Chapter 10

Restoring the Ground Layer of Longleaf Pine Ecosystems

Joan L. Walker and Andrea M. Silletti

The longleaf pine ecosystem includes some of the most species-rich plant communities outside of the tropics, and most of that diversity resides in the ground layer vegetation. In addition to harboring many locally endemic and otherwise rare plant species (Peet this volume) and enhancing habitat for the resident fauna (Costa and DeLotelle this volume), the ground layer vegetation produces fine fuel needed to carry low-intensity surface fires that perpetuate the ecosystem. Ecosystem restoration requires the restoration of both the ground layer plant community and the pine canopy.

Ground layer restoration in longleaf pine communities is an area of active investigation, through both adaptive management projects and formal research. However, there is no restoration manual for the longleaf pine community. Instead, restoration practitioners develop their action plans based on an ecological reference model and project goals, and achieve their objectives using conventional natural resources management and horticultural methods. Given the natural heterogeneity of the longleaf pine ecosystem at multiple scales and the differences imposed by a varied land use history, one could argue that there never will be a manual to adequately describe or prescribe restoration protocols for all situations; however, we believe there are general patterns within this ecological system that can guide restoration protocol development. In addition, restorationists have practical experience that is not documented in the peer-reviewed literature at this time but nevertheless converges on some necessary steps for successful restoration. In this chapter we summarize the general lessons learned from ongoing restoration efforts, and discuss ecological aspects of the ground layer vegetation that guide us in extrapolating this information to other sites. Our purpose is to share information so that we might advance the restoration of the ground cover in longleaf pine communities by minimizing avoidable mistakes and by identifying critical information needs.

In the first section we provide an overview of the ground cover vegetation in the longleaf pine ecosystem. We then describe extant conditions in longleaf pine sites often targeted for restoration, including the ways they differ from reference conditions and their derivation from widespread historical land uses. The next two sections summarize lessons learned from research and restoration projects that emphasize (1) altering canopy structure to favor ground-layer restoration or (2) starting new populations of ground cover species. We close

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with an assessment of information needed to advance ground cover restoration in the longleaf pine ecosystem.

Our review of existing restoration projects shows that they are being conducted on a relatively narrow subset of possible longleaf pine habitats. Significant projects we know of are concentrated in the Atlantic and Gulf Coastal Plains; mesic savannas and flatwoods, loamy upland sites, and xeric to subxeric sites in the Fall-line Sandhills are represented. We note the absence of projects in the middle Atlantic Coastal Plain, where few examples of remnant vegetation remain, in the mountain longleaf pine communities of the Blue Ridge and Cumberland Plateau, and in the longleaf pine–bluestem communities. Information presented in this chapter draws on projects conducted by researchers and restoration practitioners in Florida, South Carolina, and Georgia. Although many of the same issues exist in the underrepresented areas, unique species, habitats, spatial contexts, and historical land uses are bound to generate some restoration challenges that we have not addressed.

Ground Layer Vegetation in Longleaf Pine Landscapes: An Overview

Throughout the range of longleaf pine the general picture of a frequently burned high-quality natural area shows a predominantly herbaceous ground layer dominated by grasses with a diverse mixture of forbs. Woody species, if present, are short and inconspicuous. Most of the common species are sun-loving perennials with an ability to resprout after fire. Fire typically stimulates the flowering and seed production by many characteristic species, and there are apt to be species flowering at most any time during the growing season.

Grasses, legumes, and composites are the most common plant families in these burned habitats (Harcombe et al. 1993; Peet and Allard 1993; Drew et al. 1998). Other common families include the sedges, especially the beak rushes (*Rhynchospora* spp.), and lilies. More unusual plants include orchids and carnivorous species, often associated with wet, nutrient-poor sites.

Locally, ground layer composition and structure vary with fire frequency and soil conditions, typically characterized by soil texture and interpreted as variation in soil moisture status (Peet and Allard 1993). Overall, frequently burned sites have more species at small spatial scales than sites where fire has been eliminated; and intermediate-to-wet sites support more species than very dry sites (Peet this volume).

In spite of these general patterns, there is considerable compositional variation from one part of the region to another. Most herbaceous species have geographic ranges that are much smaller than that of longleaf pine. Species that have more or less restricted geographic ranges are known as endemic species, and the longleaf pine ecosystem has many subregional and local endemic species (Estill and Cruzan 2001; LeBlond 2001; Sorrie and Weakley 2001). As the geographic limit of a species' range is reached, it drops out of the local flora but may be replaced by an ecologically similar species. This results in changing species composition in the ground layer. Species with very small geographic distributions (narrow endemics) are prone to extinction and include some of the ground layer species that are federally listed as Endangered or Threatened (Walker 1998). Because there are important differences among sites, describing the ecologically appropriate composition for restoration must be done carefully.

Reference Models and Goals for Ground Layer

Restoration practitioners use "reference models" to describe the ecological potential for a project site. A reference model is a description of the restoration site as it may have looked and functioned in the past, before negative changes had occurred. Ideally the description answers questions about composition, structure, and function. Intact remnant patches of the target ecosystem, such as nearby "natural areas," are sometimes identified as "reference sites." They are selected to match the restoration project site with respect to geography and physical environment and are believed to represent the historic or contemporary potential conditions. Nearby environmentally similar sites are the best reference sites, but the condition of any proposed reference site may have been influenced by unknown stochastic events in the past (such as extreme weather or disturbance events) so that its condition may not represent the project site potential.

Besides using reference sites, restoration ecologists use other kinds of "reference information" to develop reference models (Table 1; White and Walker 1997). Ideally the project planner would conduct a site assessment to gather current information about the site to be restored, including a description of the underlying environmental conditions, and search for accurate historical information about the same site. Desirable historical information includes historical photographs, written descriptions, plant and animal species lists, frequency of burn in the area and under what conditions, and/or reports of significant disturbances or past land uses.

Practitioners sometimes use historical or contemporary information from other sites, or from less specific geographic areas. Though such information may be useful, it is important to remember that information about places is generally place- and time-specific. The more distant or more general the information source, the less likely it will accurately represent a specific project site and the less useful it will be for setting feasible objectives (Table 1). Egan and Howell (2001) recommend that restorationists use a combination of site analysis (same time, same place), historic information from the project site (different time, same place), and information from contemporary reference sites (same time, different place).

TABLE 1. Examples of reference information that can be used to develop a reference model.[a]

Time/space	Restoration project site	Different site or general location
Contemporary (Observed directly; change can be monitored)	(Site analysis) • Physical environment. Examples: soil type, fertility, hydrology, topographic position, etc. • Biotic environment. Examples: (1)canopy—composition, age, size class distribution, origin; (2) other vegetation—composition, species abundance, presence of exotic species • Disturbance evidence. Examples: fire scars, plow lines	(*Reference site* if it matches the conditions and geography of site to be restored) • Same as for site analysis data The nearer the site to the project site, the more likely that information can be used directly in reference model • General location information Examples: county species lists, herbarium records
	HIGH VALUE for reference model	*HIGH-MODERATE VALUE*
Historical (Snapshot of past; cannot observe change or know effect of stochastic events in the past)	(Site history) • Photographs, with dates • Written descriptions of physical and biotic conditions, past land uses or disturbances (sources: deeds, explorers' accounts, diaries and letters of previous owners)	(Historical information from different sites) • Similar to site history data • Fire scar data in general landscape or region • Regional land use history • Pollen data (prehistorical)
	HIGH VALUE	*LOW VALUE*

[a] Reference information can be classified into four categories based on geographic source of data (the site to be restored versus a different or general location) and whether the data represent current (contemporary) or historical conditions. Modified from White and Walker 1997 with permission from Blackwell.

A variety of restoration goals may be compatible with the site's ecological potential, for example, establishing fine fuels to facilitate fire use in timber management, improving habitat for a bobwhite quail, or creating an aesthetically desirable setting. Goals like these examples may be viewed as restoring a subset of the composition, structure, and function that historically characterized a site, in contrast to the ambitious goal of restoring the entire complement of species and their interactions. In practice, such "partial restoration" goals are far more likely to be achieved than "complete restoration of biodiversity" (Lockwood and Pimm 1999). The feasibility of project goals must be examined in light of the ecological capability of the restoration site including limitations imposed by spatial scale and context (White 1996), as well as the resources that are available to do the work and to maintain it (White and Walker 1997; Ehrenfield 2000).

Recent Land Uses and Legacies: Starting Points for Restoration

Altered fire regimes, plantation establishment, and conversion of forest lands to agriculture have resulted in loss of the ground cover diversity throughout the longleaf pine range (Wear and Greis 2002). Ongoing and completed restoration projects that we reviewed all fall into one of these recent land use history classes. Of these classes pine plantations are the most heterogeneous. They differ in canopy species (primarily loblolly or slash pine), in age, and in methods of establishment. Also, preplanting site histories vary, most significantly in whether they have a history of modern cultivation in contrast to continuously forested or lightly cultivated. Finally, they may have experienced a period of fire suppression. As a result of diverse management histories, plantations may resemble both agricultural sites and sites with altered fire regimes.

Although these land use groups do not represent mutually exclusive conditions, we think it useful to consider them because they differ from reference conditions in different ways and thus represent somewhat distinct challenges to restoration (Fig. 1). These largely anthropogenic disturbances have generated very different starting points in terms of physical conditions and especially of biotic legacies, which are the remnant components of the undisturbed longleaf ecosystem. Effort needed to restore a site will vary inversely with the amount of biotic legacy remaining (Fig. 2).

Altered Fire Regimes

The historical fire regime has been described as one of frequent, low-intensity surface fires. The extent of individual fire events and return interval are likely to have varied with topography, thus among different parts of the longleaf range (Frost 1998). It is assumed that most acres of longleaf pine habitat ignited by lightning burned during the early to mid-growing season, but Native American ignitions spanned the seasons (Robbins and Myers 1992). Over the last 60 years land managers have reduced the spatial extent of fires, shifted the predominant season to winter burning (which may be associated with lower intensity fires owing to high fuel moistures and low air temperatures), and reduced fire frequency or eliminated fires altogether. These practices are associated with increased densities and expanded distributions of woody species (Platt et al. 1991; Robbins and Myers 1992; Waldrop et al. 1992; Streng et al. 1993; Glitzenstein et al. 1995; Gilliam and Platt 1999; Drewa et al. 2002) and decreased abundance of herbs (Walker and Peet 1983; Peet and Allard 1993).

The hardwood component increases with fire exclusion or reduced fire frequency, but the specific composition varies both geographically and with site conditions within a landscape (Gilliam et al. 1993; Harcombe et al. 1993; Liu et al. 1997; Gilliam and Platt 1999; Varner et al. 2003). The losses in the ground cover after long periods without fire (more than two decades) are so profound that studies of extant old growth with significant fire exclusion focus almost exclusively on the woody species component (e.g., Gilliam and Christensen 1986; Gilliam et al. 1993; Gilliam

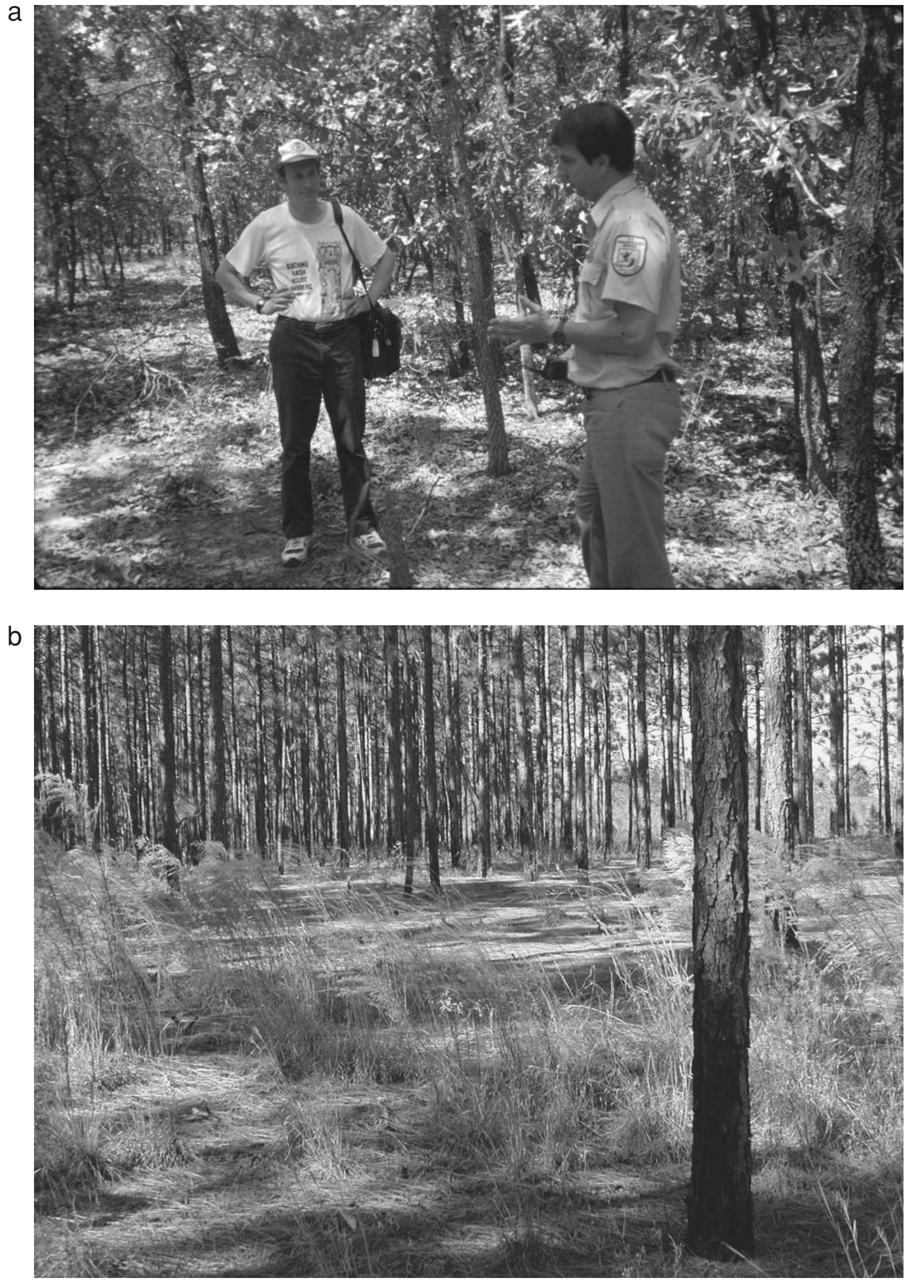


FIGURE 1. Different starting conditions for longleaf pine community restoration: (a) Xeric site where fire was excluded for about 30 years; (b) slash pine plantation on a mesic site once occupied by longleaf pine. Note increased turkey oak with fire exclusion, in contrast to absence of hardwoods in the plantation where hardwoods were controlled. Both have abundant pine straw or leaf litter, but lack a diverse herb layer.

and Platt 1999; Varner et al. 2000). Descriptions of these sites note low richness and sparse cover of herbaceous species, as in the Gilliam et al. (1993) description of the Boyd Tract, an old-growth remnant in the North Carolina sandhills: “sparse and relatively species-poor, typical of pine forest herb layers under chronic no-fire conditions.” The most abundant species

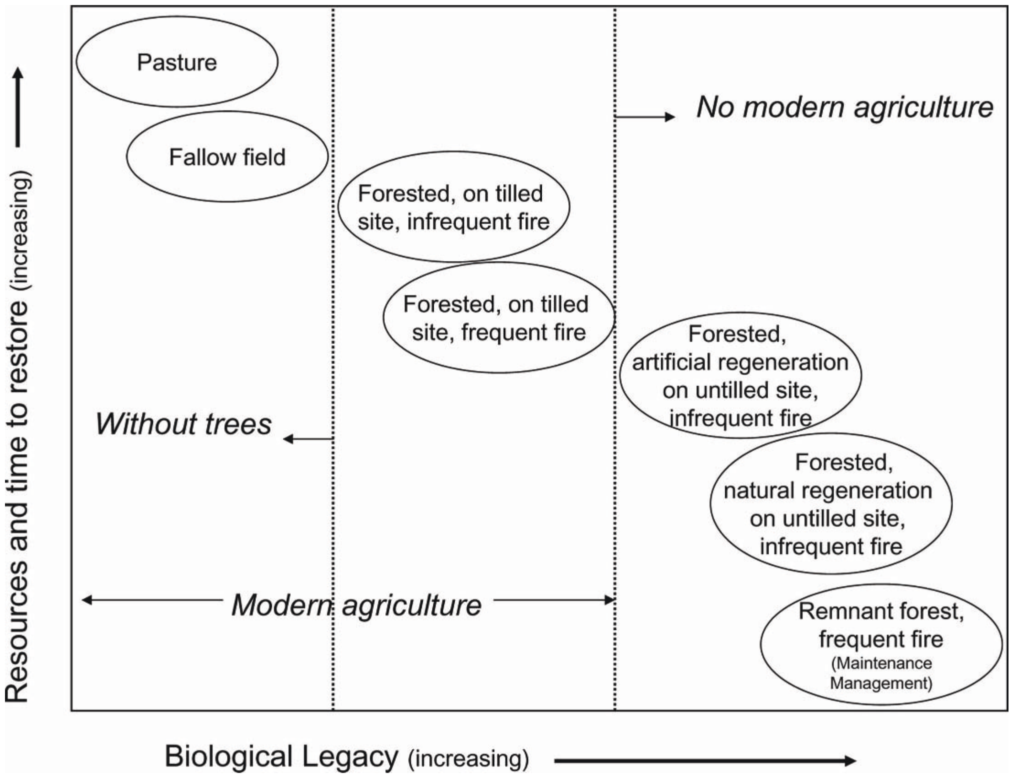


FIGURE 2. Relationship between time and resources needed for restoration and the abundance of remnant biota (biological legacy) on the site to be restored. Ovals indicate the relative position of common starting conditions as defined by land use history. Sites subjected to modern agricultural methods (repeated machine tilling) are distinct from sites that have remained in forest or escaped intense agriculture. Nonforest sites require planting trees, and all previously tilled sites are likely to require species additions. Infrequently burned forests may need hardwood removal or other canopy manipulations. The abundance of remnant biota on forested sites varies inversely with the intensity of any site preparation used for pine regeneration.

in the ground layer were seedlings of pine and oaks and other hardwoods (such as flowering dogwood, mockernut hickory, and black gum). After 45 years of fire exclusion in an old-growth site in Escambia County, Alabama, a single herb, *Acalypha virginica*, was present prior to restoration fire treatments (Varner et al. 2000). Results of fire frequency experiments, generally sampled through several fires over a decade or less, indicate that increased woody species dominance can occur in relatively short periods of time (Mehlman 1992; Beckage and Stout 2000; Glitzenstein et al. 2003).

Reduced fire frequency leads to scale-dependent decreases in herbaceous species richness: decreases in richness are most evident at small spatial scales (less than or equal to 1.0 m^2 plots) and less evident at larger scales (greater than 600 m^2). This pattern has been shown both in mesic productive savannas (Walker and Peet 1983; Glitzenstein et al. 2003) and in xeric sites (Walker 1998). Species retained at larger scales may provide on-site seed sources for restoring the ground layer via natural dispersal and establishment. How long species will persist is not known; if retention is short-lived, opportunities for restoring residual populations with fire alone will diminish with time.

Rates of species loss associated with reduced fire frequency vary with plant groups. Among the species most likely to be lost or significantly reduced in mesic to wet longleaf pine savannas are the dominant rhizomatous and bunch grasses (Walker and Peet 1983; Glitzenstein et al. 2003), species present as basal rosettes (many composites), many sedges and other small monocots, and insectivorous species. Mehlman (1992) found predictable patterns of species loss, or conversely of persistence, with fire exclusion in drier upland longleaf pine forests. He identified more species persisting in high-frequency than in low-frequency, burned or unburned sites. While all three groups of stands included ruderal and "climax" longleaf pine associates, legumes were significantly associated only with burned groups, and only woody species were significantly associated with fire exclusion. Based on work in prairies, which resemble longleaf pine ground cover vegetation in their dominance by bunch grasses, and abundance of composites and legumes, Leach and Givnish (1996) confirmed higher than expected losses of nitrogen-fixing legumes and small-seeded species, and that losses were more pronounced on more productive sites. Regionally rare species were lost at a rate more than twice the average for all species. We expect similar patterns for longleaf pine savannas. We do not know whether species associated with high fire frequencies persist as a result of fire-associated vigor, or if persistence requires continued seedling establishment in fire-created "safe sites" (*sensu* Harper 1977).

The most obvious and consistent effects of season of burning are effects on woody stems, with growing season fires being more effective at reducing both size and density compared to dormant season burning (Robbins and Myers 1992 and references therein). Drewa et al. (2002) reported shrubs sprouted more vigorously following dormant season fires than growing season fires, and further, that repeated growing season fires reduced the size but not the number of stems of established shrubs. Others have suggested that trees once established are not easily removed by fire (Rebertus et al. 1989; Platt et al. 1991; Glitzenstein et al. 1995), even after 30 years of annual or biennial summer burning (Waldrop et al. 1992).

Despite reports that growing season burning stimulates flowering and increases synchrony of flowering (Platt et al. 1988; Streng et al. 1993; Brewer and Platt 1994) and that dominant grasses flower only infrequently without growing season burning (Robbins and Myers 1992), there have been no convincing changes in abundance and composition directly related to season of burning (Streng et al. 1993; Brockway and Lewis 1997). But, fire season may affect the herbaceous community indirectly through changes in canopy structure and consequent changes in the environment (reduced resource availability, particularly light and water) for herbs (Harrington and Edwards 1999).

In summary, fire frequency is likely to be more important than season of burning for maintaining longleaf pine communities; sites with a history of frequent dormant season fire are likely to have retained most of the species found in a nearby reference site. If a substantial period of fire exclusion has occurred, however, it is not likely that simply restoring the fire regime will restore the herb layer.

Plantation Establishment and Management

The condition of the ground layer in plantations varies with land use history, site preparation methods, stand age, treatments applied during stand development, and site type. A history of machine tilling is likely to have the greatest adverse impacts on the ground layer. For example, Hedman et al. (2000) showed that as little as 2 years of cultivation prior to site preparation and planting resulted in sites with reduced species richness and cover compared to reference longleaf pine stands in southern Georgia. Effects of other factors (stand age, canopy composition, site preparation, recent fire history) were small by comparison.

Site preparation effects vary with the type of method and with intensity. Mechanical methods include treatments such as drum chopping (crushing with a roller) and leaving the vegetation, or shearing (cutting at the ground level) and piling the organic materials. Intensity may be increased, for example by weighting the chopper and rolling the site more than once, for more complete competition control. Mechanical methods generally reduce the cover of both woody and herbaceous species directly, but many individuals survive to resprout. All mechanical methods expose some mineral soils, and may inadvertently redistribute topsoil with nutrients and organic matter.

Herbicides (chemical methods) can be used to target specific plant groups, and are effectively used to reduce woody species with presumably low impacts on herbaceous species. Treatments can be broadcast or applied to individual stems, further increasing the specificity of applications. Chemical treatments do not disturb soil, reducing opportunities for weeds to become established. Both mechanical and chemical methods are often coupled with fire, which maintains pine dominance and benefits herbaceous species, especially grasses.

Regardless of the method, the general objective of site preparation is to favor the establishment and early growth of planted pines, and often results in increased herbaceous cover in the first few years. Residual herbaceous species may increase, and exposed mineral soil provides a seed bed for both weedy and desirable climax species (species of undisturbed longleaf communities). Because many climax species do not have adaptations for rapid dispersal and establishment, the short-lived flush of herbaceous growth following site preparation is relatively enriched with ruderal species and depleted of climax herbs (Swindel et al. 1986; Glitzenstein 1993).

Herbaceous cover and richness tend to decline with plantation age, and without intervening fire treatments herb cover can decline significantly by age six (Zutter and Miller 1998) while woody species increase. Additional silvicultural treatments may reduce herbaceous species, for example the reduction of pineland threeawn with fertilization (White 1977); or invigorate the herb layer, as by thinning (Grelen and Enghardt 1973; Means 1997; Harrington and Edwards 1999). Over a range of site conditions, high herbaceous cover has been associated with frequent burning and inversely related to basal area of the canopy trees, suggesting the potential benefits of burning and thinning in plantations to restore the ground layer (Hedman et al. 2000). The ground layer in plantations (on untilled sites) often includes a surprisingly large number of the species found in remnant forests on similar site types (Hedman et al. 2000; Smith et al. 2001). A study of xeric communities in the Carolina Sandhills National Wildlife Refuge showed that 40-year-old plantations had nearly identical species-presence lists as remnant longleaf pine stands (Walker and van Eerden unpublished data). Importantly, however, *Aristida stricta*, the dominant bunch grass, and *Gaylussacia dumosa*, the second most abundant ground cover species in remnant sites, were essentially eliminated from plantations. Compared to the xeric sandhills sites, more productive sites are likely to lose herb species and cover relatively quickly, and to provide fertile ground for weedy species (Smith et al. 2001).

In summary, except on old agricultural sites, plantations are likely to support many characteristic native species, and thus might be restored without species additions. However, the loss of grasses and dominant ground cover species may limit the effectiveness of fire as a restoration tool. We do not know how long populations of nonweedy species can persist in longleaf pine plantations; thinning may increase their longevity, but early postestablishment stands are most likely to have residual populations to "rescue." In this way they resemble sites where reduced fire frequency was the primary disturbance. In other plantations desirable trees may be present, but characteristic herbs missing, indicating the need for modifying canopy structure and adding characteristic herbaceous species. The need to establish or augment herbaceous species populations makes them similar to conditions in agricultural sites.

Agricultural Sites

Established pastures and recently cultivated fields present a predictable condition nearly devoid of any vestiges of the former ground cover. An agricultural history can have long-lasting impacts on the vegetation, soils, and microorganisms of other forest types (Foster et al. 2003), but there is little information available about the long-term effects of agricultural use on longleaf pine systems and how those effects impact restoration efforts. Much of what is known comes from project reports and proceedings of regional restoration conferences, mainly from sites where the primary agricultural use was management of improved pasture. These sites are characterized by the complete absence of longleaf pine, a depauperate to nonexistent native species pool, and domination by cultivated grasses such as bahia (*Paspalum notatum*) or early successional old-field weeds. Consequently, most of the time, energy, and money invested in restoring such sites go to eliminating the nonnative and undesirable vegetation and establishing new populations of longleaf pine ground cover species.

Restoration Tasks

Based on conditions described in the previous sections, we recognize some general conditions requiring management action (Table 2). The canopy may be dominated by species other than longleaf pine, and at altered densities (often greater than the reference model) and distributions (more regular in pine plantations than reference conditions). Similarly, the composition and structure of the ground layer vegetation may be changed, including species richness and relative abundance of species. Common or rare species may be absent; native ruderal species and exotics species may

TABLE 2. Summary of ecosystem changes that may have to be treated to achieve restoration goals. The necessity to treat any of these depends on specified project goals.

Condition	Alternatives: general treatments	Can fire alone fix it?	Does it matter for biodiversity conservation and sustainability?
Woody species			
Canopy/subcanopy density higher than reference	Prescribed fire Mechanical treatments Chemical treatments	Depends: yes, if fuels adequate and long time; no, if no fuels and short time constraint	Yes
Canopy composition altered	Regenerate to longleaf pine; approaches may vary from clearcutting through progressive thinning and patch regeneration	No	Yes, for long-term success
Herbs			
Absence or scarcity of dominant or common species	Prescribed fire Direct seeding Plant plugs	No; possibly increase sparse population, but probably take a long time	Yes
Absence or scarcity of rare species	Prescribed fire Direct seeding Plant plugs	Probably not	Sometimes; depends on objectives for site
Presence of persistent weeds (natives)	Prescribed fire Hand/mechanical "weeding" Chemical treatments	Depends on identity of weeds and available time; some are really difficult	Sometimes; depends on nature of "weed," but probably not
Presence of exotic species	Prescribed fire Hand/mechanical "weeding" Chemical treatments	Depends, but for noted species in longleaf pine systems, they seem to tolerate fire	Sometimes; depends on nature of "weed," but probably should be remedied
Site conditions			
Hydrology altered	Restore drainage	No	Yes
Soil structure/fertility altered	Burn off excess organic capital	Maybe	Yes

be present. Finally, the physical condition of the site itself may have been altered, for example by attempts to drain wet sites or to alter microsites for pine seedling establishment. All changes in structure and composition may be combined with the elimination of fire.

It is not necessary to remedy all altered conditions in order to achieve some restoration goals. The addition of rare species may be optional, and should be pursued if restoring the biodiversity in a nature preserve is the goal; or if their establishment supports a rare species conservation goal, and then only if postrestoration management can maintain high-quality habitat conditions (Gordon 1994). The presence of native weeds may go untreated if they are not aggressively displacing desired climax species (D'Antonio and Meyerson 2002), but we favor eliminating exotic species where possible as ecological ramifications may not be known at this time.

Except for restoring altered physical conditions, such as site hydrology changed by drainage ditches, prescribed burning is essential for rectifying and maintaining the restored condition of nearly all aspects of community change (Table 2). Additional possible treatments can be grouped based on two overall goals: (1) restore canopy structure to a condition that promotes ground layer establishment and vigor and (2) start new populations or augment existing populations of native ground layer species. This chapter focuses on actions required to restore the ground layer vegetation, and does not address establishing the longleaf pine. However, approaches to restoring the longleaf component can affect ground layer development, and successful restoration will require coordinating longleaf and ground layer restoration.

Changing Canopy Structure to Enhance Ground Layer Vegetation

Aside from establishing longleaf pine in the canopy, the most common objective for canopy management is to reduce a hardwood and shrub component. Fire, mechanical methods (e.g., felling, girdling, drum chopping, shearing), and chemical (herbicide) methods are used. All of these treatments, alone or in combinations, both reduce and control trees and shrubs, and affect existing ground layer vegetation to varying degrees.

Fire is promoted as a "natural" method with positive benefits and most restoration practitioners and researchers concur that in some cases fire alone may restore canopy structure and favorable conditions for ground cover recovery, but that restoration will require multiple fires over relatively long times (Robbins and Myers 1992; Waldrop et al. 1992; Glitzenstein 1993; Streng et al. 1993). Factors that limit the capacity for fire to restore structure include a lack of fine fuels, presence of ladder fuels that may promote crown damage, and thick duff that resists burning when moist and kills trees when it does burn. The problem is particularly vexing when the site contains desirable old trees with heavy duff accumulations at their bases (Varner et al. 2000; Kush et al. 2004). Compared to the presumed historical fire regime, a prescribed fire regime for restoration may differ in seasonality, frequency, and intensity, or be combined with pretreatments to protect desirable biological legacies like remnant old trees or trees with red-cockaded woodpecker cavities (see Box 10.1). An initial series of cool, winter burns may effectively reduce duff accumulations and protect old trees in fire-suppressed stands (Kush et al. 2004).

The effectiveness of fire for changing canopy structure can be enhanced by combining burning with mechanical and/or chemical treatments (Tanner et al. 1988; Outcalt 1994; Walker and van Eerden 1998; Provencher et al. 2001; Kush et al. 2004; Walker et al. 2004). In general, mechanical or chemical treatments reduce hardwoods and subsequent fires consume fuels and maintain hardwoods as basal sprouts.

The best-documented study of the effects of treatments to restore canopy structure in a longleaf pine ecosystem was conducted in a large-scale experiment in the sandhill communities at Eglin Air Force Base in the

Florida Panhandle (Provencher et al. 2001). The study plots were second-growth longleaf pine stands that had a long history of fire suppression. Consequently, the midstory had become dominated by a variety of oak species and there was a very sparse understory, with mats of hardwood leaf litter interspersed with bare ground. The goal of the study was to use management techniques commonly employed to reduce hardwood midstory in longleaf pine systems, and to document their effects on both target (oak) and nontarget (herbaceous) species, thereby testing the hypothesis that restoration of the habitat structure would be sufficient to return the understory vegetation to reference conditions. Three hardwood reduction treatments were used: spring burning, application of a hexazinone herbicide, and mechanical felling/girdling of hardwoods. The herbicide and felling/girdling treatments were followed by fuel reduction burns in the year after treatment. These plots were compared to both untreated controls and reference plots to determine the effect of oak reduction treatments on herbaceous species richness and densities. They predicted an increase in plant species richness and in densities of herbaceous plants that qualitatively tracked increasing levels of hardwood reduction.

All treatments were effective for reducing oaks; however, 4 years after treatment, results suggested that fire alone was the least effective hardwood reduction method, but yielded the greatest increases in ground cover species richness and densities. Brockway and Outcalt (2000) similarly reported that hexazinone followed by burning more effectively reduced turkey oak and shrub density and enhanced ground layer recovery in an oak-dominated site than did burning alone. Provencher et al. (2001) concluded that if gradual reduction of hardwood densities were acceptable, fire was an effective and cost-efficient means of hardwood control and would benefit the ground layer vegetation. Chemical and mechanical control were recognized to be viable options for situations where hardwood reduction is needed immediately, but they cost up to eight times more than burning, showed less understory improvement, and were judged to be effective for restoring community structure in the long term only if followed by prescribed burning.

Among mechanical options, drum chopping has been widely applied to reduce hardwoods, especially small oaks (*Quercus laevis, Q. incana, Q. margaretta*), and other woody species such as saw palmetto (*Serenoa repens*) (Tanner et al. 1988). Light chopping treatments (single passes with an empty drum chopper) have short-lived impacts on dominant bunch grasses in dry sites (*Aristida beyrichiana* in Florida flatwoods [Grelen 1959] and *A. stricta* in South Carolina sandhills [Walker and van Eerden 1998; Walker et al. 2004]), but more intensive treatments are likely to substantially reduce or eliminate the dominant wiregrass (Grelen 1962; Moore 1974).

Mechanical treatment effects vary with season of treatment, and when applied in the same year as prescribed fire. In a field experiment at the Carolina Sandhill National Wildlife Refuge prescribed fire (growing season, dormant season, and no-burn treatments) was combined with light drum chopping (growing season, dormant season, and no-chop treatments), and treatment effects on wiregrass and turkey oak recovery were evaluated. Wiregrass recovered to pretreatment levels within two growing seasons in all growing season burn treatments, regardless of chopping treatment; dormant season burn plots recovered more slowly, the impact exacerbated by extreme drought (Walker et al. 2004; Fig. 3). The plots showing the slowest recovery were chopped after dormant season burning, perhaps as a result of chopping without a layer of pine straw to protect wiregrass roots and crowns. Other tools that cut or crush understory trees without intense ground disturbance are available and we would expect similar effects. Chemical applications can effectively reduce hardwoods within pine stands on a range of site conditions. Hexazinone formulations are often used on oaks and shrubs typically found on mesic to dry sites; treatments for mesic sites are more variable including glyphosate, triclopyr, and 2,4-D formulations (Litt et al. 2001).

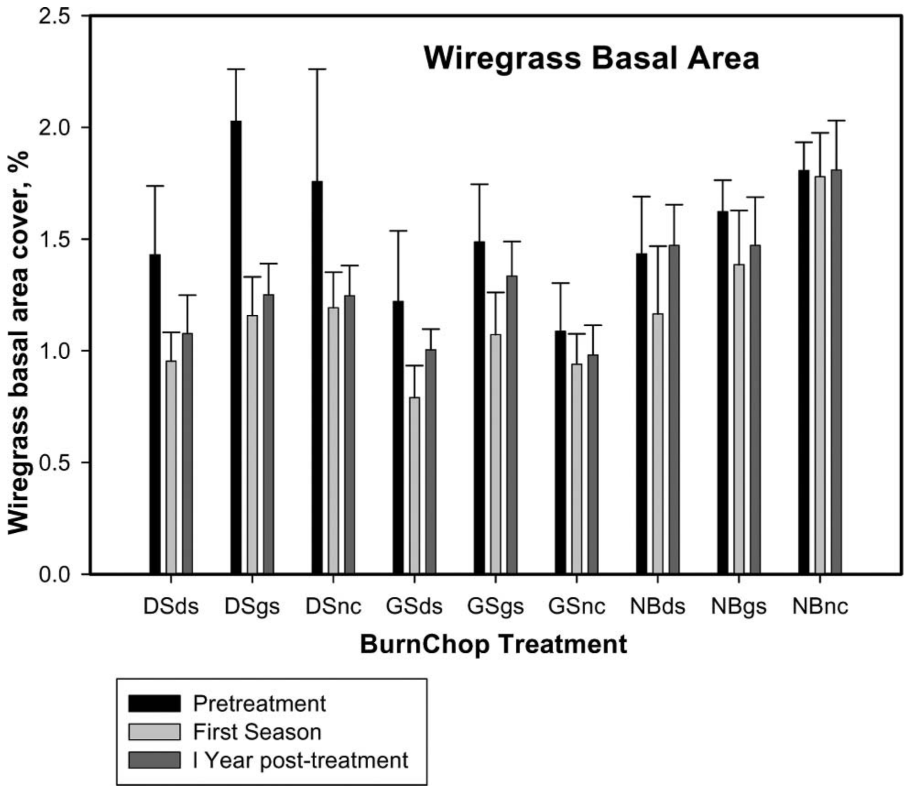


FIGURE 3. Basal area of wiregrass (*Aristida stricta*) before and following experimental burning and drum chopping at the Carolina Sandhills National Wildlife Reserve, South Carolina. Study sites were longleaf pine saw timber or pine-scrub oak stands on Alpin soils. Three burn and three chopping (single pass, unweighted drum) treatments were defined by season: dormant season (DS), growing season (GS), and not treated (that is, not burned [NB] or not chopped [NC]). Treatments: Uppercase letters indicate burn season; lowercase indicate chopping season. Measurements shown are pretreatment, after one growing season, and after two growing seasons. NB treatments did not change through time; GS burns recovered to pretreatment levels; DS burns had not recovered to pretreatment levels in two seasons (see Walker et al. 2004).

Although target woody species are successfully controlled with chemical applications, the effects on nontarget species of the ground layer are not fully understood. A recent review of herbicide application studies to determine effects on native, nontarget species (Litt et al. 2001 and references therein) found that extremely variable treatments and their application mostly in plantations rather than natural stands make it difficult to evaluate herbicide use for restoration of ground layer vegetation. The effects of herbicide use on the ground layer varied with habitat and with the specific herbicide, or combination of herbicides, used. Hexazinone herbicides were most widely used as they are especially effective against common midstory hardwood species such as oaks, sweetgum, and sumacs.

In flatwoods habitats, all herbicides used reduced species richness and cover of herbaceous and woody ground layer plants. Decreases ranged from 5.1% in herbaceous species richness compared to control using a form of hexazinone, to 71.8% in total species richness using a mixture of three herbicides. The only study to document vegetative cover reported declines in the cover of both herbaceous (27.2%) and woody (58.6%) vegetation after hexazinone application.

In sandhills habitats, the effects were more varied. Woody cover and density were reduced 10.3% to 55.9% by hexazinone application, but woody biomass increased 105.3% with use of 2,4-D. Graminoid density and cover generally increased with hexazinone application, but the response of nongraminoid herbaceous plant cover ranged from a 49.8% increase to a 33% decrease with hexazinone use. The response of ground layer species richness to herbicide use in sandhills was dependent on the type of herbicide used and the application rate. Total species richness increased anywhere from 6.4% to 81%, while herbaceous species richness was shown to increase 55.2% in the one study for which it was reported.

Among pine plantation studies, treatments were especially variable with respect to both herbicide or herbicide combination used and application rate, making it difficult to describe any general response patterns. Herbicide treatments generally increased herbaceous species richness (10.5% to 84.7%), and reduced woody species richness to varying degrees, never exceeding a 17.2% decline. Graminoid species richness increased by 30.8% in one study, decreased by 16.7% in another, and showed intermediate responses in the rest. Herbicides tended to decrease total species richness in plantations, with declines as much as 11.2% reported. However, triclopyr and glyphosate herbicide application increased total species richness by 10.9 and 8.7%, respectively. In plantation studies competition control was the motivation for herbicide use; however, differences between control of desirable ground layer plants and weeds are not reported. Thus, it is impossible to determine the contribution of each group to the reported changes in species richness.

Very few studies have reported herbicide effects on individual species of concern, such as wiregrass or other herbaceous species. With respect to wiregrass, study results range from increases of up to 7480% to decreases of 142%, depending on the specific chemical and application rate used. Even studies using the same herbicide have shown a wide range of responses, and responses within the same study can vary widely from year to year. At this point in time, it is difficult, if not impossible, to draw any general conclusion about the effects of herbicide use on wiregrass, simply because the little information that we do have shows no consistent pattern. The same is true for any individual species of interest, although it is important to note that responses of three threatened species in Mississippi to herbicide use were all negative.

In summary, herbicide use is generally successful in reducing mid- and understory hardwoods in all systems; however, there remain significant unknowns about impacts on native species, especially those in the herbaceous ground layer. Additional well-designed studies in natural systems would provide much needed information and would be advised before large-scale application of herbicides is used as a restoration method, especially in those areas with remnant native plant populations.

Most studies of restructuring the canopy to restore diverse ground layer vegetation have been conducted in comparatively dry sites. It seems likely that higher productivity sites might differ in the following ways: need for more frequent retreatment; need for more intensive initial treatments relative to the period of fire exclusion; greater challenge from exotic species; more profound species losses because mesic sites will develop more intense competitive species interactions, mesic sites have more species to lose, and mesic sites have more relatively rare species which are prone to elimination (Leach and Givnish 1996). As a result of more species losses, we suggest that mesic sites are more likely to require species reintroductions.

Plantation Restoration Strategies

Several research groups have proposed strategies for restoring plantations. Based on the results from an experiment to study the relative importance of light and soil water availability and litterfall in limiting herbaceous density and cover in longleaf pine plantations, Harrington and Edwards (1999) concluded that conventional silvicultural treatments, including thinning, herbicides, and prescribed fire, can be used to create a stand structure that favors herb layer diversity and production. Although the study was conducted in sites where the herbaceous composition differed substantially from an undisturbed ground layer, they suggest similar conditions would favor climax species. That assertion may be generally true, but we suspect that once established, climax species would respond more slowly than old-field species to changing conditions. Harrington and Edwards (1999) caution that prescribed fire (every 2 to 3 years) and thinning must be applied periodically to maintain an open structure that favors herbs. Alternatively, managing the stand for herbaceous layer diversity and productivity could begin with site preparation, using herbicides (for control of woody species) and prescribed fire to benefit pine seedlings and existing herbs. Missing herbaceous species may be added at this time to restore the composition of the herbaceous community. (See related information in the section on Direct Seeding.)

Kirkman and Mitchell (2002) describe a progressive thinning strategy to restore even-aged slash pine plantations to multi-aged longleaf pine communities with diverse ground cover. The work is being conducted in an upland site in southwest Georgia and in a flatwoods site in the Florida Panhandle. Gradual thinning leaves pines producing litter to support surface fires and providing for future timber harvest, while creating conditions that favor herbaceous species. This research group is investigating the effects of gap size, and of different methods (including herbicide and mowing treatments) to control woody species growth and promote a grassy ground layer. Treatments also include seeding *Aristida beyrichiana* in experimental gaps. Researchers will monitor herb layer development with burning to determine the need for additional species introductions. No results are published yet, but this approach has promise for restoring longleaf plantations as well as for restoring longleaf to sites currently planted in other pines. Methods such as these could be especially helpful to land managers with responsibilities to recover red-cockaded woodpecker populations challenged to restore both the canopy and ground layer of existing plantations (U.S. Fish and Wildlife Service 2001). A gradual conversion and restoration would retain the value of the plantation as woodpecker foraging habitat, while developing future habitat.

Altering Species Composition

Species composition may differ from reference conditions by the absence of common or rare species, or the presence of weedy natives or exotic species. In this section we focus on starting new populations of native species, although exotic species effects can pose significant problems for ecological restoration in the longleaf pine system as elsewhere (Hobbs and Humphries 1995; D'Antonio and Meyerson 2002). For example, cogon grass (*Imperata cylindrica*), a well-studied exotic rhizomatous grass invasive in the southern part of the longleaf pine range, can displace native grasses and alter the fire regime because it burns more intensively than the native bunch grasses (Lippincott 2000; Jose et al. 2002). By changing the fire regime, cogon grass has the potential to alter patterns of species recruitment and persistence through time.

Exotic species clearly challenge restoration efforts, but an exhaustive treatment of the topic is beyond the scope of this chapter. For more details we refer the reader to the rapidly expanding literature on exotic species, including excellent sources of information for identification and control of exotic plant species (e.g., Miller 2003). Especially helpful are websites devoted to management of nonnative plants, including a site with information from U.S. federal and state governments (http://www.invasivespecies.gov), and from the Nature Conservancy's Invasive Species Initiative (http://tncweeds.ucdavis.edu).

TABLE 3. Comparison of direct seeding and outplanting options.

Direct seeding	Outplanting
Advantages	*Advantages*
Economical ($3K/acre)	Can choose individual target species
Simultaneously introduce multiple species known to co-occur	No need to disrupt existing conditions
Can create custom seed mixes by varying timing and methods of collection	No special planting tools
Can be done concurrent with site preparation	Can be done on slopes where seeding equipment cannot be used safely
Can be done in winter, before frost, when competition for labor is lower	Conducive to volunteer assistants
Mechanized approaches can treat large areas	Good success for many species
Genetically diverse seeds can be used so that site conditions "select" most suitable individuals	Reduced susceptibility to drought at early stages
	Appropriate for rare species
	Few seeds are needed to ensure establishment objectives
	Stock can be propagated any time when seed is available
	Shorter period of competition control needed in many cases
Disadvantages	*Disadvantages*
Unreliable establishment requires large seed supplies	Expensive (up to $10K/acre)
Not as useful for rare species	Introduce only one species at a time
Special care needed to create seed mixes	Available stock may be limited by the need for hand-collecting seed and size of nursery
Seeding rates difficult to determine to ensure outcome	Germination and initial establishment in greenhouse conditions; may favor genotypes less suitable for future establishment in field conditions
Competition control essential	

Options for Starting New Populations

Options for starting new populations include direct seeding, out-planting nursery stock, or transplanting wild stock (Guerrant 1996). In the context of biodiversity conservation the latter approach is generally regarded as a last resort, reserved for rescuing native plants from sites destined for destruction, and will not be addressed further. Both direct seeding and outplanting nursery stock have been used successfully in longleaf pine restoration projects and have advantages and disadvantages (Table 3). Economic considerations give direct seeding a clear advantage over planting plugs. Costs for using plugs, which include seed collection, nursery personnel, site preparation, and planting, can run from $3000 (van Eerden, unpublished report to North Carolina Department of Agriculture) to as high as $12,000/acre (Seamon, in Disney Wilderness Preserve 2000); cost estimates for direct seeding were estimated at $155–650 and $300–400/acre at the same sites, respectively, and include maintenance of the seed collection site, seed collection, site preparation, and seeding. Machine planting options for direct seeding make it possible to treat large areas, and when seed mixes (mixed species, or mixed collections from more than one site) are used, established individuals will represent genotypes that are successful as seedlings in field conditions rather than greenhouse conditions. Outplanting approaches allow for selecting individual species (e.g., rare species), controlling the genetic composition of the new population, and for establishing plant cover quickly, but may be best suited for small areas. Native seed is not available commercially, so seed may have to be supplied to a grower for seedling production by special order.

Key issues associated with seeds include what species to plant; where, how, and when to collect seed; how to clean and store native seed; seed viability, germination requirements, and factors that affect seedling establishment.

Species Selection

Criteria for species selection include: (1) the species' habitat is similar to the restoration site conditions; (2) the restoration site is within the natural distribution range of the target species; (3) the species is needed to meet the project goal. For examples, restoring fine fuel production, restoring the diversity of vascular plants to a site, and restoring habitat for a rare butterfly require different suites of species. In order to maintain a restoration project, burning must be possible, and we recommend fuel production, through the establishment of dominant perennial grasses and retention of onsite fuel sources (e.g., pine straw), as an objective for all restoration projects. If restoration goals do include the introduction of uncommon species, there is as yet no general consensus about whether to add these species at the beginning of the restoration process (Weber 1999), or to wait to add them until after a matrix of dominant native species is established (Packard and Mutel 1997). Gordon (1994) developed a dichotomous key to support or guide management decisions to introduce (or not) a native species. Although this tool highlights issues associated with individual species, especially "at-risk" species, some of them are directly applicable to restoration, such as considering genetic and environmental suitability of the donor site, considering impacts on any remnant populations on the recipient site, and the potential for managing the site after the species introductions.

Seed Sources

Abundant seed production is expected in sites with abundant flowering, often resulting from burning in the current or previous growing season (Platt et al. 1988; Robbins and Myers 1992; Streng et al. 1993). However, viable seed production in native plant populations is a complex process dependent on successful pollination, fertilization, seed development, and seeds escaping predation or destruction by pathogens. In theory, all of these processes could be affected through various mechanisms by season of burning. Independent of recent fire history, year-to-year and site-to-site variation in seed production is typical of natural plant populations (Fenner 1985). Thus, abundant flowering does not necessarily predict abundant seed production.

There are very few direct measurements of the magnitude of seed production in natural populations of longleaf pine associates. In *Pityopsis graminifolia* (Brewer and Platt 1994) and *Aristida stricta* (van Eerden 1997) viable seed production (seeds/plant) following growing season burns was significantly greater than after dormant season fires, while Hiers et al. (2000) reported that effects of burn season on seed production in legumes varied with species. Greater losses of some legume species' seed to predators occurred after winter compared to growing season fires, but that also varied among species (Hiers et al. 2000).

Genetic Considerations

The genetic composition of populations at the seed donor site can affect the success of the new population by providing genotypes suitable for the environmental conditions at the restoration sites. Donor composition can also affect the genetic structure of residual populations in or near the restoration site by introducing new genes and creating novel genotypes via genetic recombination. To minimize potentially adverse consequences, collection sites should be as near as possible and as similar as possible with respect to physical environment to the planting site.

Widespread species, such as some of the dominant grasses, may harbor considerable genetic diversity across their ranges (Hamrick et al. 1991; Millar and Libby 1991). Based on morphological, geographic, and ecological factors, Peet (1993) divided *A. stricta* (*sensu* Radford et al. 1968) into a more northerly species, *A. stricta*, and more southerly taxon, *A. beyrichiana*. *Aristida stricta* and *A. beyrichiana* dominate the ground cover in many longleaf pine communities, and despite disagreement as to the taxonomic status (Walters et al. 1994; Kesler et al. 2003), the bunchgrass is undoubtedly variable within its geographic range. Further, species with wide habitat tolerances within the same landscape may exhibit ecotypic differentiation, as Kindell et al. (1996) demonstrated for *A. beyrichiana*. They reported a differential performance of seedlings from different habitats (xeric sandhills versus mesic flatwoods in north Florida) in common gardens and reciprocal plantings, such that individuals grew better in sites similar to their habitat of origin. Brewer (1995) showed that for the widespread *Pityopsis graminifolia*, individuals from different locations, with potentially different ecologically limiting conditions, responded differently to fire.

Matching environmental conditions of donor and recipient sites may be more important for species that have limited potential for gene flow among populations, including shorter-lived rather than long-lived perennials, animal rather than wind pollinated, and species with no adaptations for widespread dispersal (Hamrick et al. 1991). In such species, populations tend to be genetically distinct (compared to species with ample gene flow among populations), and consequently more finely adapted to local environmental conditions. If no good collection site match is available, Huenneke (1991) suggests that collecting from multiple suitable sites may be advantageous in producing a genetically diverse propagule mix, and thereby increasing the likelihood of including a suitable environmental match to the restoration site.

Removing seed from a donor site may have adverse effects at the donor site, particularly if the persistence and structure of the community rely on frequent establishment from sexual reproduction, or if collected species provide critical food resources for native fauna. Because most species are perennial in this system, and there have been few observations of seedling establishment, effects of periodic seed removal on donor site composition are not expected to be significant. Out of concern for potential adverse effects of collection, collectors often follow informal "rules" such as: take less than 50% of a strong perennial or less than 10% of an annual; take only what you are prepared to handle responsibly; avoid trampling; collect as close to the restoration sites as is practical (Apfelbaum et al. 1997). The Center for Plant Conservation developed collection guidelines for preserving the diversity of rare plant species (Center for Plant Conservation 1991).

Seed Collection and Handling

Timing

Because each species has a specific phenology, there is no one best time to collect seeds. Plants that are ready for harvest have full-sized seeds with seed coats changing color, usually from green to a darker hue, and dry stems (Apfelbaum et al. 1997). Baskin and Baskin (1998) recommend harvesting when the seeds would naturally disperse. Not only are there differences among species, but seeds of the same species can mature both at different times across the range of longleaf pine systems due to differences in climate and topography, and at different times from year to year due to variations in weather. Seed maturation may also be affected by season of burning, but effects likely vary with species. Some guidelines for seed collection have been published, such as those by Pfaff et al. (2002), which list collection dates for several species of grasses and forbs. But, because of the variations listed above, these types of recommendations should be used with caution and paired with direct observation of the maturity of the plants. More is known about the timing of seed collection for wiregrass than for most other species. Although wiregrass seeds seem to ripen in midfall (October) there is an "after-ripening" effect, such that seeds collected later in the fall and into winter have higher germination rates. van Eerden (1997) found that *Aristida stricta* seeds collected in December had higher germination rates than seeds collected from the same North and South Carolina sandhill sites in November. Similar results were found for *A. beyrichiana* collected in Georgia sandhills (Walker and Silletti unpublished data).

Seed Harvest, Cleaning, Storage

Methods for collecting, cleaning, and storing seed for prairie restorations (Apfelbaum et al. 1997; Clinebell 1997) are mostly applicable for seed handling for longleaf pine restoration projects (Glitzenstein et al. 2001). Generally, seed can be collected by hand, which is especially useful for rare or infrequent species or when individual species are needed to enrich an existing site, or mechanically, which is very effective for collecting seed mixtures (Fig. 4). Hand collection methods vary from simply stripping individual seed heads by hand, to collecting entire infructescences with clippers, to collecting small seeds with a hand-held vacuum.

Several types of seed harvesting machines are available, but often prohibitively

FIGURE 4. Bulk seed collection with an ATV mounted seed stripper in a remnant upland site (a) and emptying the collection hopper into a storage bin (b). Seed collections include seed from all species in fruit at the collection time, e.g., common large grasses and composites. (Photo courtesy of Lin Roth.)

expensive. Sharing the cost of equipment may provide a feasible option, but requires cooperation in collection efforts. Green silage cutters harvest and collect all aboveground plant material. The resulting "green" harvest contains seeds as well as other vegetation and must be distributed quickly so as to avoid seed-destroying mildew as the plants decompose. Pull-type and front-end mounted seed strippers harvest seeds plus accessory plant parts (mostly dry) with rotating brushes. Seed stripper types, available in sizes suitable for mounting on four-wheelers and larger, have been used in longleaf pine systems, but smaller models are most convenient for harvesting seed from sites with trees. Pfaff et al. (2002) provide more details on seed harvester equipment and sources.

Seed harvests are processed to varying degrees depending on how long they are to be stored, how pure the seed must be, and such practical considerations as how much space is available for storing (see Apfelbaum et al. 1997 for details; Baskin and Baskin 1998). Except for fleshy fruits, such as blueberries and huckleberries common to the longleaf system, harvests are usually dried before processing further. [Fleshy fruits require special handling to separate seed and pulp. See Phillips (1985) for suggestions.] Experience supports that collecting seeds on low-humidity days and spreading them out of the weather in a warm place provides adequate drying. Collections generally include a variety of other plant parts and are cleaned in several stages (threshing, scalping, final cleaning), depending on the desired final condition. Methods can be simple such as hand sorting, to more complex screening, and milling of various forms. (See Packard and Mutel 1997 for details and references.)

Seeds of many longleaf-associated native species stored indoors in paper or grass seed bags retain viability for at least a year. Glitzenstein et al. (2001) report acceptable germinability for 2 years, but much reduced viability and deformed seedlings after 2 years of storage at room temperatures. Storing seeds in dry unheated areas (e.g., unheated storage shed) will expose seed to temperature variations similar to field conditions, and may be useful for seed collected in the fall and intended for planting the following season (Glitzenstein et al. 2001; Pfaff et al. 2002). However, Pittman and Karrfalt (2000) report that viability of wiregrass seed drops rapidly after 8 months of storage at ambient temperatures, and they used annually collected seed for seedling production.

Factors Affecting Germination and Establishment

Properly collected seeds of many longleaf pine associates readily germinate without elaborate pretreatments. Germination rates across common plant families are similar and highly variable, ranging from zero to greater than 80% in laboratory, greenhouse, or outdoor trays exposed to ambient environmental variations (Pfaff and Gonter 1996; van Eerden 1997; Glitzenstein et al. 2001; Pfaff et al. 2002). Results of a study of 42 species characteristic of Atlantic coastal plain savannas indicate that germination rates within a species vary from site to site and year to year, but are not related to time of burning or time since burning (Glitzenstein et al. 2001). In that study, most trials exceeded 30% germination. Glitzenstein and colleagues compared germination rates in laboratory trials with germination in flats exposed to outdoor conditions and found that for some species, especially fall-seeding composites, field germination exceeded lab trials.

Several treatments have been reported to increase germination rates in some common longleaf pine associates. Cold stratification increases germination in fall-fruiting composites such as *Liatris* spp. (Pfaff and Gonter 1996), and perennial grasses including *Andropogon gerardii, Schizachyrium scoparium, Ctenium aromaticum, Erianthus giganteus, Aristida beyrichiana* (Glitzenstein et al. 2001), and *A. stricta* (van Eerden 1997). A period of after-ripening reportedly benefits germination rates in *Aristida beyrichiana*, with germination increasing for up to 5 months in dry storage (Pittman and Karrfalt 2000). Finally, heat treatments, which can be as simple as pouring boiling water over seeds and allowing them to cool slowly, increase germination in various legume species (Cushwa et al. 1968; Pfaff and Gonter 1996; Baskin and Baskin 1998). Testing germinability is the most reliable basis for calculating seeding rates and for determining timing of harvest; but as a general rule, mature seeds should be planted at the same time they are naturally dispersed (Baskin and Baskin 1998). Delays in planting some species result naturally in induced dormancy (Baskin and Baskin 1998). Consult references in this section for more information about native seed germination and growing native species.

Although seedlings of many native species have been established and grown under greenhouse and nursery conditions (Pfaff and Gonter 1996; Glitzenstein et al. 2001; Dagley et al. 2002; Pfaff et al. 2002) and even commercially produced (Pittman and Karrfalt 2000), there is little information about factors that affect seedling establishment either from naturally dispersed seed in intact longleaf communities or from seed introduced into field conditions. Experimental results suggest that seedling establishment in intact longleaf pine communities is rare, and that general failure of seedling establishment can be attributed to competition from established dominant species (Brewer et al. 1996; van Eerden 1997; Glitzenstein et al. 2001); higher establishment in mesic compared to xeric sites suggests that competition for water may be the specific cause of mortality (van Eerden 1997; Glitzenstein et al. 2001).

In a garden experiment using a variety of species, Glitzenstein et al. (2001) found that each species was most successful in soil and drainage conditions that most closely matched the environments where it grows naturally. Thus, matching species and probably matching seed source habitats for species found on a broad environmental gradient (especially soil moisture in the longleaf pine system) will most surely enhance establishment success.

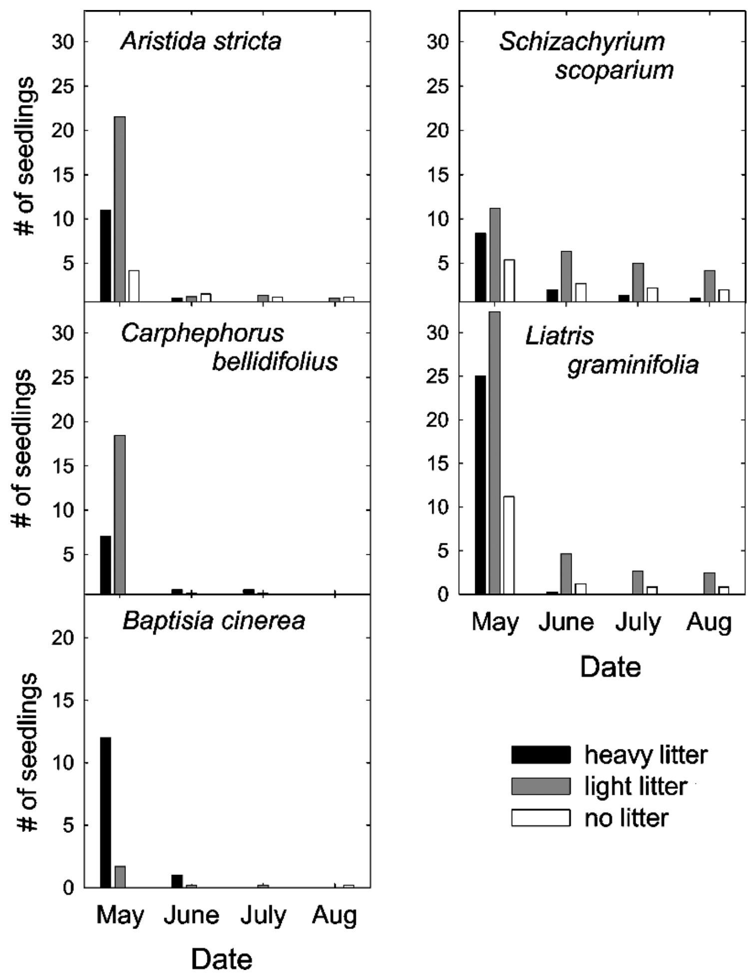
The presence of litter likely affects germination and establishment (Fowler 1986; Facelli and Pickett 1991) and species-specific responses to experimental litter treatments were observed at the Carolina Sandhills National Wildlife Refuge (Walker unpublished data; Fig. 5). The effects of pine straw litter on the germination and establishment of ten common sandhills species were monitored for one growing season. Germination of common grasses and composites benefited from light litter. Heavy litter seemed to benefit germination among legumes, but overall germination rates were low and at the end of the first season only one seedling of *Baptisia cinerea* remained in a no-litter plot. In summary, available information suggests that planting in an appropriate site with respect to a moisture gradient, with low competition, and low litter loads favors seedling establishment under field conditions. Similar conditions may be achieved via site preparation for direct seeding projects.

Site Preparation and Sowing Treatments

The challenges for controlling competition vary markedly with site history. As a general rule, in previously forested sites where exotic herbaceous species are not dominant in the ground layer, site preparation suitable for planting longleaf pine seedlings will also favor ground cover establishment, as long as a sufficient amount of bare soil is available for plant establishment. Experimental evidence suggests that more complete competition control is likely to benefit seedling establishment. However, we observe acceptable wiregrass establishment (about two clumps per square meter; from about 15.4 kg cleaned seed/ha; Walker and Silletti unpublished data) from broadcast seeding soon after planting trees in sandy sites where piling harvest slash left a mosaic of bare soil, litter, and residual plant cover. Using a cultipacker to press seed into the soil did not increase establishment success on these uneven forest site surfaces. Acceptable establishment was similarly achieved on mesic savanna sites at Fort Stewart, Georgia (Dena Thomson personal communication).

Pasture lands and abandoned agricultural fields present the dual challenges of removing existing vegetation, including nonnative perennial pasture grasses, and reducing the numbers of weed seeds present in the soil

Figure 5. Effect of pine straw litter on seedling germination and establishment in selected common sandhills species. Small garden plots at the Carolina Sandhills National Wildlife Refuge were treated with a low litter (comparable to litter deposited in the first year after burning) and heavy litter (twice the low level) application. Bars represent the mean of five replicates per species per treatment. Seedlings were counted in the same plots in four successive months during a single growing season. Number of seeds varied among species, but was constant within a species; thus internal comparisons can be made, but conclusions about species differences cannot be drawn. (Unpublished data).



(the seed bank). Recent projects have demonstrated that removal of unwanted species takes at least 1 year of treatment before planting native species. The generally recommended protocol requires herbicide to remove all vegetation from the site (Disney Wilderness Preserve 2000) followed 3 to 4 weeks later with disking to expose weed seeds allowing them to germinate. Disking is repeated every 4 to 6 weeks for about 6 months prior to planting. Immediately before sowing desired species, the soil is compacted by rolling, and a final herbicide treatment is applied 2 to 3 weeks before planting. Variations on this protocol were shown to effectively prepare sites once dominated by pasture grasses or with cogon grass (*Imperata cylindrica*). If populations of native plants are quickly established after this treatment protocol, additional weeds can be controlled through periodic spot application of herbicide and eventually reduced as they are outcompeted by natives.

Comprehensive studies of sowing treatment effects on establishment of wiregrass and other species were conducted at Apalachicola Bluffs and Ravines Preserve in north Florida (Hattenbach et al. 1998; Seamon 1998; Cox et al. 2004). They examined the effects of eight treatments in a three-factor experiment: sowing native seed alone or with winter rye as a cover crop, rolling the seed in after sowing, or not and adding supplemental water for the first 4 months after sowing or not. They found that neither supplemental water nor sowing an annual cover crop increased ground layer species richness or density. Rolling seeds

FIGURE 6. Standard hay blower distributing wiregrass seed at Fort Gordon, GA. This equipment is effective and widely available.

in immediately after sowing, however, significantly increased wiregrass establishment and survival, as others have reported (Pfaff and Gonter 1996; Bissett 1998).

Additions of fertilizer and mulch to sites after sowing are not recommended. Neither treatment significantly increases establishment of native species under most conditions, but both favor the growth of native and exotic weeds that tend to outcompete natives (Bissett, in Florida Institute of Phosphate Research 1996; Clewell, in Florida Institute of Phosphate Research 1996; Pfaff and Gonter 1996; Jones and Gordon unpublished report to Florida Department of Transportation; Jenkins et al. 2004).

Direct Seeding: How Much, How, When?

Several options for sowing seed including hand broadcasting, hydroseeders, cultipackers, fluffy-seed drills, and fertilizer spreaders have been tested with varying results. The device most often recommended for quick, efficient distribution of native seed, especially wiregrass, is a standard hayblower (Fig. 6), which allows for relatively even distribution of seed over a large area with some control over seed placement (Disney Wilderness Preserve 2000; Jones and Gordon unpublished report to Florida Department of Transportation). See Pfaff et al. (2002) for a more detailed discussion of seeding methods.

The question of at what rate to spread seed (or seed bearing material) highlights the lack of consensus in longleaf pine restoration projects. At a discussion of restoration methods at the Disney Wilderness Preserve Conference on Uplands Restoration, the range of seeding rates for seed stripper collected seed was 25 kg material/ha. The participants agreed on a recommendation of at least 56 kg/ha of material that is 10–11% wiregrass seed by weight, and 8–10% other seed by weight. Their goal was at least three established wiregrass clumps per square meter. For material collected with a green silage cutter, they estimated that approximately 1500 kg/ha would yield the desired establishment rates. One estimate for distributing clean seed was 2.2–2.8 kg/ha (Disney Wilderness Preserve 2000). Other rates found in the literature include 133 kg/ha (Seamon 1998) for stripped material, 4.4–8.8 kg/ha of hand-collected and cleaned seed (van Eerden unpublished report to North Carolina Department of Agriculture), 3.3–4.4 kg seed/ha (Pfaff et al. 2002), and 91 kg/ha (Hattenbach et al. 1998) which yielded 5 to 7 plants/0.5 m^2. Clearly, further experimental trials of seeding rates and resulting yields for different materials are needed.

Adequate soil moisture during early establishment is essential for native plant species. Planting should occur just prior to the season of most reliable moisture (Pfaff and Gonter 1996); in most cases this is during the winter rainy season, from November to February (Pfaff and Gonter 1996; van Eerden 1997). In projects where soil moisture stress is severe, and the site is small enough to make it manageable, irrigation can be applied for the first 3 to 4 months after planting to increase seedling establishment (Jones and Gordon unpublished report to Florida Department of Transportation; Jenkins et al. 2004).

Seedling Plugs: How Many, When, Where?

Seedlings for outplanting are best grown under conditions that ensure adequate growth and survival, while maintaining an environment that is stressful enough to select for stress-tolerant plants and natural root-to-shoot ratios. Glitzenstein et al. (2001) discuss considerations for cultivation including germination and growth media (this can include horticultural media or soil taken from the restoration site, which has the added advantage of providing mycorhizal innoculum), watering regime, and overwintering of seedlings, all of which prepare seedlings for successful outplanting. The results of several studies suggest that, at least for wiregrass, plugs should be at least 6 months old before they are outplanted because younger, smaller seedlings are more susceptible to the effects of drought (van Eerden 1997; Outcalt et al. 1999) and competition (Mulligan and Kirkman 2002a). There is no consensus on the best time of year to plant seedlings; reported planting times ranged from April (Outcalt et al. 1999) to November (van Eerden 1997, unpublished report to the North Carolina Department of Agriculture) for wiregrass and plantings of other species occurred throughout the year (Glitzenstein et al. 2001). Seedling density is also species dependent, but for wiregrass three plugs per square meter is commonly used for experimental purposes (Mulligan and Kirkman 2002a).

In general, survivorship and growth of outplanted plugs in field situations are high, with survivorship rates of 90% (Glitzenstein and Streng, in Florida Institute of Phosphate Research 1996) and 60% (Outcalt et al. 1999) after one growing season, and 80% after two (Glitzenstein and Streng, in Florida Institute of Phosphate Research 1996). Both survivorship and growth are reduced by competition from neighboring plants (Outcalt et al. 1999; Mulligan and Kirkman 2002a). Regarding underplanting seedlings to restore plantations, seedling performance is likely to be maximized when planted in large canopy openings with minimal root competition from both woody and other herbaceous species (Dagley et al. 2002) and low inputs of pine straw litter (van Eerden 1997; Dagley et al. 2002).

Post-planting Management

Prescribed fire is essential to encourage flowering in many species and to control the growth of woody and exotic species. Clewell (in Florida Institute of Phosphate Research 1996) advocates burning as soon as the site is able to carry a fire; however, burning too early can kill young wiregrass plants and slow the growth of those that survive (Outcalt et al. 1999; Mulligan and Kirkman 2002b). Additionally, reports indicate that wiregrass seeds may remain dormant for a year after sowing and germinate in the second season (Seamon 1998; Mulligan and Kirkman 2002b; Cox et al. 2004). It has therefore been recommended that new plants be given at least one to two complete growing seasons and as long as four to five seasons (Outcalt et al. 1999) before prescribed fire is introduced. After that, a 2- to 3-year burn cycle has been suggested, as competition begins to negatively impact wiregrass plants after 3 years (Glitzenstein and Streng, in Florida Institute of Phosphate Research 1996).

Population Establishment: Does It Work?

Population establishment can be considered a success when it results in a self-maintaining population with sufficient genetic diversity for long-term persistence (Pavlik 1996). While few studies have been in place long enough to reach this ultimate goal, there are many encouraging results thus far. Seedling recruitment has been observed in populations of both outplanted wiregrass plugs (Mulligan et al. 2002) and in plots that were direct-seeded (Bissett, in Florida Institute of Phosphate Research 1996). Glitzenstein et al. (2001) monitored six species of outplanted grasses and forbs, including both wiregrass and the rare forb *Parnassia caroliniana*, for 5 years and are optimistic about their chances of long-term success. At the Nature Conservancy Apalachicola Bluffs and Ravines Preserve seeds were collected from 4- and 5-year-old direct-seeded populations, and a direct seeding study for the Florida DOT (Jones and Gordon unpublished report to the Florida Department of Transportation) resulted in a stand that was within the natural range of species cover and able to carry fire in 3 years.

Filling Information Gaps: Adaptive Management and Research

Knowledge about restoring the ground layer in longleaf pine communities has increased substantially in recent years, and results from established projects promise a bright future for restoration. Restoration projects and research efforts underway in various places through the region will yield still more information in the near future (for example, see Box 10.2). We expect that continued knowledge development would benefit from increased collaboration and coordination among research and restoration trials, and further that a widely accessible outlet for developing information will generate even more landowner interest in ground cover restoration.

In addition to the need for increased communication, we have identified some specific information gaps. Restoration research or adaptive restoration projects conducted in other locations within the range of longleaf pine would advance the restoration cause, as well as contribute to understanding the natural variability of the ecosystem. In the absence of more specific information, research projects designed to understand the variation in ecosystem functions across gradients, especially a productivity gradient, may be useful for targeting the most difficult and most pressing restoration needs. There is always a need for more species-specific information about the biology and habitat requirements of both common and rare species, especially regarding reproductive biology. Because species reintroductions are needed for many sites, a more comprehensive understanding of population processes in experimental as well as natural species matrices is essential. Information about persistent native seed banks is scarce (Cohen 1998; Jenkins 2003), but would be especially useful in developing restoration protocols. Finally, while there are suggestions that small fragments of this diverse herbaceous community can persist (Heuberger and Putz 2003), the effects of fragmentation and isolation on the persistence of the ground cover of longleaf are not well known; such knowledge could ensure that feasible restoration goals are established and that restoration resources are targeted where they can be successful.

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