clearcut strips being greater than that from single overstory trees (Boyer 1963). The relationship of declining seedling growth rates with increasing amounts of overstory competition (i.e., overstory basal area) follows that of a general exponential decay curve. The root collar diameter for 4-year-old seedlings has been reported to sharply decrease from 1.2 cm to 0.7 cm as overstory basal area increased from 0 to 6.9 m^2/ha. More recent work has substantiated the suppressive effect of overstory adults upon longleaf pine seedlings on redhills sites (Grace and

Platt 1995) and flatwoods sites (Gagnon et al. 2003, 2004) and the exponential relationship between seedling growth and overstory basal area (Palik et al. 1997).

Overstory hardwood trees are even greater competition for longleaf pine seedlings. While 60% of the seedlings in the 0–3 m zone near adult longleaf pines reached sufficient root collar diameter by age 9 to begin height growth (Smith 1962), only 24% of the pine seedlings near oak trees had initiated height growth. Removal of overstory oaks significantly improved height growth of longleaf seedlings (Walker 1954). Understory vegetation, including other longleaf pine seedlings and herbaceous plants, also competes with longleaf pine seedlings. Single season growth increases of 18% were measured in seedling densities of 247,100/ha and increases of 64% were observed at densities of 2471/ha (Pessin 1938). When herbaceous competition was removed, growth increased by 25 and 456% for the same respective seedling densities. Thus, intraspecific competition in the understory appears much less important than competition from other species in this layer.

Ascertaining the underlying causes of seedling growth reduction has proven challenging. Root competition was believed to be much more important than light because growth depression extends well beyond the height of adjacent overstory trees (Walker and Davis 1956; Croker and Boyer 1975). This inhibitory effect is also greater on sites with poor soils, another indication of belowground competition. The importance of belowground competition was more recently substantiated by research on xeric sandhills sites in Florida, where total daily light influx did not differ significantly with distance from adult trees, but the fine root biomass of overstory trees did decline with distance (Brockway and Outcalt 1998). Others working on more fertile soils with higher densities of woody plants have shown that light does increase with distance from gap edge (Palik et al. 1997; McGuire et al. 2001; Gagnon et al. 2003). Palik et al. (1997) also documented a positive relationship between available N and seedling growth. Longleaf pine seedling growth was found to be significantly related to N, soil water, and their interaction in a greenhouse study (Jose et al. 2003). Light was important only if water was not limiting. Therefore, competition affecting longleaf pine seedling growth follows the fundamental principle of limiting factors, with growth most impaired by whichever essential factor is most limited in a specific environment.

Initiation of Height Growth

Although varying considerably, longleaf pine seedlings usually begin emerging from the grass stage when their root-collar diameter reaches about 2.5 cm (Boyer 1990a). Infection by brown-spot needle blight can substantially delay grass stage emergence. The height growth of seedlings also depends on the intensity of competition in the ambient environment (Ramsey et al. 2003). Therefore, treatments that reduce competition will increase the proportion of seedlings that emerge from the grass stage (Haywood 2000). Differences in levels of intraspecific and interspecific competition and individual genetic control of growth rates and resistance to brown-spot infection result in considerable variation in emergence of longleaf pine seedlings from the grass stage. This high within-stand variation is actually beneficial as it leads to the early establishment of dominant seedlings, preventing stand stagnation even when seedlings occur at very high densities. The key to height growth initiation is accumulation of carbohydrate reserves in the root sufficient to support rapid upward expansion of the stem. This interval is known as the bolting stage in which rapid growth of the needle-covered stem occurs with limited lateral branch development, producing the characteristic "bottlebrush" structure (Fig. 7). Under favorable conditions, longleaf pine seedlings can grow 30–90 cm in a single season (Wahlenberg 1946).

Effects of Fire

Longleaf pine evolved in ecosystems subject to frequent low-intensity surface fires and has developed many adaptations for enhancing survival and growth in this environment (Landers 1991). Although newly germinated

FIGURE 7. Longleaf pine seedlings in the bolting stage. Photo courtesy of the Forestry Images Organization.

FIGURE 8. This larger grass-stage longleaf pine survived a recent fire; note the thick root collar and partially consumed needles that adequately protected its terminal bud. Photo courtesy of the Forestry Images Organization.

and small grass-stage seedlings are susceptible to fire-caused mortality, once they attain a root-collar diameter of 1.3 cm, they become quite fire-resistant (Boyer 1974b). Such larger grass-stage seedlings have thicker bark and a large tuft of needles that protect the central meristem (Fig. 8) and, as noted previously, even if the top is killed, they will often sprout. However, since many natural seedlings do not attain this size until they are 2 or 3 years old, mortality from fires can be quite high. A single growing-season fire, at age 2, can result in as much as 80% of the total seedling mortality for the 3-year period following germination. Fire can also be beneficial to longleaf pine seedlings by consuming brown-spot-infected needles. Fire stimulates height growth (Grelen 1983) by reducing competition and releasing nutrients immobilized in organic matter.

When initiating height growth, seedlings once again become more susceptible to fire-caused mortality. During this stage, the terminal bud is situated directly in the flaming zone, where it may be exposed to maximum temperatures. These seedlings are especially vulnerable during early season bud break when the candles are rapidly expanding and there is very little protective needle mass. Once they have bolted above the flame zone (about 1 m), seedlings are again quite resistant to fires of moderate intensity. Although fire does not kill many longleaf pines once they reach this small sapling stage, burning can still cause reductions in growth (Boyer 1987b).

Seedling Mortality

Seedlings are susceptible to losses from frost heaving, flooding, disease, logging, fire,

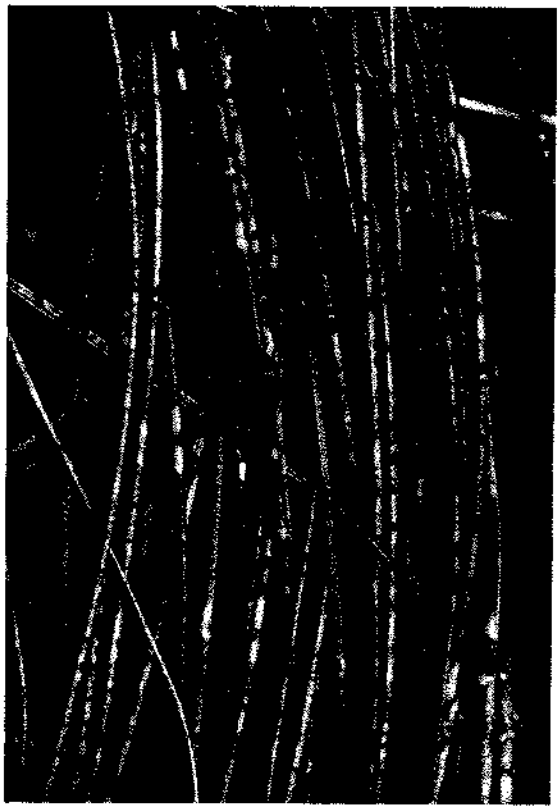

FIGURE 9. Close-up view of longleaf pine needles infected with brown-spot fungus; note highly variegated color tones and distinctive dark spots on the needles. Photo courtesy of the Forestry Images Organization.

drought, and animals. As expected, losses are greatest during the first growing season. Frost heaving is a threat only near the northern limit of the natural range on finer-textured soils. Flooding can be a problem on wet coastal plain sites where prolonged standing water can kill newly germinated seedlings (Croker and Boyer 1975). Brown-spot needle blight (Fig. 9) may at times become so severe that it destroys all the foliage and directly kills the seedling. More often, the seedling becomes so weakened that it dies during the next fire. While depending on the harvest method, season, and volume of trees removed, losses from logging generally average about 50% (Boyer 1990a). To minimize logging losses, harvesting should be done when seedlings are in the grass stage. As noted above, fire is a significant cause of seedling mortality during the first 2 years, where losses up to 90% may often occur (Grace and Platt 1995; Provencher et al. 2001b). The probability of seedling mortality from fire is greatest in the zone around adult trees, because greater needle litter accumulations there often result in hotter fires. Higher intraspecific competition in this zone also results in slower seedling growth, thus predisposing them to higher rates of fire-related mortality. Before the first fire occurs, seedlings growing close to adult pines rarely attain the 1.3 cm root-collar diameter needed for survival.

Drought can cause significant losses of first-year seedlings, especially on sandhills sites where 50% mortality is common during the spring drought period. Many of the seedlings that perish during dry periods are growing on locations where the forest floor is somewhat thicker. Although bare mineral soil is ideal for longleaf pine germination and growth, sufficient moisture is all that is needed to initiate the germination process. Therefore, many of the seedlings that germinate on thicker forest floor material in the fall, fail to survive the spring drought because their root system has not penetrated sufficiently into the mineral soil to obtain adequate moisture. Litterfall is of course not distributed evenly, but rather is highest near adult trees. The greater forest floor thickness, increased root competition, and reduced rainfall from crown interception all combine to substantially lower the probability of longleaf pine seedling survival near adult overstory trees. This typical spring mortality significantly contributes to development of the often-observed zone of seedling exclusion near adult pines (Brockway and Outcalt 1998).

Both wild and domestic animals can decimate stands of longleaf pine seedlings. Locally high populations of rabbits can cause significant damage to newly germinated seedlings by clipping off the needles (Croker and Boyer 1975). Local losses can also result from pocket gophers feeding on the starch-laden roots of grass-stage seedlings. While cattle will also graze on longleaf pine seedlings, most damage and mortality results from trampling where sites are allowed to suffer from overstocking

and excessive use. However, the most destructive of all animals is the wild hog, a nonnative species introduced from Europe. The roots of grass-stage seedlings, rich in starch, are a favorite food of wild hogs. A single hog can uproot and consume a great many seedlings in a single day. The destructive power of the vast herds of wild hogs was noted in the early 1900s (Schwarz 1907). An early fencing study demonstrated their effect on longleaf pine seedling densities, with 14,826 stems/ha occurring within the protective fence and a mere 20 stems/ha surviving outside (Mattoon 1922). In some locations, wild hogs still pose a problem for regeneration. However, removing hogs for only 2 years resulted in successful regeneration of longleaf pine in the South Carolina Coastal Plain (Lipscomb 1989).

Natural Regeneration

Regeneration Problems

Perhaps the greatest impediment to wider acceptance of longleaf pine, as a tree worthy of forest management investment, is its reputation as a difficult species to successfully regenerate, whether by natural or artificial means. Schwarz (1907) was among the first to identify poor regeneration as a major threat to the future of longleaf pine. Insufficient numbers of seed trees, infrequent seed crops, cone infestation by insects, limited dispersal distance of heavy seeds, seed predation, seed perching in litter above mineral soil, vulnerability of early germinating seed to temperature extremes, brown-spot fungus infection, slow early seedling growth, untimely fires, and fire exclusion favoring competing species are among the primary reasons for regeneration failure of longleaf pine (Wahlenberg 1946; Croker and Boyer 1975; Boyer 1979). Fortunately, the extensive research conducted on longleaf pine regeneration during the second half of the twentieth century has now reduced these problems to considerations that can be effectively addressed through appropriate management strategies and practices (Kush 2002).

Regeneration Requirements

When the fundamental requirements can be met, natural regeneration is a practical and inexpensive management option for existing longleaf pine forests (Boyer 1993a). The foremost requirements for successfully regenerating longleaf pine by natural means are an adequate seed source and a receptive seedbed (Boyer and White 1990). A sufficient number of sexually mature parent trees, having desirable characteristics and being well distributed throughout the area, typically serves to meet this need (Dennington and Farrar 1991). Since longleaf pine seed crops are infrequent, averaging one every 5 to 7 years, annual monitoring of conelet and cone production is necessary to appropriately forecast years when adequate seed will be available (Boyer 1996). For initiating even-aged stands, the size, number, and distribution of seed-bearing trees must be such that a minimum of 1860 and preferably 2470 or more cones/ha will be provided (Boyer and White 1990). Peak seed production may be encouraged in future years by reducing stand density to between 6.9 and 9.2 m^2/ha (Boyer 1979).

One of the most pervasive problems impeding the natural regeneration of longleaf pine is high-density understory and midstory layers dominated by woody plants. If preestablishment competition control is not achieved, longleaf pine regeneration success will be highly doubtful (Boyer and White 1990). Therefore, competing hardwood trees and shrubs must be effectively controlled before seed dispersal. The presence of competing woody plants is not only deleterious to seedlings as they are becoming established, but may also interfere with dispersed seeds as they attempt to reach mineral soil. Although prescribed fire conducted well in advance of seedfall may be sufficient to control these woody plants, herbicide application or mechanical treatment may also be necessary to obtain adequate control under certain circumstances (Croker and Boyer 1975).

Longleaf pine seeds need to be in contact with mineral soil for successful germination and establishment (Boyer and White 1990).

Since seed supplies are typically limited, a well-prepared mineral seedbed is necessary to provide optimum opportunity for regeneration success. A suitably prepared seedbed can be created by a prescribed fire conducted within 1 year prior to seedfall. Such a fire will remove enough forest litter to double the rate of longleaf pine seedling establishment compared to unburned sites. While only 14% of longleaf pine seeds became established as seedlings on unburned areas, 36% became established on winter-burned areas and 24% became established on fall-burned areas (Croker 1975). The lower establishment level on fall-burned areas is believed to result from lighter subsequent litter accumulation causing higher rates of seed predation by birds.

Successful regeneration requires an adequate number of established seedlings well-distributed throughout the area (Boyer and White 1990). Although exact criteria must be left up to individual land managers with specific management objectives, a reasonable goal when using the shelterwood method might be about 14,800 established 1-year-old or older seedlings per hectare. This standard allows for about 50% mortality among seedlings, when the stand is later logged, and anticipates high rates of mortality from other sources, especially brown-spot fungus, during the early years following establishment. It is reasonable to expect that at least 1235 well-distributed seedlings per hectare could result that are about 1 m in height and therefore free from brown-spot infection and relatively safe from damage by fire (Croker and Boyer 1975).

Since longleaf pine is highly sensitive to competition, established seedlings develop optimally in the absence of competitors. Although hardwood trees and shrubs comprise the most severe competition for young longleaf pine, these should be largely eliminated during preestablishment treatments. While eliminating all competitors is not practical, action to obtain postestablishment competition control is indicated when hardwood densities exceed 2.3 m^2/ha (Boyer and White 1990). Herbaceous understory plants and adult longleaf pine trees in the overstory typically remain as the major competitors for newly established seedlings. Seedling growth beneath adults remains inhibited until nearby overstory trees are removed (Boyer and White 1990). Periodic prescribed fire should adequately curtail understory plants, with herbicide application reserved for use under specific circumstances.

Control of the brown-spot fungus, the most serious pathogen of longleaf pine, is essential for successful natural regeneration (Boyer and White 1990; Boyer 1990a; Dennington and Farrar 1991). Timely application of prescribed fire, which consumes the infected needles, is the most effective remedy for this needle blight. In newly established seedlings, prescribed fire should be deferred until an adequate number of the seedlings reach a fire-resistant size. Unfortunately, seedlings beneath adult trees grow slowly and delaying fire could allow brown-spot needle blight to spread in a stand, further inhibiting seedling growth. This risk can be abated by maintaining relatively low basal areas where seedlings are less likely to be suppressed by overstory trees.

Young seedlings must also be protected from hogs, which can rapidly destroy seedlings by consuming them while in the grass stage (Boyer 1990a; Boyer and White 1990). Cattle grazing will also reduce the fine fuel needed to effectively carry fire in these ecosystems and may directly damage seedlings if conducted at high intensities (Dennington and Farrar 1991). Regenerating longleaf pine by natural means requires careful attention to details relevant to advanced planning, monitoring site conditions, prescription development, and timing of cultural treatments. Through identifying the area, assessing the seed source, monitoring cone crops, controlling competition, preparing a suitable seedbed, conducting regeneration surveys of seedlings, appropriately adjusting overstory density, and conducting postestablishment burns and other treatments, the likelihood of successfully regenerating longleaf pine forests will be substantially increased.

Unique Considerations

Largely as a result of ignorance concerning the unique life history of longleaf pine, mismanagement may be the rule rather than the

exception (Kush 2002). Unlike other southern pines, longleaf pine is both resistant to and dependent on fire and its seedlings must pass through a stemless grass stage. If unwise management or the absence of management allows competing species to grow freely while longleaf pine is in the grass stage, then it can be lost from a site and will not become reestablished and regain dominance without intervention that provides the requisite disturbance regime. Although periodic surface fires are essential for sustaining longleaf pine forests, these must be prudently timed because longleaf pine seedlings remain highly vulnerable to fire-caused mortality until they reach a groundline diameter of 7.5 mm and a height of 1 m (Kush 2002). Because of their high susceptibility to competition for aboveground and belowground resources, their slower growth near adult trees, and the greater needle litter (i.e., fuel) accumulation under tree crowns, longleaf pine seedlings located beneath adult trees are more vulnerable to mortality from fire than are those in openings (Croker and Boyer 1975). Prescribed burning, with the objectives of adequately reducing fuels and competition while affording protection for seed-bearing trees and seedlings, should be conducted within 2 to 3 days following a saturating rain, at temperatures no greater than 27°C, with relative humidity higher than 40% and wind speeds steady at 8–13 kph (Croker and Boyer 1975).

Longleaf pine is a competition-intolerant species, with its regeneration largely confined to canopy gaps (Wahlenberg 1946). Abundance and growth of seedlings have long been reported to be negatively related to the presence of adult longleaf pine (Walker and Davis 1954; Davis 1955; Smith 1961), with the competitive influence of individual trees and forest edges on seedlings observed to extend up to 16 m (less on better quality sites) from adults into forest gaps (Smith 1955; Walker and Davis 1956; Boyer 1963). This competitive effect is so pronounced that the most frequently surviving and vigorous growing longleaf pine seedlings typically cluster near the center of canopy gaps (Brockway and Outcalt 1998). Although longleaf pine seedlings may persist for years beneath the crowns of adult trees, their growth is impeded by competition from adults and continuing long-term suppression makes them highly vulnerable to mortality from a variety of individual and cumulative stress factors (Boyer 1974b; Boyer and White 1990). Therefore, unless natural or anthropogenic disturbances remove nearby adults from the canopy, it is doubtful that seedlings present beneath mature pines will ever ascend to become dominant members of the forest canopy.

The impoverished (low available moisture and nutrients) and relatively simple (very few woody plants other than longleaf pine) ecosystem represented by the well-drained and somewhat excessively drained, coarse-textured soils in north central Florida provided a unique opportunity to assess the results of gap-phase regeneration in longleaf pine that are the cumulative product of resource competition and repeated fires over several decades. In examining these long-term patterns of natural longleaf pine regeneration in numerous naturally occurring forest gaps, Brockway and Outcalt (1998) observed that most surviving longleaf pine seedlings aggregated near the center of canopy gaps and were encircled by a zone approximately 12–16 m wide from which they were generally absent. This "seedling exclusionary zone" (SEZ) was found to spatially coincide with an area of greater fine root biomass and relatively intense intraspecific root competition between adult and juvenile longleaf pines. The center of the canopy gap, where most longleaf pine seedlings cluster, spatially coincides with a fine-root gap, where seedlings are under less competitive stress and thus enjoy higher rates of survival and growth. Although all three factors are no doubt of some degree of importance, in these relatively open longleaf pine stands (57% cover) growing on xeric sandhills, competition for soil moisture and possibly competition for nutrients appear to be proportionally more important than competition for light.

Others studying gap-phase regeneration in longleaf pine have typically examined short-term responses of planted seedlings on higher quality forest sites (Palik et al. 1997; McGuire et al. 2001; Gagnon et al. 2003). On more mesic sites, with richer soils resulting in higher stand density and a greater number of woody

plants with roots innervating the surface soil layers, various root clusters are not readily distinguishable and a SEZ was not identified. On these better sites, competition for light and nutrients is reportedly more important than competition for soil water. Should the root geometry characteristic of xeric sites eventually develop on these mesic sites, it is likely that the resulting SEZ would be considerably narrower (i.e., shorter foraging distance for adult roots), perhaps only 5–10 m wide, making its effects difficult to distinguish from the influence of the 4–7 m radius directly beneath the crown of a mature longleaf pine tree.

Survival and growth of longleaf pine seedlings is negatively influenced by the density of adult trees in the canopy and the proximity of adults to the seedlings (Palik et al. 1997; Brockway and Outcalt 1998; Gagnon et al. 2004). Timely seedling release from intraspecific competition is essential to achieve successful natural regeneration. Although release can be affected through stand treatments that thin the forest to a uniform overstory density (i.e., even-aged management methods), recent appreciation for the ecological values protected by maintaining an uneven-aged structure has increased interest in achieving natural regeneration through selection silviculture techniques (Farrar 1996). Group selection, which mimics the natural stand replacement dynamics of gap-phase regeneration, may be one of the most useful approaches for regenerating longleaf pine forests. Although canopy gaps created on xeric sandhill sites should perhaps range from 0.13 to 0.8 ha (radius = 20–50 m) to sufficiently reduce the competitive influence of adults on seedlings (Brockway and Outcalt 1998), gaps as small as 0.1–0.14 ha (radius = 18–21 m) may be suitable for regenerating longleaf pine on mesic sites (Palik et al. 1997; McGuire et al. 2001; Gagnon et al. 2003).

Artificial Regeneration

Direct Seeding

Initiating a stand of longleaf pine from seed sown directly onsite can be a cost-effective regeneration method, especially for small landowners. However, this approach is potentially quite risky. Many longleaf pine stands have been successfully established by direct seeding, but there have also been many failures resulting from adverse weather, seed predation, or simply not following the required procedures. The first step in attempting to achieve successful regeneration by this method is proper seed selection. Longleaf pine has five seed zones and seed should not be transported for use more than one zone in any direction (Schmidtling 2001). Since there is no genetic evidence for east–west or ecotypic site variation, seed can be collected from anywhere within a zone for use in that zone. Seed from one zone warmer should grow faster and seed from one zone colder will typically grow slower than local seed.

Seedlots should be 95% pure and have a germination rate of at least 75% (Barnett et al. 1990). To obtain this germination rate, cones must not be collected until they are fully mature (Barnett and McGilvray 2002). Mature cones have a specific gravity of 0.89, which can be determined by the water displacement method (Barnett and McGilvray 2002). Guidelines specify that cones should not be collected until 19 of 20 cones have a specific gravity equal to 0.89, which means the average specific gravity will be about 0.81 (Wakeley 1954). Cones must be stored in a dry location having adequate ventilation. Cone storage for a short period will increase seed yields, but storage beyond 4 weeks may reduce seed quality. Cones will dry in a kiln within 24–48 hours depending on initial moisture and weather conditions. Kiln drying temperatures should not exceed 45°C (Barnett and McGilvray 2002). Once cones are dry and open, seed may be removed by using a tumbler.

Newly extracted seed will have a relatively high moisture content and, therefore, should be refrigerated and then dried to an 8–10% moisture level. Dewinging the seed requires appropriate equipment and processing techniques to prevent damage and a corresponding decline in quality (Barnett and McGilvray 2002). The wing is not really removed, but rather reduced to a stub. Debris is removed by screening and air, followed by removal of empty and partially filled seeds on a gravity

table. Processed seed can then be stored in moisture-proof containers at no more than 2°C for up to 3 years. Storage for longer periods requires a temperature of -18°C.

Seed should be tested for its germination rate prior to use or sale. Since longleaf pine seed is nondormant, stratification is not necessary. However, a 10-minute drench with benomyl fungicide prior to sowing will improve germination. Since longleaf pine seed is quite large and nutritious, some type of repellent is needed to deter consumption by birds and rodents (Nolte and Barnett 2000). On most sites, seed is best sown during the fall, when moisture is adequate and the maximum daytime temperature is below 29°C (Dennington and Farrar 1991). On other sites, such as those in northern areas with finer-textured soils prone to frost heaving or those having high rabbit populations that may damage new seedlings, seed should be sown in late winter or early spring. Seed can be broadcast onsite by air or ground equipment. Since most sites are now rather small, aerial seeding is rarely employed, but ground application with a cyclone seeder is a commonly used method. Row and spot seeders operate more slowly, but use less seed per unit area and provide increased spacing control. Following dispersal, the seed can be covered with soil, which improves seedling stocking especially on dry sandy sites.

Direct seeding should not be attempted on poorly drained soils or sites having a high water table, because new germinants are highly susceptible to mortality from wet conditions (Dennington and Farrar 1991). Steep sites where seed is likely to be displaced down slope and deep sands during drought periods are also poor candidates for direct seeding. Preparing the site prior to sowing, by burning, chemical, or mechanical means to reduce plant competition and expose mineral soil, will increase the probability of regeneration success. If competition is mostly composed of herbaceous plants and low shrubs, a prescribed fire in the spring or summer prior to sowing may be useful (Mann 1970). On sites with substantial competition from woody plants, mechanical or herbicide treatments may be required, before fire can be effectively used to prepare the seedbed. A scalper attachment may be used with the row seeder to remove competition from the area being seeded. Recommended minimum seeding rates are 32,000 repellent-treated viable seeds/ha for broadcast application. When row seeding, use 16,800 seeds/ha with one seed placed every 23–30 cm within a row. When spot seeding, 5–6 seeds should be deposited at each spot with spots arrayed at a 2 × 2 m spacing. Covering seeds lightly with about 6 mm of soil improves germination and establishment success (Barnett et al. 1990). In assessing seeding success, a minimum of 100 survey plots (each 4 m^2) per site is recommended (Mann 1970). If seedling stocking is greater than 50%, then a suitable stand of longleaf pine should develop.

Bare-Root Nursery Seedlings

The nursery management objective is to produce high-quality longleaf pine seedlings with a root-collar diameter of 10 mm, at least six primary lateral roots, a stout taproot, well-developed terminal bud, and many needle fascicles (Barnett et al. 1990). The first step in this process is to select good-quality seed with 95% purity and a germination rate of at least 75% (Cordell et al. 1990). A benomyl application to seeds will reduce fungal pathogens and improve seedling establishment in the nursery bed (Barnett et al. 1999). Seedbeds should consist of sandy or loamy sand soils with a pH of 5–6. Weeds, insects, and pathogens are reduced by seedbed fumigation prior to sowing. If mulch is used, it should also be fumigated to prevent introduction of pathogens. Seed may be sown in either fall or spring, although fall sowing will usually produce larger seedlings (Barnett et al. 1990). However, a cold winter can damage young seedlings so spring sowing may be favored at more northerly locations. Longleaf pine seedlings should be grown at a density of 108-160/m^2. Seedlings produced at higher densities have lower survival following outplanting, while growing them at lower densities increases the per unit cost of production. A precision sowing machine greatly aids in obtaining the desired planting density in the seedbed.

Irrigation and fertilization must both be carefully controlled to produce good-quality longleaf pine seedlings (Cordell et al. 1990). Too much water will promote disease, while too little will impede growth and development. The pH of irrigation water must also be controlled, maintaining it at 5–6. Substantial practical experience is needed to develop the skill necessary to determine when seedlings require watering. Fertilization decisions should be based on a chemical analysis of the soil and seedling nutrition requirements. Generally, numerous smaller applications rather than fewer larger inputs of nutrients are provided, with the highest rates applied during the phase of rapid growth. Although most large nursery operations use soluble fertilizers applied from tank sprays or as injections into the irrigation system, dry fertilizers can also be used. Standard practices should be followed for reducing fertilization during the seedling hardening phase.

Pruning of both vertical and horizontal roots improves longleaf pine seedling survival (Cordell et al. 1990). For production of 1-0 seedlings, two root-pruning treatments applied in August and October are recommended. Root pruning should be followed with irrigation to settle the soil and reduce desiccation. Needle clipping just before lifting can improve survival on dry sites (Barnett et al. 1990). The best lifting time is January and early February, but lifting should be coordinated with planting schedules to reduce time in storage. Care must be exercised during lifting to limit root system damage. Survival is improved by application of benomyl fungicide to the packing medium or as a root coating at the time of packing (Barnett et al. 1988). Grading should normally not be necessary if proper seedbed densities, fertilization, and irrigation have been used. If problems caused by nonuniform growth arise, then all seedlings with a root-collar diameter less than 7.5 mm should be discarded. Bare-root seedlings should be stored and transported in refrigerated containers maintained at a temperature of 1–3°C. Seedlings are best planted as soon as possible after lifting, with the duration in cold storage limited to 1 week. Seedling health declines rapidly when kept in cold storage longer than 2 weeks and survival becomes correspondingly low (White 1981).

Containerized Nursery Seedlings

Superior containerized longleaf pine seedlings are best grown outdoors in full sunlight. During initial germination, a 30% shade cloth is used to prevent seed wash from containers (Barnett and McGilvray 2000), but this material should be removed as soon as germination is complete. A 1:1 mixture of sphagnum peat moss and number 2 grade vermiculite is an optimum growing medium. Prior to mixing, the peat moss should be screened to remove large sticks and woody fragments. If necessary, medium pH should be adjusted to 4.5–5. Containers having a minimum depth of 11 cm, volume of 100 cm^3, and density of less than 535 seedlings/m^2 are recommended for growing longleaf pine (Barnett and McGilvray 1997). If possible, good-quality seed with a viability of at least 80% should be sown. Treatment with benomyl prior to sowing will reduce pathogens and improve germination, especially for lower quality seedlots. Seeds should be sown during spring, from March to May, putting one seed per cavity for good-quality seedlots or two per cavity if viability is 65–80% (Barnett and McGilvray 2000). The seed is then covered with a thin 3-mm layer of growing medium, grit, or vermiculite. Seedlings should be thinned to one per cavity when seedcoats are being shed.

Because longleaf normally germinates in the fall, it will do best if sown during cooler temperatures when the daily range is 15–27°C and the mean is 22°C. During the germination phase, seedlings need frequent but light watering. Following germination, water application is based on container weight. A weight of 80–85% of field capacity during rapid growth and 70–75% during the hardening phase is a good guideline for determining when water is needed. Sufficient water is typically added to wet the entire plug (Starkey 2002). While many nursery managers

now incorporate slow-release fertilizers into the growing medium, water-soluble fertilizers can also be applied as needed. Starkey (2002) recommends starting with three fertilizer applications per week, adjusted as needed for rainfall amounts, using a balanced N-P-K fertilizer like 20-20-20 or 15-15-15. After germination is completed, use 50 ppm for 2 weeks during the establishment phase, followed by 200 ppm for 14–16 weeks and then 25–50 ppm during the hardening phase. If weeds become a problem, oxyfluorfen should be applied at about one-fourth the recommended rate to prevent seedling damage (Barnett and McGilvray 2000).

Watering to field capacity makes plug extraction easier. Poor-quality seedlings, where the root plug does not hold together or root-collar diameter is less than 7 mm, should be culled. Good-quality seedlings are then put into cardboard boxes and placed in cold storage at 1–3°C. Storage intervals in excess of 2 weeks should be avoided, as seedling quality will decline. Containerized seedlings can be planted in Florida during July and August because rainfall is normally plentiful. In other areas, seedlings should be planted in the fall as soon as soil moisture is adequate, to reduce the risk from freezing winter temperatures (Barnett and McGilvray 2000).

Planting Longleaf Pine Seedlings

In the past, longleaf pine was often not chosen for reforestation because high mortality showed it to be very difficult to establish using bare-root seedlings and, even if survival was acceptable, many seedlings remained in the grass stage for extended periods. More recently, however, longleaf pine has been shown to survive well and begin height growth quite rapidly if seedlings are planted properly. Successful regeneration with bare-root seedlings requires healthy, fresh planting stock and precision planting on a well-prepared site (Barnett 1992). The average survival and growth of containerized longleaf pine, however, remains better than those of bare-root seedlings. At five locations in Georgia, containerized seedling survival was 76%, while that for bare-root seedlings was only 51%, after 5 years (Boyer 1989). Although containerized seedlings are more costly, they are clearly the better choice especially on droughty sites prone to moisture stress and when planting outside the normal dormant-season period (Barnett 2002).

Since longleaf pine is sensitive to competition, some form of site preparation is required before seedlings are planted. Prescribed burning may be all that is required if the site has been regularly burned and is dominated by herbaceous species. On sites with heavy competition from woody plants, mechanical or herbicide treatments will be required. Intensive mechanical site preparation is often a poor choice for longleaf pine ecosystems because it destroys most native understory plants, can promote rapid growth of annual weeds, and may lead to soil erosion. Herbicide and fire in a combination sequence of "brown then burn" treatments may be used to prepare harvested sites for planting. A combination of herbicide and strip scalping works well on sites with native understory plants. The herbicide should target woody species, while the scalp reduces herbaceous competition within the planting zone. The native grasses will recover and reoccupy the scalped strip, providing the fuel necessary for future management with fire (Outcalt 1995). Herbicide and scalping is also a very effective site preparation technique for old-field sites (Hainds 2001).

Longleaf pine requires careful handling and seedlings must be kept in cold storage until they are planted. For small operations, bales or boxes of seedlings can be brought to the planting site a couple of times each day and kept in the shade until planted. For large operations, it is best to have a refrigerated truck present onsite. Both bare-root and containerized seedlings can be hand or machine planted, although machine planting is preferable for bare-root seedlings because of their large root system. Bare-root seedlings should be root pruned before lifting and not in the field. Obvious culls, which are too small or have poorly formed root systems or plugs, should be discarded. Planting depth is a critical factor in survival and growth. The bud of bare-root seedlings should be placed at ground level or

slightly below to allow for soil settling (Barnett et al. 1990). Shallow planting, with the bud above the soil surface, is better for containerized seedlings that have smaller buds more prone to being buried (Hainds 2001).

Containerized seedlings can be planted anytime from July to March, when soil moisture is adequate. Winter planting should be avoided in northern portions of the range because cold temperatures may lead to mortality from freezing. Bare-root seedlings should be planted only during the dormant season from December to February, with January the best month in most areas. The planting objective is typically 740 well-distributed seedlings/ha, which means 1000–1200 seedlings/ha must be planted, assuming a survival rate of 60–75%. If the survival rate is lower, containerized seedlings can be used to fill in or, if survival is very low, the site can be burned and replanted the next season (Barnett et al. 1990). Seedling surveys, conducted 1 year after planting between October and February, are very important. Some sites may require post planting treatments to control competition and speed seedling emergence from the grass stage.

Forest Reproduction Methods

Concern for renewing the forest, through timely and successful regeneration, is the most significant difference between silviculture and exploitive logging. Reproduction methods describe the manner in which forests will be cut to ensure regeneration and are a component of silvicultural systems that define in a more comprehensive way the manner in which forest stands will be tended, harvested, and replaced (Daniel et al. 1979). Reproduction methods that are effective in achieving successful regeneration are not only important for the continuation of overstory tree species, but also have a profound impact on composition and structure of the understory plant community which provides habitat for numerous associated species and indicates to a substantial degree the ecological health of an ecosystem. Properly selecting and implementing forest reproduction methods that contribute to numerous conservation and utilitarian goals requires extensive knowledge of longleaf pine ecology, silviculture, and the variation in longleaf pine ecosystems across an extensive natural range. Although no single approach to obtaining longleaf pine regeneration can be appropriately prescribed everywhere, methods that seek to holistically sustain longleaf pine ecosystems need to be compatible with (1) frequent use of surface fires, (2) maintaining native understory vegetation, (3) retaining appropriate numbers of overstory trees onsite well beyond economic maturity, and (4) creating and maintaining small-scale canopy gaps interspersed among forest patches of varying ages within an uneven-aged landscape mosaic at larger scale (Landers et al. 1990).

Clearcutting Method

The clearcutting method consists of removing all overstory and midstory trees, resulting in an open site that is influenced little by the edge of adjacent forests. The principal objective of clearcutting is to establish a new forest stand that will have an even-aged structure (Daniel et al. 1979). Clearcutting may be prescribed for removing stands in poor condition owing to damage by insects, pathogens, or fire and may also be used to quickly remove an overstory composed of undesirable species prior to reforesting a site with longleaf pine. An area so cleared may more easily be treated with mechanical site preparation and subsequently regenerated by artificial means. Clearcutting may also be combined with natural regeneration, through application of alternative-strip or progressive-strip clearcutting. However, application of these techniques is somewhat challenging, considering the short dispersal distance of large longleaf pine seeds and the care that must be taken to protect the usually scarce advanced regeneration (Kush 2002).

Certain disadvantages of the clearcutting method suggest that it should not be applied to perpetuate existing longleaf pine forests in good condition. Clearcutting mature longleaf

pine stands can destroy much of their advanced reproduction (Boyer and Peterson 1983), thus requiring reliance on more expensive planted seedlings rather than established natural regeneration. Managing longleaf pine in accordance with a "clearcut and plant" model is very expensive, because advanced regeneration is destroyed and all stand establishment costs must be carried through a long rotation period until harvest. Although longleaf pine is a competition-intolerant tree species, its does not require complete canopy removal to regenerate and its need for sunlight cannot be used as an appropriate rationale for implementing the clearcutting method (Brockway and Outcalt 1998). Also, complete canopy removal through clearcutting can diminish aesthetics and degrades habitat quality for certain at-risk species. If clearcut longleaf pine sites are somehow captured by other tree species, not only does this contribute to further attrition of these endangered ecosystems, but plant community succession on such areas will be driven along very different trajectories that can fundamentally alter important ecological processes and structures (Brockway and Lewis 2003).

Seed-Tree Method

The seed-tree method consists of removing most of the mature overstory while leaving enough good seed-producing trees scattered across a site to ensure acceptable future stocking (Daniel et al. 1979). The 20–25 trees/ha typically left as residuals afford some degree of site amelioration and ensure an even distribution of seed over the area (Kush 2002). The residual seed-trees can provide a more aesthetic appearance and improve composition of the future stand if good-quality phenotypes (and presumably genotypes) are selected. The seed-trees are typically harvested after regeneration becomes established; however, in a variation of this method known as "deferment" cutting, these residuals may be retained onsite along with the regeneration throughout the entire next rotation (Smith et al. 1989). While the objective of the seed-tree method is usually to establish a new forest with an even-aged stand structure, use of the deferment-cut variation will result in more than one age-class present in the future forest.

The seed-tree method has a number of disadvantages for longleaf pine. Very rarely will the low number of residual overstory trees be capable of producing sufficient quantities of longleaf pine seed to obtain satisfactory natural regeneration. Therefore, a longer time period will typically be needed to achieve regeneration success with the seed-tree method. The limited seed dispersal distance of longleaf pine seed requires that cleared areas be within about 30 m of residual seed-trees (Boyer and Peterson 1983). If a good seed crop does not occur for a number of years, open areas can become occupied by competing hardwoods and other southern pines. The sparse longleaf pine overstory will produce very little needle litter, resulting in surface fires that may burn with insufficient intensity to satisfactorily control this competition (Kush 2002). If these invaders escape to grow to fire-resistant size, then chemical and/or mechanical treatments may be necessary (Boyer and Peterson 1983). Also, seed-trees retained onsite represent a timber volume loss to managers interested in maximizing the output of forest products (Kush 2002). However, the greatest problem with application of the seed-tree method in existing longleaf pine forests is that most or all of the large overstory trees will be removed, changing ecosystem structure and degrading habitat that supports numerous at-risk species.

Shelterwood Method

The shelterwood method consists of removing a moderate portion of the overstory while retaining onsite sufficient numbers of seed-bearing trees so that regeneration becomes established under the protective partial shade of mature residual trees (Fig. 10). Compared with the relatively rigid conditions resulting from application of clearcutting and seed-tree methods, the shelterwood method is the most flexible method for establishing new forests of longleaf pine having an even-aged structure and is

FIGURE 10. Longleaf pine forest being regenerated by the shelterwood method; an overstory of 60 trees/ha having a basal area of 7 m^2/ha remains following the seed cut. Photo courtesy of the Forestry Images Organization.

capable of producing a variable degree of site amelioration (Daniel et al. 1979). When applied in longleaf pine forests, the 50–62 residual trees/ha typically produce an abundance of seed that is uniformly distributed across a site (Kush 2002). Selecting high-quality phenotypes as residual trees provides an opportunity to improve genetic composition of the future stand. With no large areas left barren, a substantial forest canopy deposits sufficient needle litter to support surface fires with intensities high enough to control competing woody plants (Kush 2002). The more substantial forest canopy of this method also enhances environmental aesthetics and improves habitat for numerous wildlife species. The principal disadvantages of most forms of the shelterwood method are related to the eventual removal of all overstory trees. During overwood harvest, excessive damage may occur to established longleaf pine seedlings and, following overstory removal, forest structure is substantially transformed and habitat quality for at-risk species may remain reduced for decades.

The shelterwood method can be applied only in existing stands with sufficient dominant and/or codominant trees of seed-bearing size (Boyer and Peterson 1983). The most commonly used approach is the uniform shelterwood method, which may be implemented with either a two-cut or three-cut technique. As the name suggests, each cut in the uniform shelterwood method is applied throughout the entire stand resulting in a uniform appearance and even-aged structure. If a forest is highly stocked and requires thinning or improvement cutting, the three-cut technique is necessary. The first cut in the three-cut technique is the preparatory cut, which is optional in regularly tended stands and normally performed 10 years before the planned overwood harvest. The preparatory cut should leave a well-distributed population of dominant and codominant trees totaling

13.8–16.1 m^2/ha (Boyer and Peterson 1983). This will promote crown development and enhance cone production in the residual seed-bearing trees. If the density of competing woody plants is greater than 2.3 m^2/ha, herbicide and/or fire treatments should be implemented (Kush 2002).

The second cut in the three-cut technique and the first cut in the two-cut technique is the seed cut (Croker and Boyer 1975). The seed cut is performed 5 years or more before the planned overwood harvest to reduce the stand density to 6.9 m^2/ha, leaving well-distributed high-quality seed-bearing trees in the overstory (Kush 2002). The most desirable residuals are trees equal to or greater than 40 cm diameter at breast height that have evidence of past cone bearing ability. Large hardwood and other undesirable trees may also be removed during the preparatory cut, and smaller hardwoods can subsequently be controlled by prescribed fire conducted during the growing season (Boyer and Peterson 1983).

Seed crops are then monitored by annual springtime counts of flowers and conelets, watching carefully for crops that produce 1860–2470 cones/ha, the range typically required for adequate natural regeneration (Boyer and Peterson 1983). Once an acceptable cone crop is noted, a seedbed preparation burn can be conducted during the year prior to seedfall (Kush 2002). While prescribed fire during summer or autumn will control woody plant competition better than earlier cool-season burns, increased seed predation by birds has been associated with fire during the fall season. Annual seedling surveys are also conducted to assess the degree of regeneration success, the principal criterion being a minimum of 9880–14820 seedlings/ha that are at least 1 year old and well distributed across the site (Boyer 1993a). This abundance provides sufficient seedling numbers to compensate for future mortality during overwood removal and from other factors (Kush 2002). Once an adequate number and distribution of established longleaf pine seedlings are present, the residual seed-bearing trees in the overstory may be harvested by the removal cut (Boyer and Peterson 1983). Although longleaf pine seedling survival beneath overstory trees may be unaffected for 8 or more years, seedling damage during overwood harvest is minimized if the removal cut is conducted when seedlings are no more than 2 years old and in the stemless grass stage (Boyer 1975, 1993a). While overwood harvest may be scheduled with a reasonable amount of flexibility to meet economic and other management objectives, conducting the removal cut on overstories of higher density above seedlings of increased size will result in substantially greater seedling mortality rates (Maple 1977). When the residual overstory density is equal to or greater than 9.2 m^2/ha, overwood harvest is best accomplished by two separate removal cuts. The principal postharvest need is application of prescribed fire to control competing plants and the brown-spot fungus; however, timing is crucial, since mistimed fires can harm vulnerable seedlings (Boyer and White 1990). Prescribed burning should be avoided during the first 2 years following the removal cut, because accumulated logging slash will produce fires too hot for newly released seedlings (Boyer and Peterson 1983). Periodic burning should generally not resume until dominant longleaf pine seedlings have attained a root-collar diameter of 7.5 mm (Boyer 1979). Prescribed fire is indicated when surveys reveal a brown-spot fungus infection rate of equal to or greater than 20% among dominant seedlings (Boyer 1993a).

Variations of the shelterwood method include its application in block, strip, and group configurations (Boyer and White 1990; Boyer 1993a). The block approach is associated with even-aged forests and identifies stands typically from 4 to 40 ha as management units delineated by various natural or artificial boundary features such as creeks and roads. While each unit may be regenerated individually, several adjacent blocks could also be treated at the same time, resulting in a relatively large area being in the same stages of regeneration. The progressive strip approach can convert a large even-aged stand into a number of smaller even-aged stands covering an entire range of age-classes from seedling to mature. Strips created by cutting are long and narrow, not

exceeding 60 m in width, so that most or all of the strip will be within seed-dispersal range of the adjacent mature trees. Within each strip, the uniform shelterwood method is applied as described above, using either the three-step or two-step technique. When the seed cut is made in the first strip, a preparatory cut is made in the second strip. When seedlings are established in the first strip, a removal cut is made there, with a seed cut then made in the second strip and a preparatory cut made in an entirely new third strip. Thus, a "rolling wave" of regeneration may proceed indefinitely across the landscape. The group approach is applied to management units that are too small to be considered blocks, typically 0.2–2 ha. Using this approach, numerous patches are treated with either the three-step or two-step technique. When the first patches are treated with a seed cut, the second group of patches is treated with a preparatory cut. Once seedlings are established in the first patches, they are treated with a removal cut, the second patches are treated with a seed cut, and a third group of patches are treated with a preparatory cut. The substantial dispersion and smaller size of areas under treatment at any one time allow this shelterwood approach to more closely achieve management objectives related to aesthetic and ecological values. However, eventually removing all canopy trees still raises objections from those concerned about the rarity of older forests and welfare of associated species.

By contrast, the irregular shelterwood method retains a moderately light (less than 7 m^2/ha) canopy of mature trees onsite throughout an entire stand rotation. This method may be applied using any of the above techniques and variations, except the removal cut is mostly or entirely eliminated (Boyer 1999). Unlike the uniform method, the irregular shelterwood method can maintain a residual canopy of mature trees onsite over many rotations and potentially in perpetuity. Mature overstory residuals plus newly regenerated seedlings initially comprise a two-aged forest that may be maintained by thinning from below or allowed to eventually achieve an uneven-aged structure, as successive waves of regenerating seedlings establish and develop during ensuing decades. With this method, overstory residuals may range in age from newly mature (50–100 years) to very mature (300–400 years), depending on the health of individual trees and specific management objectives. Although the growth of longleaf pine seedlings will no doubt be slowed by competition from residual adult trees (Table 1), the continuously maintained forest canopy is beneficial in sustaining species dependent on such structural conditions (Boyer 1993b). The irregular shelterwood method is the most rapid way to convert an even-aged longleaf pine forest (or plantation) to a two-aged and eventually an uneven-aged stand structure (Boyer 1999).

Uneven-Aged Silviculture

In the most recent decade, ecosystem management policies have substantially increased interest in managing forests through uneven-aged silviculture (Guldin 1996). The chapter by Guldin (this volume) discusses uneven-aged silviculture of longleaf pine forests in greater detail. Protecting the native plant community, maintaining a continuous forest canopy, and facilitating development of large, old trees are among the desirable habitat features potentially resulting when uneven-aged silviculture is applied in an adaptive ecosystem management framework. Interest has also grown in methods for converting even-aged stands to uneven-aged forests, like uniform partial cutting and patch cutting combined with thinning (Nyland 2003). Whether by even-aged or uneven-aged methods, silviculture is fundamentally applied at varying spatial and temporal scales to mimic disturbance and guide succession in a forest. Considering the wide natural variation in frequency, intensity, and area impacted by disturbance, forests tended according to ecosystem management principles might well contain a mixture of even-aged and uneven-aged stands. Where stages of advanced succession are sought and perpetuating those stages is desirable (and ecologically feasible), uneven-aged silviculture can

TABLE 1. Inhibitory influence of residual overstory trees on stand growth during a 40-year period (1957–1996) for longleaf pine forests treated with the uniform shelterwood (initial basal area = 0) and irregular shelterwood (initial basal area > 0) methods (tree dbh > 8.9 cm).

Initial stand basal area (m^2/ha)	Residual pine		Ingrowth pine		Total pine	
	Basal area (m^2/ha)	Volume[a] (m^3/ha)	Basal area (m^2/ha)	Volume[a] (m^3/ha)	Basal area (m^2/ha)	Volume[a] (m^3/ha)
Block A						
0	0	0	18.2	131.9	18.2	131.9
0	0	0	17.0	125.7	17.0	125.7
2.1	2.2	18.6	11.7	70.4	13.9	89.0
4.1	7.3	62.0	6.8	30.1	14.1	92.1
6.2	8.9	74.7	2.3	6.2	11.2	80.9
8.3	12.9	109.6	0.8	4.4	13.7	114.0
10.4	15.4	126.8	0.2	1.1	15.6	127.9
Block B						
0	0	0	20.1	139.9	20.1	139.9
2.1	2.5	21.4	11.8	68.7	14.3	90.1
4.2	6.3	53.7	4.6	17.6	10.9	71.3
6.2	9.3	78.8	1.8	5.2	11.1	84.0
8.3	12.7	106.9	0.4	1.5	13.1	108.4
10.4	16.1	135.8	0.1	0.2	16.2	136.0

[a] All volumes reported as inside bark and derived from local forest volume tables.

be used to achieve such conditions (Guldin 1996).

Uneven-aged silviculture affords a major advantage, in that natural regeneration is more or less continuous, as late successional forest dynamics are emulated (Guldin 1996). The Dauerwald (i.e., continuous forest) of Germany is a prime example of the uneven-aged, continuously regenerating forest that can result (Schabel and Palmer 1999). Loblolly pine and shortleaf pine, growing on gentle terrain, under aggressive or limited competition, with the worst trees cut and the best trees left to serve as seed-bearing residuals, have been successfully managed with uneven-aged methods (Guldin 1996). Although longleaf pine was formerly thought to be too competition-intolerant for uneven-aged silviculture, recent evidence suggests this to be a viable and desirable forest management alternative (Farrar and Boyer 1990; Farrar 1996; Palik et al. 1997; Brockway and Outcalt 1998; McGuire et al. 2001; Gagnon et al. 2003). The group selection method and the single-tree selection method are the principal means by which uneven-aged silviculture can be practiced.

Group Selection Method

As an uneven-aged mosaic of even-aged patches distributed across the landscape (Platt and Rathbun 1993), natural longleaf pine forests maintain a continuous overstory canopy while establishing naturally regenerated seedlings in canopy gaps created by lightning and other local disturbance agents. Of all available forest reproduction methods, group selection most closely mimics this natural gap-phase regeneration pattern and is perhaps best suited in the long term for sustaining the ecological character of longleaf pine ecosystems (Brockway and Outcalt 1998). The group selection method can be used to create circular, elliptical, and irregularly shaped gaps ranging from 0.1 to 0.8 ha distributed throughout the forest to effectively simulate the desired uneven-aged mosaic (Fig. 11). If volume control is preferred, the volume-guiding diameter limit (V-GDL) and basal area-maximum diameter at breast height-q (BDq) stand regulation procedures in a modified group selection method are suitable for managing longleaf pine forests, when used in combination with prescribed fire on a 3-year

FIGURE 11. Longleaf pine regeneration freely ascending within a forest canopy gap (background); note numerous seedlings that remain suppressed by intraspecific competition from nearby adults (foreground). Photo courtesy of the Forestry Images Organization.

cycle to control competing vegetation and maintain seedbeds in appropriate condition (Farrar and Boyer 1990; Farrar 1996). Alternatively, longleaf pine stands may be quite easily regulated using an area control procedure.

Group selection implementation begins during year 0, with an entry to create the first series of canopy gaps by cutting groups of overstory trees, placing emphasis on removing poor-quality trees and retaining good-quality seed-bearing trees around the periphery of each gap (Table 2). Ideally, gaps should be cut in areas where advanced longleaf pine regeneration is already present, thereby decreasing the likelihood that newly created gaps will become occupied by competing woody species. Gaps should be created of sufficient size (at least 0.1 ha) to minimize the suppressive effects of intraspecific competition between longleaf pine adults and seedlings. The forest will be burned several times during this decade to maintain good-quality seedbeds and control woody competitors. If a 10-year cutting cycle is used, the forest will be again entered during year 10 to create a second series of gaps. If longleaf pine seedlings are established in the first series of gaps, they can be protected by skipping one fire cycle, if necessary, and allowing dominant seedlings to reach a more fire-resistant size. Overstory trees impeding seedling development along the gap periphery may now be removed. During year 20, another entry is made to create a third series of gaps in the canopy. Periodic surface fires need to be conducted throughout this decade. The seedlings in the first series of gaps should be sapling size by now and young seedlings may be present in the second series of gaps. Competing adults may be removed here as needed. During the next entry in year 30, a fourth series of canopy gaps is initiated. Seedlings may now be present in the third series of gaps and competing adults along the periphery may be removed where necessary. Seedlings in the

TABLE 2. Schedule for implementing the Group Selection Method using a 10-year cutting cycle during the first 100 years of application.

Year	Create gaps; retain cone-bearing trees along edges	Seedlings established in openings; may remove adjacent size adults; skip one fire cycle	Seedlings grown to sapling size	Saplings grown to pole size	Poles grown to sawlog	Sawlogs continue to increase in size
			gap series			
0	1st					
10	2nd	1st				
20	3rd	2nd	1st			
30	4th	3rd	2nd	1st		
40	5th	4th	3rd	2nd	1st	
50	6th	5th	4th	3rd	2nd	1st
60	7th	6th	5th	4th	3rd	2nd
70	8th	7th	6th	5th	4th	3rd
80	9th	8th	7th	6th	5th	4th
90	10th	9th	8th	7th	6th	5th
100	11th	10th	9th	8th	7th	6th

second series of gaps should be sapling size by now while saplings in the first gap series should have grown to pole size. By year 40, a fifth series of gaps will be created, seedlings should become established in the fourth series of gaps, saplings will have developed in the third series, poles will have grown in the second series, and sawlogs will have emerged in the first series of gaps. If retained for a prolonged period, these sawlogs will eventually become very large trees. This continuous serial pattern of entry, cutting, and reproduction in the longleaf pine forest may be continued, along with application of periodic prescribed burning and other cultural treatments, to create a potentially infinite series of regenerating canopy gaps that indefinitely sustain an uneven-aged mosaic.

The principal advantages of the group selection method include (1) high-forest cover is constantly maintained with no degradation of habitat for at-risk species, (2) the diversity of tree size-classes results in an aesthetically pleasing environment, (3) regeneration is continuous and not confined to short high-risk periods, (4) regeneration develops under even-aged conditions within canopy gaps, (5) the larger openings permit establishment of intolerant species, (6) more concentrated harvest results in lower logging costs, less damage to seedlings and residual overstory trees, and easier conduct of inventories compared to the single-tree selection method, (7) full stand regulation is more easily achieved, with area control being an easier-to-apply procedure than volume control procedures (i.e., BDq, V-GDL), (8) even small areas can be economically managed for regular, even product flow, (9) larger trees may be grown by adjusting the cutting cycle and/or maximum diameter at breast height with no change in stand area, and (10) the stand is afforded a greater degree of protection from disturbance-induced losses, because regeneration is present to replace fallen overstory trees (Daniel et al. 1979; Farrar and Boyer 1990; Farrar 1996; Kush 2002). Among the disadvantages of group selection are (1) if healthy groundcover is not maintained through periodic prescribed burning, gaps without advanced regeneration may become occupied by woody competitors, necessitating costly mechanical or herbicide treatments, (2) need for periodic vegetation control treatments other than prescribed fire (e.g., herbicide application every 20 years) on better quality sites with more severe woody plant competition, (3) higher management costs, greater inventory information needs and lower product outputs relative to even-aged management methods, (4) higher logging costs and greater logging damage of residuals compared with those for even-aged methods, and (5) it can be difficult to apply on sites with severe understory competition such as saw palmetto

(*Serenoa repens*) dominated flatwoods (Farrar and Boyer 1990; Farrar 1996; Kush 2002).

Single-Tree Selection Method

In the single-tree selection method, individual trees are removed from the forest canopy and regenerating seedlings become established in their place. Since only small openings are created by this method, it is best applied to tree species that are tolerant of competition for site resources (Daniel et al. 1979). Individual trees are harvested in a series of partial cuts that typically occur in a stand at 10-year intervals (though the actual cutting cycle may be somewhat shorter or longer). Application of this method results in development and maintenance of an uneven-aged forest structure, having a reverse-J size-class distribution that can be quantified by the diminution quotient, q. The q factor is derived from de Liocourt's law, ranges from 1.2 to 1.5, and is applicable to all uneven-aged forests (de Liocourt 1898; Meyer 1952).

Selection was first applied in southern pines using annual harvests for the initial 15 years, followed by periodic cuts every 5–7 years thereafter (Reynolds 1969; Reynolds et al. 1984). Although this approach was neither group selection nor single-tree selection, volume control was successfully achieved in loblolly pine and shortleaf pine stands by using the V-GDL regulation procedure and following the rule of "cut the worst and leave the best" trees (Guldin 1996). The keys to successful regeneration with application of the single-tree selection method in this forest type are regulation of stocking and stand structure, careful logging, and control of competing vegetation (Shelton and Cain 2000). Uneven-aged stands are generally easier to create and maintain on poor-quality sites because of less competing vegetation and greater ease of obtaining natural pine regeneration. Implementing the single-tree selection method with the BDq stand regulation procedure calls for postcutting guidelines of 10–14 m^2/ha for basal area, 35–55 cm for maximum diameters, and a q factor of about 1.2 for 2.5 cm diameter at breast height size classes (Shelton and Cain 2000). However, since the q factor is the most difficult to control (and least important of the variables), most operational-scale applications result in pine stands consisting of multiple size classes, rather than strictly corresponding to a classically balanced reversed-J distribution. With seed-bearing trees greater than 40 cm diameter at breast height favored as residual overstory trees, basal area should not exceed 17 m^2/ha to limit the adverse influences of shading and root competition on regenerating seedlings (Shelton and Cain 2000). Application of the single-tree selection method results in a pine stand with an irregular canopy and many gaps of various sizes, up to 0.1 ha. Although seedlings become established throughout stands managed under single-tree selection, those in gaps created by harvest are of greatest interest since they have the greatest potential to eventually ascend to a dominant position in the forest canopy.

Application of the single-tree selection method in longleaf pine forests has received less study than other southern pines. The infrequency of good seed years and inclination of seedlings to be suppressed by competition from nearby adults, appears to make longleaf pine a less suitable candidate for application of the single-tree selection method. Guidance for implementing the single-tree selection method in longleaf pine forests emphasizes thinning removal of individual trees (especially those of poor quality) on a 10-year cutting cycle, establishment of seedlings in small gaps, and removal of adjacent overstory trees to progressively enlarge these gaps thereby releasing seedlings from competition with adult longleaf pine trees (Moore 2001). Although each tree is marked and harvested as an individual, application of this guidance eventually results in the removal of groups of overstory trees, creating canopy gaps that approach the dimensions of those created by the group selection method. The principal difference is that two or more stand entries are required to create sufficiently large gaps using the single-tree selection method, while only a single entry is typically needed using the group selection method. Such dependence on multiple stand entries for multiple-tree gap

creation to achieve successful regeneration, raises concerns regarding suitability of the single-tree selection method for regenerating longleaf pine forests. Nonetheless, a management approach identified as "the single-tree selection method" has been applied for several decades on quail hunting plantations in southern Georgia (Nature Conservancy 2002). While regeneration has been obtained on these sites, the absence of an objective stand regulation procedure, such as V-GDL or BDq, impairs reliable replication of management results among different practitioners.

Advantages of the single-tree selection method include (1) forest cover and habitat for at-risk species is constantly maintained, (2) the variety of tree sizes creates high-quality aesthetics, (3) regeneration is continuous, (4) full stand regulation is easily and rapidly achieved, (5) small areas can be economically managed for regular, even product flow, (6) large trees can be produced by increasing the cutting cycle or maximum diameter at breast height without changing the stand area, and (7) the stand is afforded a higher degree of protection from windthrow, insect, pathogen, and fire losses, since regeneration is always present to replace damaged overstory trees (Daniel et al. 1979; Farrar and Boyer 1990; Farrar 1996; Shelton and Cain 2000; Kush 2002). The disadvantages of single-tree selection are (1) requirement of well-trained staff, highly skilled in applying more difficult stand management concepts and procedures, (2) large amounts of stand information from inventory examinations and growth and yield projections that are difficult and time-consuming, (3) crop trees are scattered throughout the stand resulting in higher logging costs, greater logging damage to residuals, and lower product outputs relative to other forest reproduction methods, (4) very small single-tree gaps provide conditions unfavorable for establishment and growth of intolerant longleaf pine, (5) the resulting forest environment may be less suitable for some wildlife species, such as bobwhite quail (*Colinus virginianus*) that prefer low vegetation and edge areas created by other methods, (6) fire damage of pine seedlings that are often present in the youngest and most vulnerable size-classes, (7) need for periodic vegetation control other than prescribed fire on better quality sites with more severe woody plant competition and the difficulty in efficiently applying area-wide mechanical and chemical treatments, and (8) it is very difficult to apply on sites where intense competition from native plants, such as saw palmetto, or exotic plants, especially vines like kudzu (*Pueraria lobata*) and Japanese honeysuckle (*Lonicera japonica*), severely limit pine regeneration success (Daniel et al. 1979; Farrar and Boyer 1990; Farrar 1996; Shelton and Cain 2000; Kush 2002).

Since little saleable product results, intermediate cuts in the younger-age classes necessary for maintaining an uneven-aged stand structure have a tendency to be neglected (Daniel et al. 1979). Also, among the most serious dangers inherent in the single-tree selection method is the always present temptation to violate the "cut the worst trees first and leave the best" rule. In not observing this discipline, errant practitioners will harvest the best trees first, thereby allowing the single-tree selection method to degenerate into exploitive timber "high-grading" (Farrar 1996). Finally, it is important to note that applications of the selection methods in longleaf pine forests are still in their infancy and flawless results cannot be expected without substantially more scientific study and management experience.

Silviculture that Mimics Natural Disturbance

The above forest reproduction methods were first developed by foresters in Europe during the eighteenth century, when the newly created profession of forestry was confronted with the challenge of repairing the extensive damage done to forests by centuries of exploitive logging (Daniel et al. 1979). During the ensuing 300 years, various clearcutting, seed-tree, shelterwood, and selection methods have been employed by foresters in Europe and on other continents to regenerate and rehabilitate many forest types. Although their principal focus was often limited to renewing the forest overstory, many early foresters can rightly be considered among the first practitioners of restoration. With ecologists, foresters, and

wildlife biologists more recently broadening the focus of forest management to include understory flora and fauna, appropriate forest reproduction methods applied through the practice of silviculture remain the fundamental means by which forest ecosystems will be restored and sustained.

Despite longtime recognition of the inherent efficiency of working in concert with nature, silviculture has traditionally placed little emphasis on the importance of natural disturbance dynamics in the development and maintenance of forests. Indeed, forest management has often implemented silvicultural systems that prescribe stand homogeneity to optimize stand-level tree growth. However, as the primary emphasis on timber production has shifted to also include the stewardship goals of sustaining ecological functions, conserving biological diversity, and protecting at-risk species, natural disturbance has become recognized as a potential source of guidance for forest management (Coates and Burton 1997). The fundamental hypothesis for such an approach is that the species, structures, and processes that characterize natural ecosystems are more likely to persist in managed forests if anthropogenic disturbances like logging and prescribed burning mimic the dynamics of natural disturbances (Mitchell et al. 2002). The greater spatial and temporal heterogeneity of natural disturbance regimes cause higher variation in the size and age structure of living trees and distribution of dead woody debris than typically result from application of traditional silviculture (Franklin et al. 1997; Spies 1997). Silviculture might achieve a more natural basis by striving to mimic this heterogeneity and leaving onsite appropriate patterns and suitable numbers of residual trees, snags, logs, and other woody debris as biological legacies (Mitchell et al. 2002). These legacies of the past can substantially influence forest development following disturbance and contribute to future conservation of biological diversity (Palik et al. 2002).

The forest reproduction methods of traditional silviculture are in some ways analogous to various natural disturbance events. The clearcutting method eliminates or greatly reduces the forest canopy, with results similar to those caused by a powerful windstorm (e.g., hurricane) or other large-scale disturbance (Fig. 12). However, tree removal from the site is not normally associated with such natural events and the magnitude and pattern of accompanying soil disturbance are very different (e.g., skid trails from logging rather than tip-up mounds from windthrow). Results of the seed-tree method are also like those produced by major windstorms, where a few large trees remain scattered across a site. Once again, removal of trees from the site and the resulting soil disturbance pattern are unnatural consequences. The shelterwood method is thought to closely mimic stand replacement dynamics following a damaging tropical storm, leaving the forest canopy moderately intact and facilitating prolific regeneration (Croker and Boyer 1975). While this may be true for the irregular shelterwood method (where seed-bearing trees of the overwood are retained onsite as biological legacies), eventual harvest of the overstory trees makes the uniform shelterwood method appear less similar to natural disturbance. The two selection methods result in stand conditions not unlike those created by small-scale disturbances (e.g., lightning, localized fire, disease, or insect outbreaks), where individuals or groups of trees suffer mortality and fall from the forest canopy. The major difference between these two methods is related to gap size and dispersion pattern. Group selection normally results in canopy gaps of at least 0.1 ha and well dispersed, while single-tree selection produces smaller gaps less than 0.1 ha (and often as small as the area under an individual tree crown about 0.01 ha) requiring less dispersion. As additional overstory trees are removed through time, these smaller gaps may coalesce, forming larger gaps difficult to distinguish from those created by the group selection method. Although tree removal from the site and periodic soil disturbance are also unnatural aspects of both selection methods, the abundant biological legacies retained onsite following each harvest make both of these methods appear consistent with the characteristics of a more natural version of silviculture that mimics natural disturbance.

As in numerous tropical and other temperate forest types (Brokaw 1985; Denslow

FIGURE 12. Naturally regenerating even-aged longleaf pine stand following Hurricane Camille. Photo courtesy of the Forestry Images Organization.

1987; Spies and Franklin 1989; Veblen 1989; Liu and Hytteborn 1991; Lertzman 1992), the importance of canopy gaps as fundamental ecological structures in the natural regeneration of longleaf pine ecosystems has also been recognized (Palik et al. 1997; Brockway and Outcalt 1998; McGuire et al. 2001; Gagnon et al. 2003). Canopy gaps are essential in maintaining the fine-scale variability created by small-scale natural disturbances and are also generated by forest reproduction methods that remove overstory trees in a patch configuration (Coates and Burton 1997). Forests having a wide range of gap sizes afford a diversity of microenvironments for regeneration, with habitat conditions varying among gaps, within gaps (gap centers versus gap edges), and beneath the forest canopy. The resulting variation in available light, soil moisture, and nutrient resources will differentially affect regeneration success, as will the presence of advanced regeneration prior to gap formation. Gap sizes and distribution resulting from initial harvest and subsequent stand entries will have a substantial influence on the colonization of individuals and development of advanced regeneration, therefore the type and timing of silvicultural treatments will have important impacts on forest population dynamics (Coates and Burton 1997).

Canopy gaps in longleaf pine forests naturally result from a variety of disturbance agents that operate over a wide range of spatial and temporal scales (Palik and Pedersen 1996). Disturbances that remove single trees ultimately create canopy gaps of suitable size for unimpaired growth of regeneration (about 0.14 ha) as effectively as single events that remove groups of trees, a major difference being the longer time required for many episodes of single-tree removal to occur (Palik et al. 1997). Although different pathways are followed,

the essential result is that similar outcomes for stand structure are eventually obtained (Palik et al. 2002). Thus, silviculturists may validly apply either the group selection method or single-tree selection method in achieving structures representative of natural forests as long as canopy gaps of sufficient size to facilitate regeneration are created.

Silviculture, because of social, economic, and other constraints, may be unable to perfectly emulate the forest ecosystem structures and processes sustained by a natural disturbance regime (Palik et al. 2002). However, improvements can be obtained by mitigating the negative effects of logging on understory plants, forest floor, and soil structure, and incorporating knowledge concerning ecosystem disequilibrium dynamics, the importance of biological legacies and the vital role of gap-phase replacement into appropriately implemented forest reproduction methods. The application of silviculture will then result in environmental conditions that more closely approximate those produced by natural disturbance and improve the likelihood that multiple constituencies (i.e., environmental, conservation, utilitarian, and industrial groups) will be served as longleaf pine forests are effectively regenerated and sustained in the future.

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References

Allen, R.M. 1958. A study of the factors affecting height growth of longleaf pine seedlings. Ph.D. dissertation, Duke University, Durham, NC.

Barnett, J.P. 1992. The South's longleaf pine, it can rise again! *For People* 41(4):14–17.

Barnett, J.P. 2002. Longleaf pine: Why plant it? Why use containers? In *Proceedings of Workshops on Growing Longleaf Pine in Containers*, eds. J.P. Barnett, R.K. Dumroese, and D.J. Moorhead, pp. 5–7. USDA Forest Service, Southern Research Station, General Technical Report SRS–56, Asheville, NC.

Barnett, J.P., and McGilvray, J.M. 1997. Practical guidelines for producing longleaf pine seedlings in containers. USDA Forest Service, Southern Research Station, General Technical Report SRS–14, Asheville, NC.

Barnett, J.P., and McGilvray, J.M. 2000. Growing longleaf pine seedlings in containers. *Native Plants J.* 1(1):54–58.

Barnett, J.P., and McGilvray, J.M. 2002. Guidelines for producing quality longleaf pine seeds. USDA Forest Service, Southern Research Station, General Technical Report SRS–52, Asheville, NC.

Barnett, J.P., Brissette, J.C., Kais, A.G., and Jones, J.P. 1988. Improving field performance of southern pine seedlings by treating with fungicides before storage. *South J Appl For* 12:281–285.

Barnett, J.P., Lauer, D.K., and Brissette, J.C. 1990. Regenerating longleaf pine with artificial methods. In *Management of Longleaf Pine*, ed. R.M. Farrar, pp. 72–93. USDA Forest Service, Southern Forest Experiment Station, General Technical Report SO–75, New Orleans, LA.

Barnett, J.P., Pickens, B., and Karfalt, R. 1999. Improving longleaf pine seedling establishment in the nursery by reducing seedcoat microorganisms. In *Proceedings of 10th Biennial Southern Silvicultural Research Conference*, ed. J.D. Haywood, pp. 339–343. USDA Forest Service, Southern Research Station, General Technical Report SRS–30, Asheville, NC.

Boyer, W.D. 1963. Development of longleaf pine seedlings under parent trees. USDA Forest Service, Southern Forest Experiment Station, Research Paper SO–4, New Orleans, LA.

Boyer, W.D. 1973. Air temperature, heat sums and pollen shedding phenology of longleaf pine. *Ecology* 54(2):420–426.

Boyer, W.D. 1974a. Longleaf pine cone production related to pollen density. In *Seed Yield from Southern Pine Seed Orchards*, ed. J. Krause, pp. 8–14. Macon: Georgia Forest Research Council.

Boyer, W.D. 1974b. Impact of prescribed fire on mortality of released and unreleased longleaf pine seedlings. USDA Forest Service, Southern Forest Experiment Station, Research Note SO–182, New Orleans, LA.

Boyer, W.D. 1975. Timing overstory removal in longleaf pine. *J For* 73(9):578–580.

Boyer, W.D. 1978. Heat accumulation: An easy way to anticipate the flowering of southern pines. *J For* 76(1):20–23.

Boyer, W.D. 1979. Regenerating the natural longleaf pine forest. *J For* 77:572–575.

Boyer, W.D. 1981. Pollen production and dispersal as affected by seasonal temperature and rainfall patterns. In *Pollen Management Handbook*, ed. E.C. Franklin, pp. 2–9. USDA Agricultural Handbook 587, Washington, DC.

Boyer, W.D. 1987a. Annual and geographic variations in cone production by longleaf pine. In *Proceedings of the 4th Biennial Southern Silvicultural Research Conference*, comp. D.R. Phillips, pp. 73–76. USDA Forest Service, Southeastern Forest Experiment Station, General Technical Report SE–42, Asheville, NC.

Boyer, W.D. 1987b. Volume growth loss: A hidden cost of periodic prescribed burning in longleaf pine? *South J Appl For* 11:154–157.

Boyer, W.D. 1989. Response of planted longleaf pine bare–root and container stock to site preparation and release: Fifth–year results. In *Proceedings 5th Biennial Southern Silvicultural Research Conference*, ed. J.H. Miller, pp. 165–168. USDA Forest Service, Southern Forest Experiment Station, General Technical Report SO–47, New Orleans, LA.

Boyer, W.D. 1990a. *Pinus palustris*, Mill. longleaf pine. In *Silvics of North America*, technical coordinators R.M. Burns and B.H. Honkala, pp. 405–412. Vol. 1, Conifers Washington, DC: USDA Forest Service.

Boyer, W.D. 1990b. Growing-season burns for control of hardwoods in longleaf pine stands. USDA Forest Service, Southern Forest Experiment Station, Research Paper SO–256, New Orleans, LA.

Boyer, W.D. 1993a. Regenerating longleaf pine with natural seeding. In *Proceedings of the 18th Tall Timbers Fire Ecology Conference*, ed. S.M. Hermann, pp. 299–309. Tall Timbers Research Station, Tallahassee, FL.

Boyer, W.D. 1993b. Long–term development of regeneration under longleaf pine seedtree and shelterwood stands. *South J Appl For* 17(1):10–15.

Boyer, W.D. 1996. Anticipating good longleaf pine cone crops: The key to successful natural regeneration. *Alabama's Treasured Forests* 15(3):24–26.

Boyer, W.D. 1998. Long-term changes in flowering and cone production by longleaf pine. In *Proceedings of the 9th Biennial Southern Silvicultural Research Conference*, ed. T.A. Waldrop, pp. 92–98. USDA Forest Service, Southern Research Station, General Technical Report SRS–20, Asheville, NC.

Boyer, W.D. 1999. Longleaf pine: Natural regeneration and management. *Alabama's Treasured Forests* 18(3):7–9.

Boyer, W.D., and Peterson, D.W. 1983. Longleaf pine. In *Silvicultural Systems for the Major Forest Types of the United States*, tech. comp. R.M. Burns, pp. 153–156. USDA Forest Service, Agricultural Handbook No. 445, Washington, DC.

Boyer, W.D., and White, J.B. 1990. Natural regeneration of longleaf pine. In *Management of Longleaf Pine*, ed. R.M. Farrar, pp. 94–113. USDA Forest Service, Southern Forest Experiment Station, General Technical Report SO–75, New Orleans, LA.

Boyer, W.D., and Woods, F.W. 1973. Date of pollen shedding by longleaf pine advanced by increased temperatures at strobili. *For Sci* 19(4):315–318.

Brennan, L.A., and Hermann, S.M. 1994. Prescribed fire and forest pests: Solutions for today and tomorrow. *J For* 92(11):34–37.

Brockway, D.G., and Lewis, C.E. 1997. Long–term effects of dormant-season prescribed fire on plant community diversity, structure and productivity in a longleaf pine wiregrass ecosystem. *For Ecol Manage* 96(1,2):167–183.

Brockway, D.G., and Lewis, C.E. 2003. Influence of deer, cattle grazing and timber harvest on plant species diversity in a longleaf pine bluestem ecosystem. *For Ecol Manage* 175(1–3):49–69.

Brockway, D.G., and Outcalt, K.W. 1998. Gap-phase regeneration in longleaf pine wiregrass ecosystems. *For Ecol Manage* 106(2,3):125–139.

Brockway, D.G., and Outcalt, K.W. 2000. Restoring longleaf pine wiregrass ecosystems: Hexazinone application enhances effects of prescribed fire. *For Ecol Manage* 137(1–3):121–138.

Brockway, D.G., Outcalt, K.W., and Wilkins, R.N 1998. Restoring longleaf pine wiregrass ecosystems: Plant cover, diversity and biomass following low-rate hexazinone application on Florida sandhills. *For Ecol Manage* 103(2/3):159–175.

Brokaw, N.V.L. 1985. Gap-phase regeneration in a tropical forest. *Ecology* 66(3):682–687.

Coates, K.D., and Burton, P.J. 1997. A gap-based approach for development of silvicultural systems to address ecosystem management objectives. *For Ecol Manage* 99:337–354.

Cordell, C.E., Hatchell, G.E., and Marx, D.H 1990. Nursery culture of bare-root longleaf pine seedlings. In *Management of Longleaf Pine*, ed. R.M Farrar, pp. 38–51. USDA Forest Service, Southern Forest Experiment Station, General Technical Report SO–75, New Orleans, LA.

Crofton, E.W. 2001. Flora and fauna of the longleaf pine–grassland ecosystem. In The Fire *Forest: Longleaf Pine Wiregrass Ecosystem*, ed. J.R. Wilson. *Georgia Wildlife* 8(2):69–77.

Croker, T.C. 1952. Early release stimulates cone production. USDA Forest Service, Southern Forest Experiment Station, Southern Forestry Note 79, New Orleans, LA.

Croker, T.C. 1973. Longleaf pine cone production in relation to site index, stand age and stand density. USDA Forest Service, Southern Forest Experiment Station, Research Note SO–156, New Orleans, LA.

Croker, T.C. 1975. Seedbed preparation aids natural regeneration of longleaf pine. USDA Forest Service, Southern Forest Experiment Station, Research Paper SO–112, New Orleans, LA.

Croker, T.C. 1987. Longleaf pine: A history of man and a forest. USDA Forest Service, Southern Region, Forestry Report R8–FR7, Atlanta, GA.

Croker, T.C., and Boyer, W.D. 1975. Regenerating longleaf pine naturally. USDA Forest Service, Southern Forest Experiment Station, Research Paper SO–105, New Orleans, LA.

Daniel, T.W., Helms, J.A., and Baker, F.S. 1979. *Principles of Silviculture*. New York: McGraw–Hill.

Davis, V.B. 1955. Don't keep longleaf pine seed trees too long! USDA Forest Service, Southern Forest Experiment Station, Research Note 98:3, New Orleans, LA.

de Liocourt, F. 1898. De l'amenagement des sapinieres. *Societe Forestiere de Franche-Comte et Belfort Bulletin* 6:396–405.

Dennington, R.W., and Farrar, R.M. 1991. Longleaf pine management. USDA Forest Service, Southern Region, Forestry Report R8–FR3, Atlanta, GA.

Denslow, J.S. 1987. Tropical forest gaps and tree species diversity. *Annu Rev Ecol Syst* 18:431–451.

Dickmann, D.I. 1993. Management of red pine for multiple benefits using prescribed fire. *North J Appl For* 10(2):53–62.

Engstrom, R.T. 1993. Characteristic mammals and birds of longleaf pine forests. In *Proceedings of the 18th Tall Timbers Fire Ecology Conference*, ed. S.M. Hermann, pp. 127–138. Tall Timbers Research Station, Tallahassee, FL.

Engstrom, R.T., Kirkman, L.K., and Mitchell, R.J. 2001. The natural history of the fire forest. In *The Fire Forest: Longleaf Pine Wiregrass Ecosystem*, ed. J.R. Wilson. *Georgia Wildlife* 8(2):5–11, 14–17.

Farrar, R.M. 1975. Sprouting ability of longleaf pine. *For Sci* 21:189–190.

Farrar, R.M. 1996. Fundamentals of uneven-aged management in southern pine. Tall Timbers Research Station, Miscellaneous Publication No. 9, Tallahassee, FL.

Farrar, R.M., and Boyer, W.D. 1990. Managing longleaf pine under the selection system: Promises and Problems. In *Proceedings of the 6th Biennial Southern Silvicultural Research Conference*, eds. S.S. Coleman and D.G. Neary, pp. 357–368. USDA Forest Service, Southeastern Forest Experiment Station, General Technical Report SE–70, Asheville, NC.

Franklin, J.F., Berg, D.R., Thornburgh, D.A., and Tappeiner, J.C. 1997. Alternative silvicultural approaches to timber harvesting: Variable retention harvest systems. In *Creating a Forestry for the 21st Century: The Science of Ecosystem Management*, eds. K.A. Kohm and J.F. Franklin, pp. 111–139. Washington, DC: Island Press.

Frost, C.C. 1993. Four centuries of changing landscape patterns in the longleaf pine ecosystem. In *Proceedings of the 18th Tall Timbers Fire Ecology Conference*, ed. S.M. Hermann, pp. 17–43. Tall Timbers Research Station, Tallahassee, FL.

Gagnon, J.L., Jokela, E.J., Moser, W.K., and Huber, D.A. 2003. Dynamics of artificial regeneration in gaps within a longleaf pine flatwoods ecosystem. *For Ecol Manage* 172:133–144.

Gagnon, J.L., Jokela, E.J., Moser, W.K., and Huber, D.A. 2004. Characteristics of gaps and natural regeneration in mature longleaf pine flatwoods ecosystems. *For Ecol Manage* 187:373–380.

Gilliam, F.S. ,and Platt, W.J. 1999. Effects of long-term fire exclusion on tree species composition and stand structure in an old-growth *Pinus palustris* (longleaf pine) forest. *Plant Ecol* 140:15–26.

Grace, S.L., and Platt, W.J. 1995. Effects of adult tree density and fire on the demography of pregrass stage juvenile longleaf pine (*Pinus palustris* Mill.). *J Ecol* 83:75–86.

Grelen, H.W. 1983. May burning favors survival and early height growth of longleaf pine seedlings. *South J Appl For* 7:16–20.

Guldin, J.M. 1996. The role of uneven–aged silviculture in the context of ecosystem management. *West J Appl For* 11(1):4–12.

Guyer, C., and Bailey, M.A. 1993. Amphibians and reptiles of longleaf pine communities. In *Proceedings of the 18th Tall Timbers Fire Ecology Conference*, ed. S.M. Hermann, pp. 139–158. Tall Timbers Research Station, Tallahassee, FL.

Hainds, M. 2001. Scalping aids survival of longleaf. *Alabama's Treasured Forests* 20(3):24–27.

Hardin, E.D., and White, D.L. 1989. Rare vascular plant taxa associated with wiregrass (*Aristida*

stricta) in the southeastern United States. *Nat Areas J* 9:234–245.

Haywood, J.D. 2000. Mulch and hexazinone herbicide shorten the time longleaf pine seedlings are in the grass stage and increase height growth. *New For* 19:279–290.

Heyward, F. 1933. The root system of longleaf pine on the deep sands of western Florida. *Ecology* 14:136–148.

Hilton, J. 1999. Biological diversity in the longleaf pine ecosystem. *Alabama's Treasured Forests* 18(4):28–29.

Johnson, R., and Gjerstad, D. 1998. Landscape-scale restoration of the longleaf pine ecosystem. *Restor Manag Notes* 16(1):41–45.

Johnson, R., and Gjerstad, D. 1999. Restoring the longleaf pine forest ecosystem. *Alabama's Treasured Forests* 18(4):18–19.

Jose, S., Merritt, S., and Ramsey, C.L. 2003. Growth, nutrition, photosynthesis and transpiration responses of longleaf pine seedlings to light, water and nitrogen. *For Ecol Manage* 180:335–344.

Kantola, T.A., and Humphrey, S.R. 1990. Habitat use of Sherman's fox squirrel (*Sciurus niger shermanni*) in Florida. *J Mammal* 71:411–419.

Kelly, J.F., and Bechtold, W.A. 1990. The longleaf pine resource. In *Management of Longleaf Pine*, ed. R.M. Farrar, pp. 11–22. USDA Forest Service, Southern Forest Experiment Station, General Technical Report SO–75, New Orleans, LA.

Komarek, E.V. 1968. Lightning and lightning fires as ecological forces. In *Proceedings of the 9th Tall Timbers Fire Ecology Conference*, pp. 169–198. Tall Timbers Research Station, Tallahassee, FL.

Kush, J.S., comp. 1996. Longleaf pine: A regional perspective of challenges and opportunities. Proceedings of the 1st Longleaf Alliance Conference. Longleaf Alliance Report No. 1, Auburn, AL.

Kush, J.S., comp. 1998. Proceedings of the longleaf pine ecosystem restoration symposium. Longleaf Alliance Report No. 3, Auburn, AL.

Kush, J.S., comp. 1999. Longleaf pine: A forward look. Proceedings of the 2nd Longleaf Alliance Regional Conference. Longleaf Alliance Report No. 4, Auburn, AL.

Kush, J.S., comp. 2001. Restoration and management of longleaf pine ecosystems: Silvicultural, ecological, social, political and economic challenges. Proceedings of the 3rd Longleaf Alliance Regional Conference. Longleaf Alliance Report No. 5, Auburn, AL.

Kush, J.S. 2002. Natural regeneration of longleaf pine: Adaptations to site conditions and management systems. Ph.D. dissertation, School of Forestry and Wildlife Sciences, Auburn University, Auburn, AL.

Landers, J.L. 1991. Disturbance influences on pine traits in the southeastern United States. In *Proceedings of the 17th Tall Timbers Fire Ecology Conference*, pp. 61–98. Tall Timbers Research Station, Tallahassee, FL.

Landers, J.L., Byrd, N.A., and Komarek, R. 1990. A holistic approach to managing longleaf pine communities. In *Management of Longleaf Pine*, ed. R.M. Farrar, pp. 135–167. USDA Forest Service, Southern Forest Experiment Station, General Technical Report SO–75, New Orleans, LA.

Landers, J.L., Van Lear, D.H., and Boyer, W.D. 1995. The longleaf pine forests of the Southeast: Requiem or renaissance? *J For* 93(11):39–44.

Lertzman, K.P. 1992. Patterns of gap-phase replacement in a subalpine old-growth forest. *Ecology* 73(2):657–669.

Lipscomb, D.J. 1989. Impacts of feral hogs on longleaf pine regeneration. *South J Appl For* 13:177–181.

Liu, Q., and Hytteborn, H. 1991. Gap structure, disturbance and regeneration in a primeval *Picea abies* forest. *J Veg Sci* 2:391–402.

Lynch, K.D. 1980. A phenotypic study of selected variable in longleaf pine. Ph.D. dissertation, School of Forestry, Auburn University, Auburn, AL.

Mann, W.F. 1970. Direct seeding longleaf pine. USDA Forest Service, Southern Forest Experiment Station, Research Paper SO–57, New Orleans, LA.

Maple, W.R. 1977. Planning longleaf pine regeneration cuttings for best seedling survival and growth. *J For* 75:25–27.

Mattoon, W.R. 1922. Longleaf pine. U.S. Department of Agriculture, Bulletin No. 1061, Washington, DC.

McGuire, J.P. 2001. Living on longleaf: How humans shaped the piney woods ecosystem. In *The Fire Forest: Longleaf Pine Wiregrass Ecosystem*, ed. J.R. Wilson. *Georgia Wildlife* 8(2):42–53.

McGuire, J.P., Mitchell, R.J., Moser, E.B., Pecot, S.D., Gjerstad, D.H., and Hedman, C.H. 2001. Gaps in a gappy forest: Plant resources, longleaf pine regeneration and understory response to tree removal in longleaf pine savannas. *Can J For Res* 31:765–778.

McKee, W.H. 1982. Changes in soil fertility following prescribed burning on Coastal Plain pine sites. USDA Forest Service, Southeastern Forest Experiment Station, Research Paper SE–234, Asheville, NC.

McLemore, B.F. 1977. Strobili and conelet losses in four species of southern pines. USDA Forest Service, Southern Forest Experiment Station, Research Note SO–226, New Orleans, LA.

Means, D.B., and Grow, G. 1985. The endangered longleaf pine community. ENFO, Florida Conservation Foundation, Inc., Winter Park, FL 85(4):1–12.

Meyer, H.A. 1952. Structure, growth and drain in balanced uneven-aged forests. *J For* 50:85–92.

Mitchell, R.J., Palik, B.J., and Hunter, M.L. 2002. Natural disturbance as a guide to silviculture. *For Ecol Manage* 155:315–317.

Moore, J.H. 2001. Managing the forest and the trees: A private landowner's guide to conservation management of longleaf pine. The Nature Conservancy, East Gulf Coastal Plain Ecoregional Team and Southeast Conservation Science Team, Baton Rouge, LA, Theo Davis and Sons, Inc., Zebulon, NC.

Mulligan, M.K., Kirkman, L.K., and Mitchell, R.J. 2002. Aristida beyrichiana (wiregrass) establishment and recruitment: Implications for restoration. *Restor Ecol* 10(1):68–76.

Nature Conservancy. 2002. Conserving Greenwood Plantation. Eye on Nature, Georgia Chapter, The Nature Conservancy, Atlanta, GA. Summer Issue, p. 4.

Nolte, D.L., and Barnett, J.P. 2000. A repellent to reduce mouse damage to longleaf pine seed. *Int Biodeterior Biodegr* 45:169–174.

Noss, R.F. 1989. Longleaf pine and wiregrass: Keystone components of an endangered ecosystem. *Nat Areas J* 9:211–213.

Noss, R.F., LaRoe, E.T., and Scott, J.M. 1995. Endangered ecosystems of the United States: A preliminary assessment of loss and degradation. USDI National Biological Service, Biological Report 28, Washington, DC.

Nyland, R.D. 2003. Even- to uneven-aged: The challenges of conversion. *For Ecol Manage* 172: 291–300.

Outcalt, K.W. 1995. Maintaining the native plant community during longleaf pine establishment. In Forest Research Institute, Bulletin No. 192, pp. 283–285. Rotorua, New Zealand.

Outcalt, K.W. 2000. The longleaf pine ecosystem of the South. *Native Plants J* 1(1):42–44, 48–53.

Outcalt, K.W., and Sheffield, R.M. 1996. The longleaf pine forest: Trends and current conditions. USDA Forest Service, Southern Research Station, Resource Bulletin SRS-9, Asheville, NC.

Outcalt, K.W., Williams, M.E., and Onokpise, O. 1999. Restoring *Aristida stricta* to *Pinus palustris* ecosystems on the Atlantic Coastal Plain, USA. *Restor Ecol* 7:262–270.

Palik, B.J., and Pedersen, N. 1996. Overstory mortality and canopy disturbances in longleaf pine ecosystems. *Can J For Res* 26:2035–2047.

Palik, B.J., Mitchell, R.J., Houseal, G., and Pedersen, N. 1997. Effects of canopy structure on resource availability and seedling responses in a longleaf pine ecosystem. *Can J For Res* 27:1458–1464.

Palik, B.J., Mitchell, R.J., and Hiers, J.K. 2002. Modeling silviculture after natural disturbance to sustain biodiversity in the longleaf pine (*Pinus palustris*) ecosystem: Balancing complexity and implementation. *For Ecol Manage* 155:347–356.

Peet, R.K., and Allard, D.J. 1993. Longleaf pine–dominated vegetation of the southern Atlantic and eastern Gulf Coast region, USA. In *Proceedings of the 18th Tall Timbers Fire Ecology Conference*, ed. S.M. Hermann, pp. 45–81. Tall Timbers Research Station, Tallahassee, FL.

Pessin, L.J. 1938. The effect of vegetation on the growth of longleaf pine seedlings. *Ecol Monogr* 8:115–149.

Platt, W.J., Evans, G.W., and Rathbun, S.L. 1988. The population dynamics of a long-lived conifer (*Pinus palustris*). *Am Nat* 131(4):491–525.

Platt, W.J., and Rathbun, S.L. 1993. Dynamics of an old-growth longleaf pine population. In *Proceedings of the 18th Tall Timbers Fire Ecology Conference*, ed. S.M. Hermann, pp. 275–297. Tall Timbers Research Station, Tallahassee, FL.

Provencher, L., Herring, B.J., Gordon, D.R., Rodgers, H.L., Galley, K.E. M., Tanner, G.W., Hardesty, J.L., and Brennan, L.A. 2001a. Effects of hardwood reduction techniques on longleaf pine sandhill vegetation in northwest Florida. *Restor Ecol* 9:13–27.

Provencher, L., Litt, A.R., Gordon, D.R., Rodgers, H.L., Herring, B.J., Galley, K.E.M., McAdoo, J.P., McAdoo, S.J., Bobris, N.M., and Hardesty, J.L. 2001b. Restoration fire and hurricanes in longleaf pine sandhills. *Ecol Restor* 19(2):92–98.

Pyne, S.J. 1997. *Fire in America: A Cultural History of wildland and Rural Fire*. Seattle: University of Washington Press.

Ramsey, C.L., Jose, S., Brecke, B.J., and Merritt, S. 2003. Growth response of longleaf pine (*Pinus palustris* Mill.) seedlings to fertilization and herbaceous weed control in an old field

in southern USA. *For Ecol Manage* 172:281–289.

Reynolds, R.R. 1969. *Twenty-nine years of selection* timber management on the Crossett Experimental Forest. USDA Forest Service, Southern Forest Experiment Station, Research Paper SO–40, New Orleans, LA.

Reynolds, R.R., Baker, J.B., and Ku, T.T. 1984. Four decades of selection management on the Crossett Farm Forestry Forties. Arkansas Agricultural Experiment Station Bulletin 872.

Schabel, H.G., and Palmer, S.L. 1999. The Dauerwald: Its role in the restoration of natural forests. *J For* 97(11):20–25.

Schmidtling, R.C. 1999. Longleaf pine genetics. In *Longleaf Pine: A Forward Look. Proceedings of the 2nd Longleaf Alliance Regional Conference*, Longleaf Alliance Report No. 4, comp. J.S. Kush, pp. 24–26. Auburn, AL.

Schmidtling, R.C. 2001. Southern pine seed sources. USDA Forest Service, Southern Research Station, General Technical Report SRS–44, Asheville, NC.

Schmidtling, R.C., and Hipkins, V. 1998. Genetic diversity in longleaf pine (*Pinus palustris*): Influence on historical and prehistorical events. *Can J For Res* 28:1135–1145.

Schmidtling, R.C., Hipkins, V., and Carroll, E. 2000. Pleistocene refugia for longleaf and loblolly pines. *J Sustain For* 10(3/4):349–354.

Schopmeyer, C.S., tech. coord. 1974. *Seeds of Woody Plants in the United States*. USDA Agricultural Handbook 450, Washington, DC.

Schwarz, G.F. 1907. *The Longleaf Pine Virgin Forest: A Silvical Study*. New York: John Wiley & Sons.

Seamon, G. 1998. A longleaf pine sandhill restoration in northwest Florida. *Restor and Manage Notes* 16:46–50.

Shelton, M.G., and Cain, M.D. 2000. Regenerating uneven-aged stands of loblolly and shortleaf pines: The current state of knowledge. *For Ecol Manage* 129:177–193.

Shoulders, E. 1967. Fertilizer application, inherent fruitfulness and rainfall affect flowering of longleaf pine. *For Sci* 13:376–383.

Simberloff, D. 1993. Species-area fragmentation effects on old-growth forests: Prospects for longleaf pine communities. In *Proceedings of the 18th Tall Timbers Fire Ecology Conference*, ed. S.M. Hermann, pp. 1–13. Tall Timbers Research Station, Tallahassee, FL.

Smith, H.C., Lamson, N.I., and Miller, G.W. 1989. An esthetic alternative to clearcutting. *J For* 87(3):14–18.

Smith, L.F. 1955. Development of longleaf pine seedlings near large trees. *J For* 53(4):289–290.

Smith, L.F. 1961. Growth of longleaf pine seedlings under large pines and oaks in Mississippi. USDA Forest Service, Southern Forest Experiment Station, Research Paper 189, New Orleans, LA.

Smith, L.F. 1962. Growth of longleaf pine seedlings under large pines and oaks in Mississippi. USDA Forest Service, Southern Forest Experiment Station, Paper 189, New Orleans, LA.

Snyder, E.B., Dinus, R.J., and Derr, H.J. 1977. Genetics of longleaf pine. USDA Forest Service, Research Paper WO-33, Washington, DC.

Spies, T. 1997. Forest stand structure, compositior and function. In *Creating a Forestry for the 21st Cen tury: The Science of Ecosystem Management*, eds. K.A Kohm and J.F. Franklin, pp. 11–30. Washington DC: Island Press.

Spies, T.A., and Franklin, J.F. 1989. Gap characteris tics and vegetation response in coniferous forest of the Pacific Northwest. *Ecology* 70(3):543–545.

Starkey, T.E. 2002. Irrigation and fertilization type rate and frequency of application. In *Proceedin of Workshops on Growing Longleaf Pine in Container* eds. J.P. Barnett, R.K. Dumroese, and D.J. Moo head, pp. 30–34. USDA Forest Service, Souther Research Station, General Technical Report SRS 56, Asheville, NC.

Stout, I.J., and Marion, W.R. 1993. Pine flatwoo and xeric pine forests of the southern low coastal plain. In *Biodiversity of the Southeaste United States: Lowland Terrestrial Communities*, ed W.H. Martin, S.G. Boyce, and A.C. Echternac pp. 373–446. New York: John Wiley & Sons.

Taylor, A.R. 1974. Ecological aspects of lightning forests. In *Proceedings of the 13th Tall Timbers F Ecology Conference*, pp. 455–482. Tall Timbers R search Station, Tallahassee, FL.

Veblen, T.T. 1989. Tree regeneration responses gaps along a transandean gradient. *Ecology* (3):541–543.

Wade, D.D., and Lewis, C.E. 1987. Managing sou ern grazing ecosystems with fire. *Rangela* 9(3):115–119.

Wade, D.D., and Lundsford, J. 1990. Fire as a f est management tool: Prescribed burning in t southern United States. *Unasylva* 162(41):28–

Wahlenberg, W.G. 1946. Longleaf pine: Its u ecology, regeneration, protection, growth a management. C.L. Pack Forestry Foundation USDA Forest Service, Washington, DC.

Wakeley, P.C. 1954. Planting the southern pines. S. Department of Agriculture, Agricultural Mo graph 18, Washington, DC.

Walker, J.L. 1993. Rare vascular plant taxa associated with the longleaf pine ecosystem. In *Proceedings of the 18th Tall Timbers Fire Ecology Conference*, ed. S.M. Hermann, pp. 105–125. Tall Timbers Research Station, Tallahassee, FL.

Walker, J.L. 1995. Longleaf pine ecosystem restoration: Toward a regional strategy. USDA Forest Service, Southern Research Station, Asheville, NC and Southern Region, Atlanta, GA.

Walker, J.L. 1999. Longleaf pine forests and woodlands: Old growth under fire! In *The Value of Old Growth Forest Ecosystems of the Eastern United States*, ed. G.L. Miller, pp. 33–40. Asheville: University of North Carolina.

Walker, J.L., and Boyer, W.D. 1993. An ecological model and information needs assessment for longleaf pine ecosystem restoration. In *Silviculture from the Cradle of Forestry to Ecosystem Management*, comp. L.H. Foley, pp. 138–147. USDA Forest Service, Southeastern Forest Experiment Station, General Technical Report SE–88, Asheville, NC.

Walker, L.C. 1954. Early scrub-oak control helps longleaf pine seedlings. *J For* 52:939–940.

Walker, L.C., and Davis, V.B. 1954. Forest walls retard young longleaf pine. USDA Forest Service, Southern Forest Experiment Station, Research Note 93:3, New Orleans, LA.

Walker, L.C., and Davis, V.B. 1956. Seed trees retard longleaf pine seedlings. *J For* 54(4):269.

Ware, S., Frost, C.C., and Doerr, P.D. 1993. Southern mixed hardwood forest: The former longleaf pine forest. In *Biodiversity of the Southeastern United States: Lowland Terrestrial Communities*, eds. W.H. Martin, S.G. Boyce, and A.C. Echternacht, pp. 447–493. New York: John Wiley & Sons.

White, J.B. 1981. The influence of seedling size and length of storage on longleaf pine survival. *Tree Planters' Notes* 32(4):3–4.

White, T.L., Harris, H.G., and Kellison, R.C. 1977. Conelet abortion in longleaf pine. *Can J For Res* 7:378–382.

Wright, H.A., and Bailey, A.W. 1982. *Fire Ecology of the United States and Southern Canada*. New York: John Wiley & Sons.