



History and restoration of the longleaf pine-grassland ecosystem: Implications for species at risk

David H. Van Lear^{a,*}, W.D. Carroll^a, P.R. Kapeluck^a, Rhett Johnson^b

^aDepartment of Forestry and Natural Resources, Clemson University, Clemson, SC 29634, USA

^bSolon Dixon Forestry Education Center, Auburn University, Auburn, AL 36849, USA

Abstract

The longleaf pine-grassland (*Pinus palustris-Poaceae*) ecosystem occupied over 30 million ha in the southeastern United States at the time of European discovery. Frequent low- to moderate-intensity surface fires ignited by both lightning and native Americans sustained open diverse stands in a fire climax and prevented succession to mixed hardwood forests. Disruption of pre-historical and historical fire regimes, coupled with land conversion, urbanization, and other factors, is responsible for the rapid decline of the ecosystem. Today only about 1.2 million ha remain, much in isolated fragments. Primarily because of habitat loss, many animal and plant species associated with longleaf forests are now rare or in decline. Restoration ecologists and managers face a daunting challenge—recreating an ecosystem, in the face of chronic cumulative stress from human activities, that varied widely over temporal and spatial scales. Key restoration factors include: (1) development of a general understanding of the historical condition of the longleaf ecosystem, especially unusual or unique communities and habitats embedded in the general fabric of the larger ecosystem, (2) initiation and expansion of a fire regime, where feasible, similar to that which historically shaped the ecosystem, (3) maintenance/enhancement of herbaceous diversity, (4) continued research on habitat requirements and distribution of rare species, and (5) encouragement of a multi-owner partnership approach to promote conservation across the landscape. Landowners and the public must be educated about the values of the longleaf pine-grassland ecosystem and develop a conservation ethic that considers aesthetics, wildlife, and biodiversity, in addition to economics, if the ecosystem is to be restored. Most forestry practices used to manage and restore longleaf forests are of low short-term risk to rare species in this ecosystem. The benefits of active management usually far outweigh the long-term risks associated with no management.

© 2005 Elsevier B.V. All rights reserved.

Keywords: Fire-dependent ecosystems; Prescribed burning; Endangered and threatened species; Historical and pre-historical fire regimes

1. Introduction

At the time of European settlement, longleaf pine (*Pinus palustris*) was dominant on about 30 million ha and occurred on another 7 million ha in mixed stands

* Corresponding author. Tel.: +1 864 656 4857;
fax: +1 864 656 3304.

E-mail address: dvnlr@clemson.edu (D.H. Van Lear).

(Frost, 1993). From southeastern Virginia to eastern Texas, it dominated the Coastal Plain but also extended into the Piedmont, Cumberland Plateau, Ridge and Valley, and Blue Ridge physiographic regions (Boyer, 1990; Outcalt and Sheffield, 1996). Although upland pine-grassland communities were most characteristic of this expansive ecosystem, communities of numerous rare habitats, such as sinks and other depressional

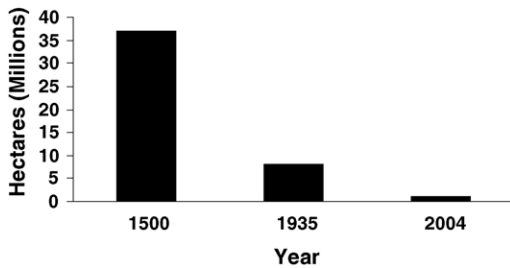


Fig. 1. Estimated area in the longleaf pine ecosystem from 1500 A.D. to 2004 A.D. Data from Frost (1993), Wahlenberg (1946), and U.S. Fish and Wildlife Service (2003).

wetlands, hammocks, and upland/wetland ecotones, were also important components.

Man and lightning combined over the millennia to make frequent fire the dominant ecological process shaping the vast longleaf pine-grassland ecosystem. However, today only about 1.2 million ha of the ecosystem remain (Outcalt and Sheffield, 1996; U.S. Fish and Wildlife Service, 2003), a 97% loss from its original extent (Fig. 1). Noss et al. (1995) ranked longleaf pine forests the third most endangered ecosystem in the United States.

In this review, we discuss the pre-historical and historical role of fire in this ecosystem and the effects of almost a century of fire exclusion, which coupled with rampant development, land conversion, and other factors, account for the loss of habitat and biodiversity. The consequences of this altered fire regime on forest succession, forest structure, and species at risk will be contrasted with the short-term risks of active management to restore ecosystem composition, structure, and function. The term “species at risk” is a comprehensive term that includes all species whose long-term survival is questionable because of habitat loss in the longleaf pine-grassland ecosystem. For conciseness, the term longleaf ecosystem will replace longleaf pine-grassland ecosystem.

2. The pre-historical role of fire in the longleaf ecosystem

2.1. Climate change and establishment of the longleaf pine-grassland ecosystem

Although the Wisconsin ice sheet of 18,000 years ago extended southward only to the present location of

the Ohio River, the massive dimensions of the glaciers and the water they contained caused a colder and drier climate in the South (Delcourt and Delcourt, 1979; Carroll et al., 2002). Longleaf pine and other southern pines found refuge mainly in coastal areas and on the exposed continental shelf from Florida to northeastern Mexico (Edwards and Merrill, 1977).

As the glaciers retreated, the climate warmed and cooled periodically, vegetation patterns in the South changed rapidly, and species migrated north and westward from their Ice Age refuges. During the Hypsithermal Period (7500–5000 years before present or ybp), the warmest period during the past 20,000 years, prairie grasses, aided by anthropogenic burning, expanded from the Midwest into the Southeast (Edwards and Merrill, 1977; Watts, 1980; Delcourt and Delcourt, 1985). At the same time, the longleaf ecosystem became dominant in the Coastal Plain (Culberson, 1993; Watts, 1980; Delcourt and Delcourt, 1985).

Although climate, soil, and topography influence the distribution of vegetation, frequent burning was the dominant ecological process that shaped and maintained the composition, structure, and function of the longleaf ecosystem (Komarek, 1974; Noss, 1989; Landers et al., 1995). Frequent fires ignited by lightning and Native Americans sustained this ecosystem (Landers, 1991; Carroll et al., 2002; Stanturf et al., 2002), which over the millennia became one of the most floristically diverse in North America (Peet and Allard, 1993; Walker, 1993).

2.2. Sources of ignition: Native Americans and lightning

It is difficult to separate the effects of lightning and anthropogenic fire on vegetative patterns or determine which was the most dominant ignition source. The southeastern United States, especially the Gulf Coastal Plain, has the highest frequency of lightning strikes in North America (Komarek, 1974). However, man domesticated fire tens of thousands of years before the first Americans brought this powerful tool to the South over 12,000 ybp, and knew how to influence vegetation with fire for his benefit (Kurten, 1972; Champion et al., 1984; Carroll et al., 2002). As Native Americans advanced through different cultural periods and became more numerous, they undoubtedly

used fire more and more (Delcourt and Delcourt, 1997; Delcourt, 2002). At the time of Columbus, it is estimated that 1.5–2.0 million people lived in the Southeast, mostly in the Coastal Plain (Dobyns, 1983). Fire was their primary tool for managing the landscape for their benefit.

Native Americans burned locally around their settlements to reduce fuels and protect themselves from wildfires (Williams, 1989; Johnson and Hale, 2002). They also influenced the character of the broader landscape by using fire to enhance wildlife habitat and increase wildlife populations, aid in hunting, favor berry- and nut-producing plants and other palatable forage, maintain open landscapes for ease of travel, and protect themselves from ambush by predators and enemy tribes (Hudson, 1976; Williams, 1989; Pyne et al., 1996; Bonnicksen, 2000; Carroll et al., 2002). Frequent burning reduced biting insects like blackflies, ticks, fleas, mosquitos, and other pests, improving the quality and health of their lives (Bonnicksen et al., 1987).

The early hunter-gatherers of the Clovis and Late Paleo Period cultures (12,000–9500 ybp) initiated a burning pattern that would dominate the Southeast until approximately 500 ybp (Pyne et al., 1996; Bonnicksen, 2000; Carroll et al., 2002). Although lightning fires were common during the growing season (Komarek, 1974; Noss, 1989), Native Americans set fires in all seasons. In all likelihood, a combination of Native American- and lightning-caused fire helped genetically fix fire-adapted characteristics in species in this ecosystem (Masters et al., 2003). Frequent fire shaped vegetative communities in the longleaf ecosystem, possibly by acting as an ecological filter that permitted access only to species compatible with this disturbance regime (Bond and Van Wilgen, 1996, p. 147) and by controlling the size and distribution of less-fire adapted hardwoods (Ware et al., 1993). Fire interacted with site and disturbance to maintain a shifting mosaic of prairies, savannas, woodlands, and other community types over the landscape (Peet and Allard, 1993; Landers et al., 1995).

In recent decades, the major role of Native Americans in shaping the Southern landscape, although controversial, has been more widely acknowledged, especially by historical geographers, historians, paleoecologists, anthropologists, and resource managers

(Delcourt and Delcourt, 1985; Williams, 1989; Pyne et al., 1996; Bonnicksen, 2000; Carroll et al., 2002). Man's use of fire allowed him to influence the landscape far out of proportion to his numbers (Hudson, 1976). Indeed, it can be argued that, at least in some places, the southeastern Coastal Plain prior to its discovery by Europeans was a cultural artifact largely molded and manipulated by Native Americans through their use of fire (Williams, 1989, p. 49; Pyne et al., 1996, pp. 236–240; Carroll et al., 2002).

2.3. Disturbances and site factors

The pre-historical fire regime, i.e., prior to 500 ybp, in the longleaf ecosystem was characterized by frequent burning which produced fires of low-to moderate-intensity and severity. In this fire regime of frequent understory burning (Brown, 2000), fires were generally non-lethal to the dominant vegetation and did not change the existing structure of woody and herbaceous components. Because the interval between fires was short, fuels did not accumulate to levels that would allow stand-replacing fires.

Fire-dependent plant communities developed that not only required fire for their maintenance, but encouraged future understory fires. Fine tinder provided by long, linear, and often overlapping leaves of bunch grasses (*Aristida* spp., *Andropogon* spp., *Sorghastrum* spp., *Schizachyrium* spp., and others) and the long, resinous needles of longleaf pine ensured that fires ignited readily and spread quickly across the open landscape (Noss, 1989; Clewell, 1989; McGuire et al., 2001). Without fire at 1–3 year intervals, there would have been invasion and replacement by communities of less fire-adapted species (Ware et al., 1993; Engstrom et al., 2001).

Combinations of disturbances and site factors contributed to the high biodiversity of the longleaf ecosystem (Hardin and White, 1989; Walker, 1993; Peet and Allard, 1993). Frequent lightning strikes, tree falls, and various animals have local influences, while tropical storms and hydrologic extremes affect larger areas and long temporal scales. These disturbances, acting over soils and sites ranging from bogs to xeric sand ridges, interacted with fire and provided temporary habitat features (coarse woody debris, hardwood thickets, etc.) and more stable features (old trees, treeless places, etc.) over the landscape.

Following major disturbances to the upper canopy from hurricanes and other wind events, more intense fires undoubtedly developed in the complex mix of fine and coarse fuels. These higher intensity fires would have had relatively long residence times—burning in large and heavy fuels—and probably killed many trees that may have survived the high winds (Outcalt and Wade, 2004). Intensely burned areas, if followed by frequent burning by Native Americans and lightning over long periods of time, would have expanded prairies and savannas (Doolittle, 1992; Gremillion, 1987; Myers and Van Lear, 1997) and contributed to this shifting vegetative mosaic that characterized the longleaf ecosystem for millennia.

3. Transition from Native American to European culture

3.1. Decline of the Native American population

European and African diseases were brought to the Caribbean around 1500 A.D. and advanced to Central America, Mexico, and the southern United States prior to the arrival of the Spanish in the region (Verano and Ubelaker, 1992). When the explorer DeSoto marched his army of 600+ men across the South in 1539–1542, he found villages of Native Americans already decimated by disease. Mortality rates as high as 90–95% have been attributed to smallpox, typhoid, bubonic plague, influenza, mumps, measles, hepatitis, and other diseases that spread rapidly in the Americas in the century after Columbus (Dobyns, 1983; Smith, 1987; Lovell, 1992). The Mississippian Culture collapsed by 1600 A.D. as a result of European intrusion and diseases. The arrival of the English in the early 17th century continued the pandemics that decimated Native Americans for another century (Hudson, 1976; Smith, 1987; Carroll et al., 2002).

With the decline in the Native American population and the still small European/African population in the southeastern United States, fire became a less common practice and was confined to smaller areas. Prairies and open savannas gradually succeeded to dense mixed hardwood forests reversing the process by which Native Americans had created them (Rostlund, 1957).

3.2. European settlement and impacts

Woods burning in the longleaf ecosystem became common once again as European settlers and their African slaves replaced Native Americans. Immigrants were primarily from western England, Scotland, and Ireland, where burning and open range herding was customary (Johnson and Hale, 2002). These new settlers burned to achieve many of the same goals of Native Americans. They burned frequently, often annually, to keep the woods open and for improved grazing and hunting. Now, however, wildlife competed with domestic livestock for palatable forage and exotic species were introduced into the ecosystem. Especially damaging to longleaf pine regeneration, feral hogs (*Sus scrofa*) saturated tidewater Virginia and northeastern North Carolina by 1750 (Frost, 1993).

Row crop farming and pasturing gradually broke the tradition of open-range burning in much of the South, although burning continued in the extensive pine-woods of the Coastal Plain. However, wealthy northerners bought plantations after the Civil War for hunting retreats and stopped extensive burning on their lands (Frost, 1993; Johnson and Hale, 2002). Northern attitudes about woods burning did not blend well with the Southern custom of firing the woods for hunting and grazing purposes.

Between 1850 and 1870, steam technology for logging developed and proliferated as logging began in earnest in the southern Coastal Plain (Frost, 1993). By 1930, most of the large longleaf pine, except those protected on hunting plantations, had been cut (Crocker, 1987). Annual burning of the cutover lands continued, but fires following logging were initially more intense as a result of heavier fuel loads from logging slash (Wade and Lundsford, 1989; Johnson and Hale, 2002).

In many cases, the longleaf ecosystem did not regenerate following harvest. Not even longleaf pine can regenerate in a regime of annual fire because small seedlings (<0.8 cm diameter at the root collar) are easily killed by fire (Boyer and Peterson, 1983) and feral hogs destroyed the occasional seedlings that had become successfully established. In addition, harvests were usually so extensive and complete that no seed source was available.

Quail populations declined on the large fire-protected plantations as understory hardwoods gra-

dually developed. Fire was gradually reintroduced on these plantations, thanks largely to the efforts of Herbert L. Stoddard, whose 1931 classic book on bobwhite quail (*Colinus virginianus*) identified lack of fire as a primary cause of the regional decline of quail (Johnson and Hale, 2002). During the last half of the 20th century, quail-hunting plantations, with their large contiguous blocks of land and tradition—dating from Stoddard—of burning, remained one of the last strongholds where the historical nature of the longleaf ecosystem was preserved.

4. Fire exclusion policy and development of an uncharacteristic fire regime

From the early decades of the 20th century, forest policy makers attempted to implement a new fire policy on the nation's forests—a policy of fire exclusion. The U.S. Forest Service and state forestry agencies were leaders in this anti-fire campaign, which followed disastrous wildfires throughout the northern tier of the country, especially in 1910 (Pyne, 2001). The American Forestry Association sponsored teams of “Dixie Crusaders” who preached fire prevention throughout the South from 1927 to 1930. Eventually, the public accepted the fervently delivered anti-fire message and a nation-wide policy of fire exclusion was established (Pyne et al., 1996; Pyne, 2001).

In the South, however, the use of fire to promote grazing, enhance hunting, and clear agricultural fields was deeply ingrained in the over-whelmingly rural population (Frost, 1993; Pyne et al., 1996; Johnson and Hale, 2002). As the young U.S. Forest Service (USFS) gained experience in the region, it grudgingly accepted the role of prescribed fire as a management tool. It had to, because early Chiefs of the Forest Service—Pinchot and Graves—recognized fire's role as researchers revealed its importance in this ecosystem (Wahlenberg, 1946; Croker, 1987; Wade et al., 2000).

By the 1940s, the USFS was using prescribed fire to reduce hazardous fuels (Pyne et al., 1996). Today, in addition to hazard reduction, resource managers use prescribed fire to prepare sites for seeding and planting, improve wildlife habitat, manage competing vegetation, control disease, improve forage for grazing, enhance aesthetic appearance, and perpetuate

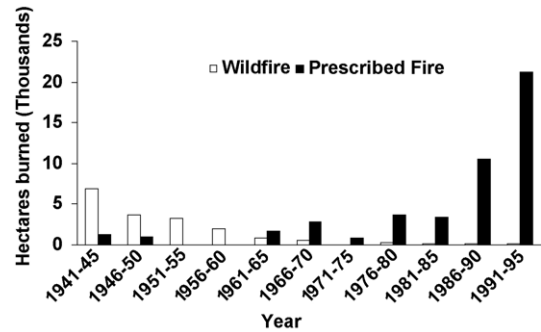


Fig. 2. Area treated with prescribed fire and area burned by wildfire on the Carolina Sandhills Wildlife Refuge 1941–1995 (from Pyne, 1997).

fire-dependent and endangered species (Wade and Lundsford, 1989). However, prescribed burning is done on a relatively small portion of this once vast ecosystem. Only about 3.2 million ha are currently prescribed burned in the entire southern United States (Wade et al., 2000).

Under the policy of fire exclusion, an uncharacteristic fire regime has replaced, in many places, the frequent, low- to moderate-intensity fire regime that sustained the longleaf ecosystem for millennia. Longer intervals between fires produced a much higher fire intensity, as witnessed by the 1998 Florida wildfire season (Outcalt and Wade, 2004). It is well established that wildfire acreage declines when prescribed burning is used to control fuel buildup (Fig. 2). Instead of the historically frequent, non-lethal understory burns that characterized the fire regime prior to 1900, the current fire regime has been one of mixed severity (Brown, 2000), where less frequent, but more severe, fires are representative. Hardwood understory species became too large to be top-killed by fires (Wade and Lundsford, 1989; Waldrop et al., 1992) and fuel loading increased (Wade et al., 2000).

There are consequences to this altered fire regime, apart from those associated with replacement of the longleaf ecosystem, that relate to restoration. For example, when wildfires occur mortality rates of overstory trees are higher (Outcalt and Wade, 2004). And when prescribed fire is used in areas where fire has been withheld for long periods, large, relic longleaf pines may be killed by smoldering combustion in the accumulated forest floors at their bases (Varner et al., 1999).

5. Species at risk in the longleaf ecosystem

The relatively sparse tree density of many longleaf pine stands allows high levels of sunlight to penetrate the canopy. Control of woody broadleaf species, typically with routine fire, allows much of that light to reach the forest floor, encouraging the species-rich understory. Sixty-nine percent of the mammal species and over one-third of the bird species characteristic of the longleaf ecosystem forage primarily on or near the ground, indicating the essential role played by fire in maintaining ground cover for mammalian and avian communities (Engstrom, 1993).

The major threats to species at risk in the longleaf ecosystem have been and continue to be conversion to other land uses—especially to agriculture and intensively managed tree plantations, urbanization, and fire exclusion (Noss, 1989; Frost, 1993; Walker, 1993; Landers et al., 1995; Noss et al., 1995; Trani, 2002). Agricultural lands are expected to decline in the next few decades, but tree plantations in the South are forecast to rise by 67% by 2040 (Wear and Greis, 2002). While about 75% of this increase in tree plantations will come from converting agricultural fields, conversion to loblolly (*Pinus taeda*) and slash (*P. elliottii*) pine plantations minimizes the possibility that some of these lands would be used for longleaf restoration. However, with proper incentives—such as the federally sponsored Wildlife Habitat Incentives Program, cost sharing would be available to landowners for practices such as planting longleaf seedlings and prescribed burning. Burning longleaf plantations on a frequent basis and restoring the herbaceous layer through management would go a long way toward restoration of a functional longleaf ecosystem.

These altered land uses are fueled by the South's rapidly growing human population, accompanied by an even greater rate of urban sprawl (Wear, 2002), and have led to habitat loss and fragmentation with major implications for species at risk, i.e., species whose conservation status is G1, G2, or G3, a ranking which indicates the relative risk of extinction for listed species (see <http://www.natureserve.org>). In addition, introduced exotic plants and animals are an ever-increasing threat and may displace native species, disrupt nutrient and fire cycles, and alter plant succession (Westbrooks, 1998). The recent Southern

Forest Resource Assessment (Wear and Greis, 2002) offers excellent reviews of these threats.

5.1. Mammals and birds

Three mammal species—red wolf (*Canis rufus*), mountain lion (*Felis concolor*), and bison (*Bison bison*)—have been extirpated from the longleaf ecosystem since European settlement. Concomitantly, feral swine, armadillo (*Dasypus novemcinctus*), coyote (*Canis latrans*), and others have become well established (Engstrom, 1993). About 14% of mammals in the longleaf ecosystem are considered to be of conservation concern (Engstrom et al., 2001). Understory grasses, legumes, and other forbs provide forage for herbivores like Sherman's fox squirrel (*Sciurus niger shermani*), listed as a species of special concern in Florida, pocket gophers (*Geomys pinetis*), and many other small mammals.

The rich herbaceous layer in the open pinelands produces seeds for granivores like Bachman's sparrow (*Aimophila aestivales*) and northern bobwhite (*C. virginianus*), and supports high insect populations for insectivores like northern bobwhite and winter cover for Henslow's sparrow (*Ammodramus henslowii*) (Tucker and Robinson, 2000; Carrie et al., 2002). The open midstory and sparse low woody brush provide excellent singing perches for Bachman's sparrows, a species of special concern, and "hawking" perches from which eastern wood-peewees (*Contopus virens*) and southeastern American kestrel (*Falco spiveyus paulus*) can hunt (Hamel, 1992).

Perhaps the bird species most frequently identified with the longleaf ecosystem is the federally endangered red-cockaded woodpecker (*Picoides borealis*). Although not limited to longleaf pine, it is found most often in association with that species. The ability of longleaf pine to live to relatively old ages (Platt and Rathbun, 1993), its copious resin flow (Bowman and Huh, 1995), and its tolerance of fire combine to make longleaf forests particularly well-suited to the red-cockaded's habitat needs (Connor and Rudolph, 1995). The open nature of fire-maintained longleaf pine forests, with few hardwoods and little midstory, provides excellent forage for the woodpeckers. In addition, the longleaf pine's production of resin in response to injury creates sticky barriers around nest cavities, deterring predators.

5.2. Plants

About 40% of the 1600+ plant species in the Atlantic and Gulf coastal plains are restricted to longleaf-dominated landscapes, an extremely high level of endemism (Walker, 1998). A large number of rare plant species (187) are associated with the longleaf ecosystem. Of the 27 species federally listed as federally threatened or endangered (Table 1), most have narrow habitat requirements (Walker, 1993; Walker, 1998). For example, American chaffseed (*Schwalbea americana*) is found in open, moist pine flatwoods, fire-maintained savannas, and ecotonal areas between wetlands and xeric uplands. Harper's beauty (*Harperocallis flava*) occurs in open pineland bogs and along moist roadside ditches in northwest Florida, and pondberry (*Lindera melissifolia*) exists

along the margins of sinks, ponds, and other depressions.

Many rare plants in the longleaf ecosystem occur in embedded wetlands that depend on periodic fire to maintain open vegetative conditions (Peet and Allard, 1993; Walker, 1993). Vegetation in ecotones between wetlands and uplands, in the absence of fire, often becomes too dense and, through transpiration, dries the soil too rapidly to sustain habitats. Periodically burning these ecotonal and seasonally wet habitats benefits many rare species (Peet and Allard, 1993).

In addition to narrow habitat requirements, almost 75% of the rare species identified in Walker's 1993 study also have narrow geographic distributions, i.e., they occur only in distinct portions of the range of the longleaf ecosystem. Many of these endangered and threatened species are found in only one state

Table 1

Federally endangered (E) and threatened (T) plant species associated with longleaf pine ecosystems and direct and indirect habitat factors cited as reasons for listing

| Common name | Scientific name | Status | Codes | Geographic distribution |
|---------------------------------|---|--------|---------------|--------------------------------|
| Hairy rattleweed | <i>Baptisia arachnifera</i> | E | b | GA |
| Pigeon wings | <i>Clitoria fragrans</i> | T | c, d, f | FL |
| Apalachicola rosemary | <i>Conradina glabra</i> | E | b, c, f, g | FL |
| Beautiful pawpaw | <i>Deeringothamnus pulchellus</i> | E | d, f | FL |
| Rugel's pawpaw | <i>Deeringothamnus rugelii</i> | E | d, f | FL |
| Scrub wild buckwheat | <i>Eriogonum longifolium</i> var. <i>gnaphalifolium</i> | E | c, d | FL |
| Telephus spurge | <i>Euphorbia telephiodes</i> | T | b, d, f, g | FL |
| Harper's beauty | <i>Harperocallis flava</i> | E | a, b, d, f, g | FL |
| Pondberry | <i>Lindera melissifolia</i> | E | a–d | MS, AR, MO, SC, GA, NC |
| Roughleaf loosestrife | <i>Lysimachia asperulaefolia</i> | E | a–f | NC, SC |
| White birds-in-a-nest | <i>Macbridea alba</i> | T | b, f | FL |
| Britton's beargrass | <i>Nolina brittoniana</i> | E | c, d | FL |
| Canby's dropwort | <i>Oxypolis canbyi</i> | E | a, b, c | MD, DE, NC, SC, GA |
| Texas trailing phlox | <i>Phlox nivalis</i> ssp. <i>texensis</i> | E | a, b, d, f | TX |
| Godfrey butterwort | <i>Pinguicula ionantha</i> | T | a, b, d, f | FL |
| Small Lewton's milkwort | <i>Polygala lewtonii</i> | E | c, d | FL |
| Chapman's rhododendron | <i>Rhododendron chapmanii</i> | E | b | FL |
| Michaux's sumac | <i>Rhus michauxii</i> | E | b–f | VA, NC, SC, GA |
| Alabama canebrake pitcher-plant | <i>Sarracenia rubra</i> spp. <i>alabamensis</i> | E | a, c, g, h | AL |
| Chaffseed | <i>Schwalbea americana</i> | E | b, c, d, f | NJ, NC, SC, GA, FL, AL, MS, LA |
| Florida skullcap | <i>Scutellaria floridana</i> | T | b, f | FL |
| Gentian pinkroot | <i>Spigelia gentianoides</i> | E | b, c, f | AL, FL |
| Cooley's meadowrue | <i>Thalictrum cooleyi</i> | E | a–c, f, g | NC, FL |
| Wide-leaf warea | <i>Warea amplexifolia</i> | E | c, d | FL |
| Carter's mustard | <i>Warea carteri</i> | E | c, d | FL |
| Florida ziziphus | <i>Ziziphus celata</i> | E | c, d, f | FL |

Habitat-related listing factor codes: a: drainage/fire plow lines/road work; b: silviculture activities; c: agriculture conversion; d: residential/commercial/recreational development; e: other human activities; f: fire suppression; g: herbicide/pesticide use; h: mining. States with known populations are listed under geographic distribution. Listing data (U.S. Fish and Wildlife Service, <http://www.fws.gov/>) were current October 15, 2004. Adapted from Walker (1998).

(Table 1). Most of these imperiled species are perennial, suggesting they are capable of resprouting if top-killed by fire, and many occupy wetland habitats such as bogs that, without fire, succeed to hardwood forests.

5.3. Reptiles and amphibians

Effects of habitat reduction in this ecosystem on the herpetofaunal community have not been directly assessed (Trani, 2002), although a cursory examination indicates that an alarming percentage of the specialist fauna is imperiled (Guyer and Bailey, 1993). As with many birds and mammals, it is well established that grasses, legumes, and other forbs provide excellent forage for gopher tortoises (*Gopherus polyphemus*) and other herpetofauna (Garner and Landers, 1981; MacDonald and Mushinsky, 1988). The gopher tortoise is federally listed in its western range and has declined by 80% over the last century (White et al., 1998).

Other listed herpetofauna include the federally threatened eastern indigo snake (*Drymarchon corais couperi*), the federally endangered Mississippi gopher frog (*Rana capito sevosa*), and the Louisiana pine snake (*Pituophis ruthveni*). Species at risk include the dusky gopher frog (*Rana sevosa*), eastern diamond-back rattlesnake (*Crotalus admanteus*), black pine snake (*Pituophis melanoleucus lodingi*), Florida pine snake (*Pituophis melanoleucus mugitus*), and Southern Hognose snake (*Heterodon simus*). The federally threatened flatwoods salamander (*Ambystoma cingulatum*) uses longleaf pine and other flatwoods habitats during a portion of its annual life cycle (Mount, 1975).

Gopher tortoises are particularly important in the longleaf ecosystem; they excavate burrows in sandy soils common to many longleaf pine sites, feed on foliage and fruits of the lowest plant strata, and bury their eggs in the frequent sun-warmed openings (Landers and Speake, 1980; Diemer, 1986). The dens they excavate serve as refuges for at least 332 species of vertebrates and invertebrates, including rare gopher frogs and the indigo snake (Landers and Speake, 1980; Means and Campbell, 1981). Retention of snags, stumps, and downed trees as habitat components is desirable for herps (Guyer and Bailey, 1993). An often overlooked habitat component of coarse woody debris are decomposing root channels. Recent studies

(Duran, 1998) have shown the importance of decomposing root channels of pine trees as hibernacula and den sites for the state endangered black pine snake (*Pituophis melanoleucus lodingi*).

6. Short-term risks associated with management activities to restore the longleaf ecosystem

Most management activities necessary to restore structure, function, and diversity to this ecosystem carry few risks for species of special interest. In fact, some management activities, i.e., prescribed burning, are essential to their long-term persistence (Fig. 3). Fire was so pervasive in this ecosystem that species not adapted to survive in fire-created habitats were likely lost long ago. Even intense wildfires during the 1998 fire season in Florida apparently had little effect on at least one rare species, the federally endangered Rugel's pawpaw (*Deeringothamnus regelii*), whose numbers actually increased in a local population (Grace, 2004).

Periodic fire can control the size of understory hardwoods, but only annual summer burning is likely to completely remove hardwood sprouts (Waldrop et al., 1992). Burning schedules should vary to provide variable habitat conditions because not all species prefer the same habitat (Walker, 1998; Wade et al., 2000). Prescribed fire, in conjunction with appropriate timber management, can sustain or enhance biological diversity at both stand and landscape levels (Mitchell et al., 2000; Masters et al., 2003). However, burning is not always feasible and carries with it risk to human habitation, liability concerns, difficulties in obtaining burning permits, and the costs of applying, controlling, and monitoring burns (Wigley et al., 2002). In addition, how different fire regimes affect specific plants are often not known (Walker, 1998).

Herbicides can satisfy some, but not all the ecological functions of fire, e.g., they cannot scarify leguminous seeds to enhance germination nor stimulate flowering in certain plants as fire does (Brennan et al., 1998). However, newer and more selective herbicides can be used with little risk to favor herbaceous species and enhance northern bobwhite habitat (Welch et al., in press; Wigley et al., 2002), create a two-tiered stand structure by controlling understory hardwoods too large to be killed by fire



Fig. 3. Prescribed burning is essential in the longleaf ecosystem to sustain structure, function, and composition.

(Conner, 1989; Waldrop et al., 1992), and augment effects of prescribed fire in restoring longleaf ecosystems (Brockway and Outcalt, 2000). Herbicides must be used with caution or not at all in wetlands or wetland-upland ecotones, however, because little is known about their effects on reptiles and amphibians (Guyer and Bailey, 1993). Herbicides should be applied by skilled applicators who recognize important plant species to avoid unintended consequences. In addition, herbicides applied on a wide scale could result in invasion by exotics or highly competitive weed species (Clewley, 1989; Provencher et al., 1998).

Both uneven- and even-aged harvest methods successfully regenerate longleaf pine (Boyer and Peterson, 1983; Masters et al., 2003). Uneven-aged management is often promoted because it allows most of the forest structure, including high-value large trees, to be retained between harvests and provides stable habitat for some species (Franklin, 1997; Georgia Wildlife Federation, 2001). Among even-

aged systems, clearcutting, seedtree, and shelterwood systems have been used to regenerate longleaf pine. However, even-aged systems have several disadvantages. If clearcutting destroys much of the advanced seedling regeneration and ground cover, there usually is no readily available seed source. In addition, widely scattered longleaf trees retained after a seed tree harvest do not produce adequate seed to regenerate a stand. The shelterwood system is the lowest risk even-aged system for regenerating longleaf and is compatible with frequent burning to sustain herbaceous diversity (Boyer and Peterson, 1983).

Thinning is a low-risk management activity used to control stand density and promote vigor in high quality residual trees. It generally has positive effects in the longleaf ecosystem by increasing the amount of light reaching the forest floor thereby encouraging growth of many herbaceous species. Thus, thinning improves habitat for red cockaded woodpeckers (Hardesty et al., 1997), gopher tortoises (Diemer, 1986), and other

animal species that benefit from open, herbaceous-rich ecosystems.

Although most silvicultural practices, when used prudently, pose little risk to restoration goals, certain practices associated with intensive pine management, may have negative consequences. For example, mechanical site preparation using rootraking or chopping may eliminate wiregrass, as well as some endangered and threatened plant species, and may encourage invasive native or exotic species (Clewell, 1989; Provencher et al., 1998).

Bedding—the mounding of the soil surface to raise roots of planted seedlings above the water table—can fill or crush borrows of gopher tortoises and disturb underground passages used by other fossorial species (Jackson, 1989; Guyer and Bailey, 1993). Fertilization is often used in intensive forestry management but may increase the dominance of some grasses at the expense of small rosette species that inhabit spaces between the larger bunch grasses (Walker, 1985). Exotic species are a common cause of degradation of natural plant communities, and restoration practices risk introducing them to communities being restored (Clewell, 1989; Provencher et al., 1998). The South has the highest number of introduced plant species on the continent (Owen, 2002), many of which are in or near the remaining longleaf ecosystem.

Well-intentioned attempts to restore the longleaf forest may fragment habitat for endangered species. Ferral (1998) noted that the large-scale conversion of slash pine (*Pinus elliottii*) stands to longleaf pine reduced the area of foraging habitat for red-cockaded woodpeckers and indirectly affected their reproduction and cluster status. Where conversion of off-site species to longleaf forest is a management emphasis, managers should evaluate potential effects of a new landscape configuration on endangered species.

Far more important than the risk that silvicultural practices may pose to rare species, however, is the risk of no management at all. At the local level, exclusion of fire places many species at risk. For example, consider the dependence of many herpetofauna on isolated wetlands. Carolina bays, cypress ponds, shrub bogs, and other non-alluvial isolated wetlands are primary natural lentic habitats embedded in the longleaf ecosystem (Sharitz and Gresham, 1998). They are critical habitat for amphibian breeding and larval development, as well as serving as important

cover and foraging habitat for numerous reptiles (Dodd, 1992; Russell and Hanlin, 1999). Without periodic fire, hardwood succession in the ecotones between these wetlands and uplands threatens the habitats of many herpetofauna (Means and Campbell, 1981; Russell et al., 1999).

Most forestry practices used to manage and restore longleaf forests are of low risk to rare species in this ecosystem. Furthermore, the risk posed by these practices depends on the intensity, frequency, and scope of their application. Clearly, the benefits of active management far outweigh the long-term risks of doing nothing. In fact, without active management the eventual loss of the remaining portions of this once expansive ecosystem would be certain.

7. Restoring the longleaf ecosystem

7.1. Restoration realities

Restoration of the longleaf ecosystem involves restoring the structure and function of the ecosystem, as well as the ecological processes key to its maintenance, while sustaining or enhancing its native diversity. This is a daunting task and raises many questions. What structure and composition will enable us to know when restoration has been achieved? Given the nature of our society and economic realities, how much can actually be restored, and how much restoration will be enough to secure a future for its many rare plants and animals? How will restoration success at different biogeographic scales be measured? How can long-term success of restoration efforts be assured?

In actuality, restoring an ecosystem to a specific condition is neither a realistic nor relevant goal. Information is often lacking on the range of variation, dynamics, and characteristics of the ecosystem being restored. Thus, it is impossible to know the exact condition of an ecosystem at an earlier time or the disturbance history that shaped it (White and Walker, 1997). There also are many embedded communities and habitats within the longleaf ecosystem, and the restoration goals and needs for each may differ.

Instead of attempting to recreate an exact replica of a historical condition, restoration ecologists and

managers should study an ecosystem's past disturbance history, both natural and anthropogenic, and develop general intuitive models of a desired future condition for that ecosystem (Walker, 1993; White and Walker, 1997). Once this desired condition is achieved, it can be maintained with adaptive management using proven and new silvicultural practices (Van Lear and Wurtz, 2005).

Because much of the longleaf ecosystem exists in small isolated fragments, it will be difficult to achieve restoration of many declining species on a significant scale (Simberloff, 1993). Many scattered fragments have not been burned as needed to retain the open and diverse nature of the historical landscape. Most of the remnants of the longleaf ecosystem are on private land, and these landowners have varied goals (Landers et al., 1995).

Realistically, it may be only possible to double the current acreage of the ecosystem in the next few decades. If accomplished, about 6% of the pre-Columbian acreage of the longleaf ecosystem would exist, rather than 3%. Although this may improve survival prospects for many species, it probably will not be enough to prevent extinction for some extremely rare, isolated species. Genetic diversity has probably already declined in small isolated populations, further weakening species already at risk (Soule, 1980; Terborgh and Winter, 1980).

Private landowners must benefit from recovery of the longleaf ecosystem to ensure long-term restoration success (Landers et al., 1995; Franklin, 1997). There must be an economic incentive for private landowners, which is derived primarily from harvesting longleaf timber. Harvesting restrictions would be a disincentive to many landowners and encourage further loss of longleaf on private lands. If our society becomes more environmentally conscious as it matures, as speculated by Kimmins (1992), enlargement of the ecosystem may be possible.

7.2. Fire as a restoration agent

The key ecological process, fire, must be central to any restoration management strategy. Most of the diversity in the longleaf ecosystem is in the ground layer, and responses of many species in this layer to burning have not been documented. Further research is needed to monitor responses of different species to

burning, as well as other management activities, to ensure restoration success (Walker, 1998).

Burning is increasingly limited by factors associated with our expanding population and economy. Efforts to increase the capability to use fire in the longleaf ecosystem must be addressed through various means, including (1) land acquisition of critical forest core sites, (2) promotion of urban growth patterns that minimize forest parcelization and fragmentation, (3) implementation of forestry practices that maintain and restore biological diversity, and (4) formation of state Prescribed Fire Councils to reduce institutional and regulatory barriers to burning (The Nature Conservancy, 2003).

7.3. Partnerships

Partnerships are key to accomplishing restoration goals and there are numerous examples of effective partnerships. The Longleaf Alliance—a consortium of federal and state government agencies, large and small private landowners, conservation groups, universities, and others—has embarked on a major effort to restore the longleaf ecosystem, not only on public lands, but private lands as well. It is a regional effort that promotes the ecological and economic values of longleaf ecosystems (Landers et al., 1995; Gjerstad et al., 1998). The U.S. Fish and Wildlife Service partners with non-federal landowners through programs aimed primarily at endangered species, such as the Safe Harbor Program that also encourage restoration of healthy longleaf ecosystems. Private research foundations such as the Tall Timbers Research Station and the Joseph W. Jones Ecological Research Center partner with scientists and managers from universities, federal and state agencies, industries, conservation groups, and landowners in the search for answers to management questions that will help expand and restore this ecosystem (Lowcountry Conservation Project Plan, 2003; Masters et al., 2003).

Efforts to link fragments of longleaf habitat will be necessary to slow or prevent further species decline. These efforts take many forms, ranging from a variety of conservation easements and land trusts to cost-share agreements. The Longleaf Alliance administers four cost-share programs that target the restoration and management of longleaf pine ecosystems and give priority to funding landowners who meet a variety of

criteria, including potential to contribute to connecting corridors between longleaf fragments. Other criteria include willingness to restore native understory communities, restore and manage for species of special conservation concern, including listed species, and maintain forests in longleaf pine for extended periods. Funding for these cost-share agreements is currently provided by the Partners for Fish and Wildlife program of the U.S. Fish and Wildlife Service, the National Fish and Wildlife Foundation, the Georgia Forestry Commission, and the Southern Company.

Private and public interests must cooperate to return the longleaf ecosystem and its rich array of species to the prominent role it historically played in the Southern landscape. To be successful in the long-term, restoration efforts should benefit society in general and private landowners in particular (Landers et al., 1995). Without economic benefits, long-term and broad scale conservation projects are likely doomed to failure (Kimmins, 1992; Oliver, 1992).

7.4. *Implications for species at risk*

Much more research is needed regarding the distribution, population dynamics, habitat requirements, and response to management of rare species, both plant and animal, in the longleaf ecosystem (Walker, 1998; Trani, 2002). This information is essential before restoration efforts are truly science based and habitat for species with narrow niches can be restored or protected (Walker, 1993). Much is known about some of the more highly publicized species, i.e., the red-cockaded woodpecker and the gopher tortoise. For example, recent scientific gains have led to physical restoration of red-cockaded woodpeckers to uninhabited or under-inhabited suitable habitat through creation of artificial cavities and re-location of birds from established populations (Walters et al., 1995; Hess and Costa, 1995; Carter et al., 1995). Gopher tortoises also have been moved from habitats at risk to more protected and suitable habitat (Robert Bonnie, personal communication). Attempts to reintroduce less-studied species of special concern to unoccupied suitable habitat have had variable results. Eastern indigo snakes were introduced into several areas in south Alabama and the

panhandle of Florida with little success (Dan Speake, personal communication).

The establishment of mitigation banks or reserves for both gopher tortoises and red-cockaded woodpeckers has been a positive step in the preservation of these species. Cost-effective techniques for restoring understory plants are being researched and developed today by several groups, including the Jones Ecological Research Center, The Longleaf Alliance, Tall Timbers Research Station, the U.S. Fish and Wildlife Service, the U.S. Forest Service, The Nature Conservancy, the Department of Defense, and the USDA Natural Resources Conservation Service, among others. Much of the initial restoration efforts will be conducted on public lands.

8. Summary

The longleaf ecosystem was shaped over millennia by frequent, low-intensity surface fires ignited by man and lightning. This fire regime sustained the ecosystem's high biodiversity and produced prairies, savannas, and open woodlands.

The extent of the ecosystem declined dramatically when the longleaf pine timber was logged during the 19th and 20th centuries without provision for regeneration. It has continued to decline as fire exclusion, conversion to agriculture and other tree species, development, and other factors have taken their toll. A policy of fire exclusion initiated in the early decades of the 20th century has been especially damaging, as it created an uncharacteristic fire regime that allowed the longleaf ecosystem to succeed to a hardwood or mixed pine-hardwood forest. Now only 1.2 million ha remain and hundreds of plant and animal species are in peril. Over 30 species are listed as federally endangered or threatened.

Restoration efforts are underway to reestablish the historical fire regime that characterized the ecosystem for millennia. Restoration activities generally pose low short-term risk to imperiled species and are far out-weighted by the long-term loss of habitat that accompanies no management of longleaf forests. Research continues to learn the distribution, population dynamics, and habitat requirements of rare species, and the recovery methods needed for these populations. However, because it is impossible to

measure the degree to which any mix of cultural practices simulates the historical disturbance regime of a particular ecosystem, restoration efforts are as much art as science. Biological complexity and the practical realities of society in the 21st century suggest that restoration of the longleaf ecosystem will require perseverance and flexible, adaptive management that integrates knowledge gained from scientists, resource managers, and other sources.

References

- Bond, W.J., Van Wilgen, B.W., 1996. Fire and Plants. Chapman & Hall, NY.
- Bonnicksen, R., Standford, D., Fastook, J.L., 1987. Environmental change and developmental history of human adaptive patterns: the Paleoindian case. In: Ruddiman, W.E., Wright, Jr., H.E. (Eds.), The Geology of North America and Adjacent Oceans During the Last Deglaciation, vol. K-3. Geological Society of America, Boulder, CO, pp. 403–424.
- Bonnicksen, T.M., 2000. America's Ancient Forest: From the Ice Age to the Age of Discovery. John Wiley & Sons, NY.
- Bowman, R., Huh, C., 1995. Tree characteristics, resin flow, and heartwood rot in pines (*P. palustris*, *Pinus elliotii*), with respect to red-cockaded woodpecker cavity excavation, into hydrologically-distinct Florida flatwood communities. In: Kulhavy, D.L., Hooper, R.G., Costa, R. (Eds.), Red-cockaded Woodpecker: Recovery, Ecology and Management, Center for Applied Studies in Forestry. Stephen F. Austin University, pp. 415–426.
- Boyer, W.D., Peterson, D.W., 1983. Longleaf pine. In: Burns, R.M. (Tech. Comp.), Silvicultural Systems for the Major Forest Types of the United States. USDA Forest Service Agricultural Handbook, vol. 445. Washington, DC, pp. 153–156.
- Boyer, W.D., 1990. *Pinus palustris* Mill. Longleaf pine. In: Burns, R.M., Honkala, B.H. (Technical Coordinators), Silvics of North America, vol. 1, Conifers. USDA Forest Service. Washington, DC, pp. 405–412.
- Brennan, A., Engstrom, R.T., Palmer, W.E., Herman, S.M., Hurst, G.A., Burger, L.W., Hardy, C.L., 1998. Whither wildlife without fire? Transactions of the 63rd North America. In: Proceedings of the Wildlife and Natural Resources Conference of Wildlife Management Institute. Washington, DC, pp. 402–414.
- Brockway, D.G., Outcalt, K.W., 2000. Restoring longleaf pine-wiregrass: hexazinone application enhances effects of prescribed fire. Forest Ecol. Manage. 96, 167–183.
- Brown, J.K., 2000. Introduction and fire regimes. In: Brown, J.K., Smith, J.K. (Eds.), Wildland Fire in Ecosystems: Effects of Fire on Flora. USDA Forest Service RMRS-GTR-42, vol. 2, pp. 1–8.
- Carrie, N.R., Wagner, R.O., Moore, K.R., Sparks, J.C., Keith, E.L., Melder, C.A., 2002. Winter abundance of and habitat use by Henslow's sparrows in Louisiana. Wilson Bull. 114, 221–226.
- Carroll, W.C., Kapeluck, P.R., Harper, R.A., Van Lear, D.H., 2002. Background paper: historical overview of the southern forest landscape and associated resources. In: Wear, D.N., Greis, J.G. (Eds.), Southern Forest Resource Assessment. USDA Forest Service GTR SRS-53, pp. 583–606.
- Carter, J.H., Engstrom, R.T., Purcell, P.M., 1995. Use of artificial cavities for red-cockaded woodpecker mitigation: two studies. In: Kulhavy, D.L., Hooper, R.G., Costa, R. (Eds.), Red-cockaded Woodpecker: Recovery, Ecology and Management, Center for Applied Studies in Forestry. Stephen F. Austin University, pp. 372–379.
- Champion, T., Gamble, C., Shennan, S., Whittle, A., 1984. Prehistoric Europe. Academic Press, London.
- Clewell, A.F., 1989. Natural history of wiregrass (*Aristida stricta* Michx., Graminae). Nat. Areas J. 9, 223–233.
- Conner, R.N., 1989. Injection of 2,4-D to remove hardwood mid-story within red-cockaded woodpecker colony areas. USDA Forest Service Research Pa SO-251. New Orleans, LA.
- Connor, R.N., Rudolph, D.C., 1995. Excavation dynamics and use patterns of red-cockaded woodpecker cavities: relationships with cooperative breeding. In: Kulhavy, D.L., Hooper, R.G., Costa, R. (Eds.), Red-cockaded Woodpecker: Recovery, Ecology and Management, Center for Applied Studies in Forestry. Stephen F. Austin University, pp. 343–352.
- Crocker Jr., T.C., 1987. Longleaf Pine, a History of Man and a Forest. USDA Forest Service Southern Forest Experiment Station Forestry Report R8-FR 7.
- Culberson, L.C., 1993. Arrowheads and Spearpoints in the Prehistoric Southeast. University of Mississippi Press, Oxford, MS.
- Delcourt, P.A., Delcourt, H.R., 1979. Late Pleistocene and Holocene distributional history of the deciduous forest in the southeastern United States. In: Veroffentlichungen des Geobotanischen Instituts der ETH, vol. 68, Zurich, Germany, pp. 79–107.
- Delcourt, P.A., Delcourt, H.R., 1985. Quaternary palynology and vegetational history of the Southeast United States. In: Programme for Quaternary Studies of the Southeast U.S., University of Tennessee, Knoxville, TN.
- Delcourt, H.R., Delcourt, P.A., 1997. Pre-Columbian Native American use of fire on southern Appalachian landscapes. Conserv. Biol. 11, 1010–1014.
- Delcourt, H.R., 2002. Forests in Peril: Tracking Deciduous Trees from Ice-Age Refuges into the Greenhouse World. McDonald & Woodward, Blacksburg, VA.
- Diemer, J.E., 1986. The ecology and management of the gopher tortoise in the southeastern United States. Herpetologica 42, 125–133.
- Dodd Jr., C.K., 1992. Biological diversity of a temporary pond herpetofauna in north Florida sandhills. Biodivers. Conserv. 1, 125–142.
- Dobyns, H.F., 1983. Their Numbers Became Thinned: Native American Population Dynamics in Eastern North America. University of Tennessee Press, Knoxville, TN.
- Doolittle, W.E., 1992. Agriculture in North America on the eve of contact: a reassessment. Ann. Assoc. Am. Geogr. 82, 386–401.
- Duran, M., 1998. Herp Spotlight: Black Pine Snake. Mississippi Herpetological Atlas, vol. 1. <http://www.cfr.msstate.edu/gap/mhaneews3.html> (accessed 10/14/04).
- Edwards, R.L., Merrill, A.S., 1977. A reconstruction of the Continental Shelf areas of Eastern North America for the times 9,500

- BP and 12,000 BP. Archaeology of Eastern North America, Eastern States Archaeology Federation, vol. 5. Bethlehem, CT, pp. 1–43.
- Engstrom, R.T., 1993. Characteristic mammals and birds of longleaf pine forests. Tall Timbers Fire Ecol. Conf. 18, 127–138.
- Engstrom, R.T., Kirkman, L.K., Mitchell, R.J., 2001. Natural history: longleaf pine-wiregrass ecosystem. In: Wilson, J.R. (Ed.), The Fire Forest: Longleaf Pine-Wiregrass Ecosystem. Georgia Wildlife Natural Georgia Series 8 (no. 2). Georgia Wildlife Federation, pp. 5–18.
- Ferral, D.P., 1998. Habitat quality and the performance of red-cockaded woodpecker groups in the South Carolina Sand Hills. M.S. Thesis. Clemson University, Clemson, SC.
- Franklin, R.M., 1997. Stewardship of longleaf pine forests: a guide for landowners. Longleaf Alliance Report no. 2. A Joint Project of the Longleaf Alliance. Auburn University and Clemson University Cooperative Extension Service.
- Frost, C.C., 1993. Four centuries of changing landscape patterns in the longleaf pine ecosystem. Tall Timbers Fire Ecol. Conf. 18, 17–44.
- Garner, J.A., Landers, J.L., 1981. Food and habitat of the gopher tortoise in southwestern Georgia. Proc. Annu. Conf. Southeast. Assoc. Fish Wildl. Agencies 35, 12–134.
- Georgia Wildlife Federation, 2001. The fire forest: longleaf pine-wiregrass ecosystem. Georgia Wildlife Natural Georgia Series, vol. 8 (no. 2). Georgia Wildlife Press.
- Gjerstad, D.H., Johnson, R., Hains, M., 1998. The longleaf alliance: a regional effort promoting the ecological and economic values of longleaf ecosystems. In: Proceedings of the Longleaf Pine Ecosystem Restoration Symposium, Longleaf Alliance Report no. 3. Auburn University, Auburn, AL, pp. 34–36.
- Grace, S.L., 2004. Post wildfire response of plant species of concern and exotic species following the 1998 Florida wildfires. http://www.flame.fl-dof.com/joint_fire_sciences/dem009.html (accessed 18 August 2004).
- Gremillion, K.J., 1987. Plant remains from the Fredericks, Wall sites. In: Dickens, Jr., R.S., Ward, H.T., Davis, S. (Eds.), The Siouan Project: Seasons I and II. University of North Carolina, Anthropology Department, Chapel Hill, NC, pp. 275–277.
- Guyer, G., Bailey, M.A., 1993. Amphibians and reptiles of longleaf pine communities. Tall Timbers Fire Ecol. Conf. 18, 139–157.
- Hamel, P.B., 1992. Land Manager's Guide to the Birds of the South. The Nature Conservancy, Chapel Hill, NC.
- Hardesty, J.L., Gault, K.E., Percival, F.P., 1997. Ecological correlates of red-cockaded woodpecker (*Picoides borealis*) foraging preference, habitat use, and home range size in northwest Florida (Elgin Air Force Base). Final Report Research Work Order 99, Florida Cooperative Fish and Wildlife Research Unit. University of Florida, Gainesville, FL.
- Hardin, E.D., White, D.L., 1989. Rare vascular plant taxa associated with wiregrass (*Aristida stricta*) in the southeastern United States. Nat. Areas J. 9, 234–245.
- Hess, C.A., Costa, R., 1995. Augmentation from the Apalachicola National Forest: the development of a new management technique. In: Kulhavy, D.L., Hooper, R.G., Costa, R. (Eds.), Red-cockaded Woodpecker: Recovery, Ecology and Management, Center for Applied Studies in Forestry. Stephen F. Austin University, pp. 385–388.
- Hudson, C., 1976. The Southeastern Indians. University of Tennessee Press, Knoxville, TN.
- Jackson, D.R., 1989. The fauna of gopher tortoise burrows. In: Diemer, J.E. (Ed.), Proceedings of the Gopher Tortoise Relocation Symposium, Florida Game and Fresh Water Fish Communication. Technical Report 5. Tallahassee, FL.
- Johnson, A.S., Hale, P.E., 2002. The historical foundations of prescribed burning for wildlife: a southeastern perspective. In: Ford, W.M., Russell, K.R., Moorman, C.E. (Eds.), The Role of Fire in Nongame Wildlife Management and Community Restoration: Traditional Uses and New Directions. USDA Forest Service Gen. Technical Report NE-288, pp. 11–23.
- Kimmins, H., 1992. Balancing Act: Environmental Issues in Forestry. UBC Press, Vancouver, BC.
- Komarek Sr., E.V., 1974. Effects of fire on temperate forests and related ecosystems: southeastern United States. In: Kozlowski, T.T., Ahlgren, C.E. (Eds.), Fire and Ecosystems. Physiological Ecology: A Series of Monographs, Texts, and Treatises. Academic Press, NY, pp. 251–277.
- Kurten, B., 1972. The Ice Age. G.P. Putnam & Sons, NY.
- Landers, J.L., Speake, D.W., 1980. Management needs of sandhill reptiles in southern Georgia. Proc. Annu. Conf. Southeast. Assoc. Fish Wildl. Agencies 34, 515–529.
- Landers, J.L., 1991. Disturbance influences on pine traits in the southeastern United States. Tall Timbers Fire Ecol. Conf. 17, 61–98.
- Landers, J., Van Lear, L., Boyer, D.H., William, D., 1995. The longleaf pine forests of the Southeast: requiem or renaissance? J. Forestry 9, 39–44.
- Lovell, W., 1992. "Heavy shadows and black night": disease and depopulation in colonial Spanish America. Ann. Assoc. Am. Geographers 82, 426–443.
- MacDonald, L.A., Mushinsky, H.R., 1988. Foraging ecology of the gopher tortoise, *Gopherus polyphemus*, in a sandhill habitat. Herpetologica 44, 345–353.
- Masters, R.E., Robertson, K., Palmer, B., Cox, J., McGorty, K., Green, L., Ambrose, C., 2003. Red Hills Forest Stewardship Guide. Miscellaneous Publication no. 12. Tall Timbers Research Station, Tallahassee, FL.
- McGuire, J.P., Mitchell, R.J., Moser, E.B., Pecot, D.H., Gjerstad, D.H., Hedman, C.W., 2001. Gaps in a gappy forest: plant resources, longleaf pine regeneration, and understory response to tree removal in longleaf pine savannas. Can. J. Forest Res. 31, 765–778.
- Means, D.B., Campbell, H.W., 1981. Effects of prescribed fire on amphibians and reptiles. In: Wood, G.W. (Ed.), Prescribed Fire and Wildlife in Southern Forests. Belle Baruch Forest Science Institute, Clemson University, Georgetown, SC, pp. 89–96.
- Mount, R.H., 1975. The Reptiles and Amphibians of Alabama. The Agricultural Experiment Station, Auburn University.
- Mitchell, R.J., Neel, W.L., Hiers, J.K., Cole, F.T., Atkinson, J.B., 2000. A Model Management Plan for Conservation Easements in Longleaf Pine-Dominated Landscapes. J.W. Jones Ecological Research Center, Newton, GA.

- Myers, R.K., Van Lear, D.H., 1997. Hurricane-fire interactions in coastal forests of the South: a review and hypothesis. *Forest Ecol. Manage.* 103, 265–276.
- Noss, R.F., 1989. Longleaf pine and wiregrass: keystone components of an endangered ecosystem. *Nat. Areas J.* 9, 234–235.
- Noss, R.F., LaRoe, E.T., Scott, J.M., 1995. Endangered ecosystems of the United States: a preliminary assessment of loss and degradation. USDI National Biological Service, Biological Report 28.
- Oliver, C.D., 1992. Achieving and maintaining biodiversity and economic productivity. *J. Forestry* 90, 20–25.
- Outcalt, K.W., Sheffield, R.M., 1996. The longleaf pine forest: trends and current conditions. USDA Forest Service Southern Research Station. Resource Bulletin SRS-9.
- Outcalt, K.W., Wade, D.D., 2004. Fuel management reduces mortality from wildfire. *South J. Appl. Forestry* 28, 28–34.
- Owen, W., 2002. The history of native plant communities in the South. In: Wear, D.N., Greis, J.G. (Eds.), *Southern Forest Resource Assessment*. USDA Forest Service, GTR SRS-53, pp. 47–62.
- Peet, R.K., Allard, D.J., 1993. Longleaf pine-dominated vegetation of the southern Atlantic and eastern Gulf Coast region, USA. *Tall Timbers Fire Ecol. Conf.* 18, 45–82.
- Platt, W.J., Rathbun, S.L., 1993. Dynamics of an old growth longleaf pine population. *Tall Timbers Fire Ecol. Conf.* 18, 275–298.
- Provencher, L., Rogers, H.L., Galley, K.E.M., Herring, B.J., Sheehan, J., Nortrup, N.M., McAdoo, S.J., Brennan, L.A., 1998. Post-treatment analysis of restoration effects on soils, plants, arthropods, and birds in sandhill systems at Elgin Air Force Base, Florida. Annual Report to Natural Resources Division, Elgin Air Force Base, Niceville, FL. Public Lands Programme. The Nature Conservancy, Gainesville, FL.
- Pyne, S.J., Andrews, P.L., Laven, R.D., 1996. *Introduction to Wildland Fire*, second ed. John Wiley & Sons, NY.
- Pyne, S., 1997. *Fire in America: a cultural history of Wildland and Rural fire*, second ed. University of Washington Press, Seattle, WA, 680 pp.
- Pyne, S.J., 2001. *The Year of the Fires: The Story of the Great Fires of 1910*. Penguin Books, NY.
- Rostlund, E., 1957. The myth of a natural prairie in Alabama: an interpretation of historical records. *Ann. Assoc. Am. Geographers* 47, 392–411.
- Russell, K.R., Hanlin, H.G., 1999. Aspects of the ecology of worm snakes (*Carphophis amoenus*) associated with small isolated wetlands in South Carolina. *J. Herpetol.* 33, 339–344.
- Russell, K.R., Van Lear, D.H., Gynn Jr., D.C., 1999. Prescribed fire effects on herpetofauna: review and management implications. *Wildlife Soc. Bull.* 27, 374–384.
- Sharitz, R.R., Gresham, C.A., 1998. Pocosins and Carolina Bays. In: Messina, M.G., Conner, W.H. (Eds.), *Southern Forested Wetlands: Ecology and Management*. Lewis Publishers, Boca Raton, FL, pp. 343–378.
- Simberloff, D., 1993. Species-area and fragmentation effects on old-growth forests: prospects for longleaf pine communities. *Tall Timbers Fire Ecol. Conf.* 18, 1–14.
- Smith, M.T., 1987. *Archeology of aboriginal culture change in the Interior Southeast: depopulation during the early historic period*. University of Florida Press, Gainesville, FL.
- Soule, M.E., 1980. Thresholds for survival: maintaining evolutionary fitness and potential. In: Soule, M.E., Wilcox, B.A. (Eds.), *Conservation Biology*. Sinauer Assoc., Sunderland, MA, pp. 151–169.
- Stanturf, J.A., Wade, D.D., Waldrop, T.A., Kennard, D.K., Achtemeier, G.L., 2002. Background paper: fire in southern forest landscapes. In: Wear, D.N., Greis, J.G. (Eds.), *Southern Forest Resource Assessment*. USDA Forest Service GTR SRS-53, pp. 607–630.
- Stoddard Sr., H.L., 1931. *The Bobwhite Quail: Its Habits, Preservation, and Increase*. Charles Scribner's Sons, NY.
- Terborgh, J., Winter, B., 1980. Some Causes of Extinction. In: Soule, M.E., Wilcox, B.A. (Eds.), *Conservation Biology*. Sinauer Assoc., Sunderland, MA, pp. 119–133.
- The Nature Conservancy, Ducks Unlimited, The Conservation Foundation, Lowcountry Open Land Trust, South Carolina Coastal Conservation League. The J.W. Jones Ecological Research Center, and Clemson University. *Lowcountry Forest Conservation Partnership Plan*. A grant funded by the Doris Duke Charitable Foundation.
- Trani, M.K., 2002. Terrestrial ecosystems. In: Wear, D.N., Greis, J.G. (Eds.), *Southern Forest Resource Assessment*. USDA Forest Service GTR SRS-53, pp. 1–45.
- Tucker, J. W., Robinson, W.D., 2000. Influence of season and frequency of fire on Bachman's sparrows and Henslow's sparrows in longleaf pine forests of the Gulf coastal plain. Final Report. Department of Biological Sciences, Auburn University. USDA Forest Service Southern Research Station.
- U.S. Fish and Wildlife Service, 2003. Longleaf pine ecosystem fact sheet. <http://www.southeast.fws.gov/pfwpine.html> (accessed 4 November 2003).
- Van Lear, D.H., Wurtz, T.L., 2005. Cultural practices for maintaining ecosystem function. In: Stanturf, J.A., Madsen, P. (Eds.), *Restoration of Temperate and Boreal Forests*. CRC Press, Boca Raton, FL, pp. 173–192, Chapter 11.
- Varner, J.M., Kush, J.S., Meldahl, R.S., 1999. Old-growth montane longleaf pine stand structure: a preliminary assessment. In: Haywood, J.D. (Ed.), *Proceedings of the Tenth Biennial Southern Silvicultural Research Conference*. USDA Forest Series GTR SRS-30, pp. 606–608.
- Verano, J.W., Ubelaker, D.H. (Eds.), 1992. *Disease and Demography in the Americas*. Smithsonian Institution Press, Washington, DC.
- Wade, D.D., Lundsford, J.D., 1989. *A Guide for Prescribed fire in Southern Forests*. USDA Forest Service Southern Region. Technical Publication R8-TP 11.
- Wade, D.D., Brock, B.L., Brose, P.H., Grace, J.D., Hoch, G.A., Patterson III, W.A., 2000. Fire in eastern ecosystems. In: Brown, J.K., Smith, J.K. (Eds.), *Wildland Fire in Ecosystems: Effects of Fire on Flora*. USDA Forest Service RMRS-42 (Chapter 4).
- Wahlenberg, W.G., 1946. *Longleaf pine: Its use, ecology, regeneration, protection, growth, and management*. C.L. Pack Forestry Foundation and USDA Forest Service. Washington, DC.

- Waldrop, T.A., White, D.L., Jones, S.M., 1992. Fire regimes for pine-grassland communities in the southeastern United States. *Forest Ecol. Manage.* 47, 195–210.
- Walker, J.L., 1985. Species Diversity and Production in Pine-Wiregrass Savannas of the Green Swamp, North Carolina. Ph.D. Dissertation. University of North Carolina, Chapel Hill, NC.
- Walker, J.L., 1993. Rare vascular plant taxa associated with the longleaf pine ecosystem. *Tall Timbers Fire Ecol. Conf.* 18, 105–126.
- Walker, J., 1998. Ground layer vegetation in longleaf pine landscapes: an overview for restoration management. In: *Proceedings of the Longleaf Pine Ecosystem Restoration Symposium*. Longleaf Alliance Report no. 3, pp. 2–13.
- Walters, J.R., Robinson, P.P., Starnes, W., Goodson J., 1995. The relative effectiveness of artificial cavities in inducing the formation of new groups of red-cockaded woodpeckers. In: Kuhlavy, D.L., Hooper, R.G., Costa, R. (Eds.), *Red-cockaded Woodpecker: Recovery, Ecology and Management*, Center for Applied Studies in Forestry. Stephen F. Austin University, pp. 367–371.
- Ware, S., Frost, C.C., Doerr, P.D., 1993. Southern mixed hardwood forest: the former longleaf pine forest. In: Martin, W.H., Boyce, S.G., Echternacht, A.C. (Eds.), *Biodiversity of the Southeastern United States: Lowland Terrestrial Communities*. John Wiley & Sons, NY, pp. 447–493.
- Watts, W.A., 1980. Late-Quaternary vegetation history at White Pond on the inner coastal plain of South Carolina. *Q. Res.* 13, 187–199.
- Wear, D.N., 2002. Land use. In: Wear, D.N., Greis, J.G. (Eds.), *Southern Forest Resource Assessment*. USDA Forest Service GTR SRS-53, pp. 153–173.
- Wear, D.N., Greis, J.G. (Eds.), 2002. *Southern Forest Resource Assessment*. USDA Forest Service GTR SRS-53.
- Welch, J.R., Miller, K.V., Palmer, W.E., Harrington, T.B., in press. Response of understory vegetation important to northern bobwhites following Imazapyr and mechanical treatments. *Wildlife Soc. Bull.*
- Westbrooks, R., 1998. *Invasive Plants, Changing the Landscape of America: Fact Book*. Federal Interagency Committee for the Management of Noxious and Exotic Weeds, Washington, DC.
- White, P.S., Wilds, S.P., Thunhorst, G.A., 1998. Southeast. In: Mac, M.J., Opler, P.A., Puckett, C.E. (Eds.), *Status and Trends of the Nation's Biological Resources*. USDI Geological Survey, Reston, VA, pp. 255–314.
- White, P.S., Walker, J.L., 1997. Approximating nature's variation: selecting and using reference information in restoration ecology. *Restor. Ecol.* 5, 338–349.
- Wigley, T.B., Miller, K.V., deCalesta, D.S., Thomas, M.W., 2002. Herbicides as an alternative to prescribed burning for achieving wildlife management objectives. In: Ford, W.M., Russell, K.R., Moorman, C.E. (Eds.), *The Role of Fire in Nongame Wildlife Management and Community Restoration: Traditional Uses and New Directions*. USDA Forest Service GTR NE-288, pp. 124–138.
- Williams, M., 1989. *Americans and their Forests—A Historical Geography*. Cambridge University Press, NY.