Seed Bank Viability in Disturbed Longleaf Pine Sites

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Abstract

Some of the most species-rich areas and highest concentrations of threatened and endangered species in the southeastern United States are found in wet savanna and flatwood longleaf pine (*Pinus palustris* Mill.) communities. Where intensive forestry practices have eliminated much of the natural understory of the longleaf ecosystem, the potential for reestablishment through a seed bank may present a valuable restoration opportnnity. Longleaf pine sites converted to loblolly pine plantations and non-disturbed longleaf sites on the Coastal Plain of North Carolina were examined for seed bank presence and diversity. Conducting vegetation surveys and examining the seed bank using the seedling emergence technique allowed for verification of the seed bank presence, as well as evaluation of the quality of the seed bank on disturbed longleaf pine sites. Forty-three species and over 1,000 individuals germinated, and the seed banks of both the disturbed and non-disturbed stand types contained species not noted in the vegetation survey. Although many of these species were considered weedy and typical of disturbance, numerous taxa were indicative of stable longleaf pine communities. This study confirms both the presence and quality of seed banks in highly disturbed former longleaf pine sites, suggesting that the seed bank may be an important tool in restoration efforts.

Key words: flatwoods, longleaf pine, *Pinus palustris*, restoration, savannas, seed bank.

Introduction

Due to human activities, the area once occupied by longleaf pine (*Pinus palustris)* ecosystems has been reduced from an estimated 60million acres in pre-colonial times to less than 3million acres (Outcalt & Sheffield 1996). Generally categorized according to moisture conditions, longleaf pine ecosystems range from xeric sand hills to wet flatwoods and savannas. Land conversion to agriculture, as well as loblolly pine (*Pinus taeda)* and slash pine (*Pinus elliottii)* plantations, accounts for much of the reduction on the more moderate to poorly drained sites. Roughly 95% of today's remnant longleaf stands are found on xeric to dry-mesic sites generally considered not optimal to support agriculture or intensive plantation culture (Frost 1990). However, it is the wetter savanna and flatwood communities that tend to produce higher understory plant diversity (Christensen 1978). Some of the most species-rich areas and highest concentrations of endangered and threatened species in the Southeast are found on these wet sites (Walker & Peet 1983; Rome 1988; Frost 1990; Peet & Allard 1993). Although the dominant or codominant longleaf pine overstory tends to be predictable across soil types, the associated understory communities are more diverse and variable in response to many factors including landscape position, soil moisture and texture, and fire frequencies (Rome 1988; Noss 1989; Frost 1990).

Due to the increasing rarity of these wetter longleaf pine communities, restoration efforts must include land that has been converted to alternative uses. Although longleaf pine can now be successfully planted, reestablishment of the herbaceous understory has been problematic. Where the natural understory vegetation has been eliminated by severe disturbance, the potential for reestablishment through a seed bank presents a valuable opportunity (Simpson et al. 1989). Sowing and transplanting of native species is costly, time consuming, and may not be possible if geographically suitable seed is not readily available. In addition, the increasing isolation of intact, rare community types makes natural seed dispersal of desired understory species unreliable (van der Valk & Pederson 1989; Augusto et al. 2001).

Although substantial research exists on seed banks from a range of community types, longleaf pine communities have received little attention. However, several general trends from seed bank research suggest that a persistent seed bank in longleaf pine communities would be expected. Adaptation by plants found in environments subject to frequent disturbance may be the foundation for a persistent seed bank (Pickett & McDonnell 1989), and disturbance by fire is essential to the perpetuation of longleaf pine ecosystems. Many established plants survive fires and there is strong post-fire recruitment from seeds dispersed locally, either before fire or immediately after it. Frequent fires may, in fact, select for species that have local dispersal of long-lived dormant seeds (Whelan 1986). Fire may also stimulate flowering in some plant

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species such as sundews and orchids (Whelan 1986; Platt et al. 198X). Fire is known to be the flowering stimulus for *Aristida stricta* (pineland three-awn), a consistently dominant understory plant in longleaf savannas (Platt et al. 1988). Although it is generally accepted that disturbed areas accumulate large seed banks, with timing, severity, and scale of disturbance all being factors, it has also been suggested that equal, predictable disturbance, such as low-intensity and high-frequency fire, does not result in the accumulation of a large seed bank. In these types of stressed-yet-stable environments, vegetative and clonal reproduction may be more competitive than seedlings (Fenner 1985; Thompson 1992). Determining the presence of a seed bank and its composition is the first essential step before a management or restoration plan that utilizes the seed bank is attempted (van der Valk & Pederson 1989).

The Croatan National Forest, situated in the Coastal Plain of North Carolina, contains some of the finest natural longleaf stands in the Atlantic coastal region, as well as many former longleaf sites now supporting loblolly pine plantations. Many plantations on moderate to poorly drained soils, established 20-30 years ago, are proving to be much less productive than originally anticipated and restoration of those stands back to longleaf pine ecosystems is being considered (J. Cherry, USDA National Forest System, 1999, personal communication). The seed bank may provide an additional economic and time-efficient tool in the restoration of the understory component on these sites.

The objectives of this study were to verify the existence of a persistent seed bank in disturbed longleaf pine sites and, if present, evaluate its quality. Because human disturbances are so prevalent in natural communities, seed banks will often be critical in the management and restoration of an ecosystem (Thompson 1992). The presence of a high-quality seed bank will be of particular importance for the restoration of species-rich longleaf pine ecosystems.

Methods

Study Sites

The study sites are four highly disturbed and four non-disturbed longleaf pine sites in the Croatan National Forest, located in Jones, Craven, and Carteret Counties, North Carolina. All sites are predominantly on Leon (sandy, siliceous, thermic Aeric Alaquod) soils, a poorly drained fine sand with a cemented spodic horizon (Bh). The more poorly drained Murville (sandy, siliceous. thermic Umbric Endoaquod) soils and moderately drained Mandarin (sandy, siliceous, thermic Oxyayuic Alorthod) soils are often found in association with Leon soils and small inclusions occur throughout the study sites (Goodwin 1989; R. LeBlond, North Carolina Natural Heritage Program, 1999, personal communication).

All eight sites occur within several miles of each other and thus have a similar early history. In colonial times, the sites were naturally forested with longleaf pine. The old-growth longleaf pine trees were harvested between the late 1800s and early 1900s, and all sites subsequently regenerated naturally lo second-growth longleaf pine. Before purchase by the federal government in 1937, the study sites were owned by the Interstate Cooperage Company, a subsidiary of the Standard Oil Company, New Jersey (Interstate Cooperage Company 1934; Anonymous 1937). Government acquisition reports classify all of the sites as “merchantable longleaf turpentine areas with unmerchantable saw timber.” The majority of the trees were longleaf pines ranging from 15 to 25cm diameter at breast height (dbh), whereas scattered, old-growth longleaf pines showed evidence of previous turpentine activities (Interstate Cooperage Company 1934). It is unlikely that significant understory disturbance occurred before 1934 on any of the study sites. Early utilization of forests, even logging operations, did little long-term disturbance to the understory and many second- and third-growth stands now show old-growth characteristics with an open park-like structure and low-stature understory (Noss 1989).

The four highly disturbed sites have all undergone severe understory disturbance associated with forestry activities and are currently in loblolly pine plantations established between 1971 and 1975 (Croatan National Forest 1982, 1997). These sites have undergone mechanical site preparation, which includes chopping and bedding, on a minimum of two occasions and are burned every 5-10 years for fuel reduction and wildlife habitat enhancement (J. Cherry, USDA National Forest System, 1999, personal communication).

The four non-disturbed sites are fire-maintained natural longleaf stands and are forested with second-growth longleaf established in the late 1800s and early 1900s. Scattered old-growth trees occur throughout the four sites (Croatan National Forest 1982, 1997). These sites have never experienced understory disturbance and are considered to be the best approximation of pristine longleaf pine flatwood or savannas sites on Leon soils within the Croatan National Forest (Schafale 1994; R. LeBlond, North Carolina Natural Heritage Program, 1999, personal communication; R. Braham, North Carolina State University, 1999, personal observation). These sites are burned every 2-3 years, primarily during winter months (J. Cherry, USDA National Forest System, 1999, personal communication).

Sampling Procedure

The current vegetation at each site was surveyed and seedling emergence from soil collections was utilized to evaluate the presence and quality of the seed bank in each site. A modified version of the North Carolina Vegetation Survey (Peet et al. 1998) was employed to examine the standing vegetation of each site. In each site, one 20 X 50-m (0.1-ha) plot was established. Trees, woody plants equal to or greater than 2.5 cm dbh, in each plot were measured.

From these data, density and basal area by species were calculated.

Within each plot, ten 10 X 10-m modules were laid out in a 2 x 5 pattern (Peet et al. 1998). Four of the modules were intensively surveyed for shrubs (woody plants <2.5 cm dbh) and were centrally located within the plot to reduce edge effect (Peet et al. 1998). Within each of these four intensive modules, three 2 X 2-m quadrats were laid out to sample ground line species. Ground line species consist of grasses, forbs, vines, and subshrubs (woody plants not exceeding 0.25 m).

Percent foliar cover of shrubs in the intensive modules and of ground line species in quadrats was ocularly estimated and placed into one of five cover scale classes: trace to 5, 6-25, 26-50, 51-75, and 766100% (Kent & Coker 1992). Only plant cover falling within the vertical projections of the sides of the modules and quadrats was measured. Total cover basically measured leaf area and often exceeded 100% because many leaves overlapped each other (Bonham 1989; Kent & Coker 1992). Additionally, portions of the 20 X 50-m plots that were not intensively surveyed were searched for additional shrub and ground line species not previously encountered. All plots initially surveyed in July were resurveyed in the fall and after spring to add species that were previously overlooked.

Based on the primary goals of detection and evaluation in examination of the seed bank, the seedling emergence method was selected as the most appropriate. The method of placing seeds in an environment with favorable germination conditions relative to light, temperature, and moisture is commonly employed for the detection of a persistent seed bank and estimating species presence. This has been found to provide a reliable measure of composition (Thompson & Grime 1979; Baldwin et al. 1996). Additional factors including the role of fire, scarification, and temperature and moisture regimes in the germination of seeds are beyond the scope of this study.

The seedling emergence technique is preferred to meet the objectives of this study rather than methods that rely on seed extraction. which may overestimate numbers. It is not always possible to distinguish viable from nonviable seed, not to mention the extreme difficulty in seed identification (Brown 1992; Rossell & Wells 1999). However, there are recognized limitations to the emergence methodology as well. Because germination requirements vary among species and distribution of seeds throughout the soil is uneven, the number of viable buried seed tends to be underestimated, as does the number of detectable species (Fenner 1985; Simpson et al. 1989; Gross 1990; Baskin & Baskin 1998). These factors become even more important in a longleaf pine ecosystem, which typically contains many species that arc naturally rare. However, the objective of this work was not to provide a complete assessment of the seed flora, but rather to detect the presence of a high-quality, persistent seed bank. It has also been noted that with the seedling emergence method there is often a lack of ability to detect tree and shrub species (Thompson & Grime 1979; Brown 1992). This is of little concern in longleaf ecosystems because many shrubs are clonal and herbaceous plants tend to be under finer scrutiny.

Soil sample collections were made in August 1999 and May 2000, and each collection was monitored for 9 months. Only a small amount of soil could be examined at one time in the greenhouse, and the second collection contributed to the completeness of the seed bank composition. The second pre-summer collection may be more representative of a persistent seed bank, whereas the post-summer collection may contain more seeds of transients, which may have fallen through the litter layer and been collected in the soil (Thompson & Grime 1979). Additionally, soil collected before pre-summer received dormancy breaking cold stratification (Whipple 1978) just before collection. This is a condition that was not met in a heated greenhouse nor was it imposed on the collected soil.

Collections were made using a split-tube bucket auger, taken to a depth of 10 cm from within the 12 ground line quadrats of the 20 X 50-m vegetation plots, and compiled by site. Samples were cornposited to minimize the small-scale inherent heterogeneity of seed distribution in the soil. A large number of small sampling units are more appropriate than a few large sampling units for seed bank studies (Forcella 1984; Benoit et al. 1989; Simpson et al. 1989; Ware et al. 1993; Baldwin et al. 1996). Additionally, previous studies demonstrate sharp declines of seed density at deeper depths; thus, a 10-cm depth was deemed adequate to examine species composition (Baldwin et al. 1996). Samples were taken where there was no vegetation and litter was cleared away to the mineral surface. Samples were sieved through 5,660-μm mesh to remove large pieces of roots and debris.

Seed flats were placed in a greenhouse equipped with an automatic misting system, full-spectrum artificial lighting, and temperature controls. The minimum temperature maintained was 20°C, and natural plus supplemental light provided 16-hr photoperiods. Misting was continuously adjusted to maintain a moist planting medium. All equipment used in both the collection and the preparation of the soil was washed in a bleach solution to prevent cross-contamination between sites. For each collection date, 12 seed flats per site were created, for a total of 48 seed flats for the disturbed and 48 for the non-disturbed sites. The seed flats were then randomly placed on the greenhouse benches to minimize external biases, such as small variations in light and moisture intensities.

Within each seed flat was a 5.0-cm base of pre-mixed, sterilized greenhouse planting medium (perlite, vermiculite, and peat moss), on top of which was placed 300 cm” of the composite, field-moist soil sample mixed with 300cm” of potting medium. Previous observations demonstrated germination to such a heavy degree that diluting the seed bank facilitated greater germination because of less competition (Cohen 1998). Because light is the most consistent factor affecting the germination of dormant seed and does not readily penetrate the soil (Grime 1979; Pons 1992), the total depth of this seed bank-potting medium mixture was less than 1 cm. Control flats containing only greenhouse planting medium were placed throughout the greenhouse to detect seed contamination from the local area. Plants germinated from seed were collected and identified, with the date of germination and study site recorded. When necessary, plants were transplanted to pots until large enough to identify. All plants in the research study sites and seed flats were identified to species whenever possible and nomenclature largely follows Weakley (2002).

Results

Vegetation Survey

The dominant canopy species in the non-disturbed sites was *Pinus palustris*, accounting for over 95% of the basal area. There were no hardwood species over 2.5 cm diameter at breast height, and *Pinus serotina* (pond pine) was the only other species large enough to be recorded as a tree. The basal area in the disturbed sites is approximately twice that found in the non-disturbed sites and there are almost nine times as many stems per hectare (Table 1). Being plantations, loblolly pine dominated and accounted for over 85% of the basal area. *Pinus palustris* and *P. serotina* made up approximately 10% of the basal area and probably seeded in from surrounding natural areas. Expected typical hardwood species such as *Acer rubrum* (red maple), *Nyssa sylvatica* (blackgum), *Magnolia virginiana* (sweetbay magnolia), and *P. palustris* (redbay) were also present but accounted for only 3% of the basal area per hectare. *Acer rubrum* was the dominant tree of these hardwood species.

Although the disturbed and non-disturbed sites share many of the same shrub species, the abundance of these species is very different. The dominance of shrubs is dramatically evident when moving through the disturbed sites. These sites are characterized with well over 100% shrub cover per 100 m^2, with the dominant species being *Ilex glabra* (inkberry), *Ilex coriacea* (large gallberry), *P. palustris, A. rubrum*, and *Gaylussacia frondosa* (dangleberry) (Tablel; Fig. 1). A total of 30 shrub species were documented. Shrub height often greatly exceeded 1 m and thick litter layers occur throughout. The non-disturbed sites have considerably less shrub cover (Table I) and are dominated by *Vaccinium tenellum* (small black blueberry), *Morella cerifera* (wax myrtle), *I. glahra,* and *Gaylussacia* spp. A total of 22 shrub species were recorded in the non-disturbed sites. Due to the use of fire, shrub height rarely exceeds 0.5 m in these sites, and the litter layer does not accumulate for more than three seasons before it is reduced.

There is a shift from shrub to ground line vegetation dominance going from disturbed to non-disturbed sites. The disturbed sites and non-disturbed sites have 35 and 32 ground line species, respectively. Non-disturbed sites are dominated by *Aristida stricta*, *Pityopsis graminifolia* var. *latifolia* (silk grass), and *Vaccinium crassifolium* (creeping blueberry), as well as containing typical genera such as *Dichanthelium, Platanthera, Xyris*, and *Rhexia.*

Although the disturbed sites exhibit high resiliency to disturbance and contain many typical longleaf species such as *A. stricta* and *V. crassifolium,* these species contribute less to overall cover. Species typical of disturbed areas such as *Gelsemium sempervirens* (evening trumpet flower) and *Smilax* spp. dominate. Several rare species were encountered, most notably *Solidago pulchra* (Carolina goldenrod), a North Carolina endangered species and a Federal Species of Concern (Amoroso & Finnegan 2002). A complete species list is summarized in Table 2.

Seed Bank Examination

A total of 1,064 individuals representing 43 species germinated over the course of the study. Thirty-three species were recorded from the May 2000 collection and 21 from August 1999. Although there were greater numbers of species in the May 2000 collection, there were greater numbers of individuals from the August 1999 collection (Table3). Eleven species of the total 43 were common to both collection dates. More species were common to disturbed and non-disturbed sites from the same collection date. The disturbed and non-disturbed sites from the August 1999 collection shared 10 of 21 species, whereas the sites from May 2000 shared 13 of 33 species. The disturbed sites from both collection dates had both greater numbers of individuals and greater numbers of species than the non-disturbed sites (Table 3).

Species that emerged in the greenhouse were categorized as indicative, weedy, or "greenhouse" colonizers based on criteria cited in Flora of the Carolinas and Virginia (Weakley 2002), A Synonymized Checklist of the Vascular Flora of the United States, Canada, and Greenland (Kartesz 1994), Manual of the Vascular Flora of the Carolinas (Radford et al. 1964), and the North

Table 1. Basal area/hectare and stems/hectare of trees, and understory percent cover by site type.

Stand Type	*Basal Area (m^2)*	*Stems*	*% Shrub Cover*	*% Ground Line Cover*
Disturbed	21.10 (2.19)	1388.0 (307.53)	171.69 (35.90)	33.03 (11.13)
Non-disturbed	10.25 (2.07)	160.0 (17.79)	70.03 (11.41)	90.83 (26.85)

Standard error of the mean is shown in parentheses.

Figure 1. The image on the left, one of the disturbed sites, is a sharp contrast to a non-disturbed site, shown on the right.

Carolina Natural Heritage Program (Amoroso & Finnegan 2002; R. LeBlond, North Carolina Natural Heritage Program, 1999, personal communication). Species were considered indicative if regularly cited as being consistent members of intact longleaf pine communities. Species responsiveness to disturbance, such as that caused by forestry activities, was not a factor. A positive response to disturbance, such as that exhibited by several species of *Drosera* for example, does not preclude those species from being considered indicative. Native species predictably found in longleaf communities but also found in other plant communities are also considered indicative.

Weedy plants were those typical of highly disturbed areas and were frequently cited as commonly occurring in ruderal environments. These species are not adapted to and are not likely to perpetuate themselves in fire-maintained ecosystems. Greenhouse species likely originated from seeds present within the greenhouse and blown into the greenhouse from surrounding areas. These species were not found in the field sites and were not likely present in the original soil collections. There were three unknown species and five greenhouse species from the August 1999 collection and four unknowns and four greenhouse species from the May 2000 collection. Unknowns and greenhouse species were omitted from the results. The overall numbers of species, as categorized above, from the greenhouse portion of this study are summarized in Table 3.

On both collection dates, from disturbed and non-disturbed sites, over half of all species are classified as indicative. This number is more dramatic from the disturbed sites in the May 2000 collection, where the greatest number of species (29) was encountered, with over 75% of those considered indicative. Weedy species were not well represented. Many of the germinated species were notable and unexpected. ***Pinguicula*** *pumila* (small butterwort), classified as a "significantly rare species" by the North Carolina Heritage Program and considered imperiled in North Carolina by The Nature Conservancy (Amoroso & Finnegan 2002), germinated from both the disturbed and non-disturbed sites from the May 2000 collection and from the disturbed sites from the August 1999 collection. The Federal Species of Concern, *S. pulchra* (Amoroso & Finnegan 2002), germinated from the non-disturbed sites from the May 2000 collection. A complete list of species that germinated in the greenhouse is provided in Table4.

A few species constituting the majority of greenhouse individuals and many species only contributing a few individuals is the trend across all of the sites. Over half of all individuals from the disturbed sites from the August 1999

Table 2. Presence/absence list from the vegetation survey and seed bank examination

	Disturbed Sites		*Non-Disturbed Sites*	
Trees and Shrubs	*Vegetation Survey*	*Seed Bank Examination*	*Vegetation Survey*	*Seed Bank Examination*
Acer rubrum L. var. *ruhrum*	1	0	1	0
Aronia arbutifolia L.	1	1	1	0
Clethra alnifolia L.	1	0	1	1
Cyrilla racemiflora L.	1	0	1	0
Diospyros virginiana L. var. *virginiana*	1	0	1	0
Gaylussacia dumosa (Andrews) Torrey & Gray var. *dumosa*	1	0	1	0
Gaylussacia frondosa (L.) Torrey & Gray ex. Torrey	1	0	1	0
Gordonia lasianthus L.	1	0	0	0
Ilex coriacea (Pursh) Chapman	1	0	1	0
Ilex glabra L.	1	0	1	0
Ilex myrtifolia Walter	1	0	0	0
Ilex opaca Aiton var. *opaca*	1	0	0	0
Liquidambar styraciflua L.	1	0	0	0
Lyonia ligustrina (L.) Augustin de Candolle var. *foliosiflora* (Michx.) Fernald	1	0	0	0
Lyonia lucida (Lamark) K. Koch	1	0	0	0
Lyonia mariana (L.) D. Don	1	0	1	0
Magnolia virginiana L.	1	0	1	0
Morella cerifera (L.) Small	1	0	1	0
Morella pensylvanica (Mirbel) Kartesz	1	0	1	0
Nyssa sylvatica Marshall	1	0	1	0
Persea palustris Rafinesque	1	0	1	0
Pinus palustris Mill.	1	0	1	0
Pinus serotina Michx.	1	0	1	0
Pinus taeda L.	1	0	1	0
Quercus lyrata Walter	1	0	0	0
Quercus nigra L.	1	0	0	0
Rhus copallinum L. var. *copallinum*	1	0	1	0
Rubus L. sp.	0	0	1	0
Sassafras albidum (Nuttall) Nees	1	0	0	0
Vaccinium fuscatum Aiton	1	0	1	0
Vaccinium tenellum Aiton	1	1	1	1
Ground line				
Agalinis purpurea (L.) Pennell	1	0	1	0
Amianthium muscitoxicum (Walter) Gray	1	0	0	0
Andropogon L. sp.	1	0	1	0
Andropogon virginicus L. var. *virginicus*	1	0	1	1
Aristida L. sp.	1	0	0	0
Aristida stricta Michx.	1	0	1	0
Arundinaria gigantea (Walter) Walter	1	0	1	0

Aster L. sp.	0	0	1	0
Aster paludosus Aiton	1	0	1	0
Balduina uniflora (Nuttall)	1	0	1	0
Bartonia virginica (L.) Britton, Sterns, & Poggenberg	0	0	1	0
Carex striata Michx. var. *brevis* Bailey	1	0	1	0
Carphephorus odoratissimus (J. F. Gmelin) Herbert	1	0	1	0
Carphephorus tomentosus (Michx.) Torrey & Gray	0	0	1	0
Centella erecta (L.) Fernald	1	0	0	0
Cleistes bifaria (Fernald) Catling & Gregg	0	0	1	0
Cleistes L.C. Richard ex. Lindley sp.	1	0	1	0
Conyza canadensis (L.) Cronquist	0	1	0	1
Coreopsis L. sp.	0	0	1	0
Cyperus L. sp.	0	0	0	1
Dichanthelium (A. S. Hitchcock & Chase) Gould sp.	0	1	0	0
Dichanthelium chamaelonche (Trinius) Freckmann & Lelong	0	1	0	1
Dichanthelium dichotomum (L.) Gould var. *dichotomum*	1	0	0	0
Dichanthelium dichotomum (L.) Gould var. *nitidum* (Lamark) LeBlond	0	1	0	1
Dichanthelium laxiflorum (Lamark) Gould	0	1	0	1
Dichanthelium mattamuskeetense (Ashe) Mohlenbrock	0	1	0	1
Dichanthelium portoricense (Desvaux ex. Hamilton) B. F. Hansen & Wunderlin	0	0	1	0
Dichanthelium tenue (Muhlenberg) Freckmann & Lelong	1	1	1	1
Dichanthelium = *Panicum lancearium* (Trinius)	1	0	1	0
Dichanthelium = *Panicum webberianum* (Nash)	1	0	0	0
Drosera brevifolia Pursh	0	1	0	1
Drosera capillaris Poiret	0	1	1	1
Eleusine indica (L.) Gaertner	0	1	0	1
Eriocaulon decangulare L. var. *decangulare*	1	1	0	1
Eupatorium album L.	1	0	0	0
Eupatorium capillifolium (Lamark) Small	0	1	0	1
Eupatorium pilosum Walter	1	1	1	0
Euthamia tenuifolia (Pursh) Nuttall	1	0	0	0
Fimbristylis puberula (Michx.) Vahl var. *puberula*	0	0	1	0
Gamochaeta purpurea (L.) Cabrera	0	1	0	1
Gelsemium sempervirens St. Hilaire	1	0	0	0
Gnaphalium obtusifolium L. var. *obtusifolium*	0	1	0	1
Hypericum crux-andreae (L.) Crantz	0	1	0	0
Hypericum densiflorum Pursh	1	0	0	0
Hypericum galioides Lamark	0	0	1	0
Hypericum hypericoides (L.) Crantz	1	0	0	0
Hypericum reductum (Svenson) P. Adams	1	1	1	1
Ionactis linariifolia (L.) Greene	0	0	1	0
Iris verna L. var. *verna*	1	0	1	0
Juncus L. sp.	1	1	0	1
Juncus canadensis J. Gay ex. Laharpe	0	1	0	1
Lachnanthes caroliana (Lamark) Dandy	0	1	0	0
Liatris graminifolia Willdenow	0	0	1	0
Lobelia nuttallii J. A. Schultes	0	0	1	1
Ludwigia alternifolia L.	0	1	0	0
Lysimachia loomisii Torrey	0	1	0	0
Osmunda cinnamomea L. var. *cinnamomea*	1	0	0	0
Osmunda regalis L. var. *spectabilis* (Willdenow) Gray	1	0	0	0

(*Continued*)

Table2. Continued

Trees and Shrubs	Disturbed Sites: Vegetation Survey	Disturbed Sites: Seed Bank Examination	Non-Disturbed Sites: Vegetation Survey	Non-Disturbed Sites: Seed Bank Examination
Oxalis dillenii (Jacquin)	0	1	0	1
Parthenocissus quinquefolia (L.) Planchon	1	0	0	0
Phytolacca americana L.	0	0	0	1
Pinguicula pumila Michx.	0	1	0	1
Pityopsis graminifolia (Michx.) Nutall var. *latifolia* Fernald	0	0	1	0
Platanthera L. C. Richard sp.	0	0	1	0
Platanthera blephariglottis (Willdenow) Lindley var. *conspicua* (Nash) Luer	0	0	1	0
Polygala lutea L.	1	1	1	1
Polygala cruciata L. var. *cruciata*	1	0	1	0
Polygala curtissii Gray	1	0	0	0
Pteridium aquilinum (L.) Kuhn var. *pseudocaudatum* (Clute) Heller	1	0	1	0
Rhexia alifanus Walter	1	0	1	0
Rhexia nashii Small	1	0	0	0
Rhexia petiolata Walter	1	1	0	1
Rhynchospora Vahl sp.	0	1	0	1
Rhynchospora chapmanii M. A. Curtis	0	1	0	0
Rhynchospora fascicularis (Michx.) Vahl var. *fasciculuris*	0	0	1	0
Rhynchospora plumosa Elliott	0	0	1	0
Sabatia Adanson sp.	0	0	1	0
Schizachyrium scoparium (Michx.) Nash var. *scoparium*	1	0	1	0
Scleria Bergius sp.	1	0	0	0
Scleria ciliata Michx. var. *ciliata*	0	0	1	0
Scleria muhlenbergii Steudel	0	1	0	0
Seymeria cassioides (J. F. Gmelin) Blake	0	0	1	0
Solidago pulchra Small	1	0	1	1
Smilax glauca Walter	1	0	1	0
Smilax laurifolia L.	1	0	1	0
Smilax rotundifolia L.	1	0	0	0
Sonchus asper (L.)	0	1	0	1
Stellaria media (L.)	0	0	0	1
Toxicodendron radicans (L.) Kuntze var. *radicans*	1	0	0	0
Utricularia juncea M. Vahl	0	1	0	0
Vaccinium crassifolium Andrews	1	1	1	0
Vitus rotundifolia Michx.	1	0	0	0
Woodwardia virginica (L.) J. E. Smith	1	1	1	0
Xyris ambigua Beyrich ex. Kunth.	0	1	0	0
Xyris baldwiniana J. A. Schultes	0	1	0	0
Xyris caroliniana Walter	1	0	1	0
Xyris jupicai L. C. Richard	0	1	0	0
Zigadenus densus (Desrousseaux) Fernald	0	0	1	0
Total	78	38	69	30

A "1" indicates presence whereas a "0" indicates absence.

Table 3. Summary table of greenhouse seedling emergence results.

	August 1999 Collection		*May 2000 Collection*	
	Disturbed[a]	*Non-Disturbed*	*Disturbed*	*Non-Disturbed*
Total number of individuals	467	193	350	54
Total number of species	17	15	29	17
Total number of indicative[b] species	11	9	22	11
Number of indicative species found only in the seed bank	5	3	15	6
Total number of weedy species	4	3	6	4
Number of weedy species found only in the seed bank	4	3	6	4

Values are absolute numbers.
[a]Refers to disturbed or non-disturbed study sites.
[b]Species were considered indicative if regularly cited as being consistent members of intact longleaf pine communities.

collection were *Dichanthelium chamaelonche* (carpet witch grass), an occasional to rare grass species frequently found in moist longleaf pine savannas and flatwoods (Weakley 2002; R. LeBlond, North Carolina Natural Heritage Program, 1999, personal communication). The genus *Dichanthelium* was well represented in the greenhouse and very typical longleaf pine species germinated from both dates and sites. *Drosera brevifolia* (dwarf sundew) and *Drosera capillaris* (pink sundew) were also well represented and germinated in very large numbers. The dominant plants grouped by disturbed and non-disturbed sites, from each collection date, are listed in Table 5.

Almost half the germinated species classified as indicative, which germinated in the greenhouse from the disturbed sites in the 1999 collection, were not found in the standing vegetation. That number increased to almost 75% from the disturbed sites from the 2000 collection (Table 2). Within the non-disturbed sites, the dominant understory plants from the vegetation survey were completely absent from the seed bank. The most notable absence was that of *A. stricta* from the non-disturbed sites. Table2 provides a complete greenhouse species list as well as indicating which of those were identified in the vegetation survey.

Discussion

Vegetation Survey

The overall vegetative structure of the non-disturbed sites is classic with its open park-like overstory, lack of a midstory, and low-growing understory. Although not the case in these particular sites, high fire tolerance does not always result in a monospecific overstory, and pristine longleaf savannas and flatwoods often contain other pines and scattered hardwood species that establish themselves during unusually long fire intervals (Christensen 1988; Schafale & Weakley 1990). Many tree species typically occurring in moderate to poorly drained longleaf pine sites have not reached tree size in these sites due to the very regular use of prescribed fire as a management tool.

The higher occurrence of shrubs on the non-disturbed sites is probably due to the dormant-season fire regime versus a more natural growing-season fire regime. Shrubs will persist under fire regimes of periodic winter burns (once every 3-6 years), annual winter burns, and under periodic summer burns (Lewis & Harshbarger 1976). Although the fire frequency retards overall shrub growth and prevents shading of herbaceous species, the high occurrence of shrubs may eliminate some herbaceous species due to increased competition. Although the non-disturbed sites contain fewer herbaceous species than the disturbed sites, the species they do contain are much more indicative of longleaf pine savanna and flatwood sites and the percent cover is generally higher than that of disturbed sites.

Within the disturbed sites, development of a dense canopy of species other than longleaf pine, growth of a thick shrub midstory. and loss of the fire-adapted, shade-intolerant understory species are promoted by fire suppression (Christensen 1988; Frost 1990). In this case, of course, the canopy species is planted loblolly pine. The hardwoods, which only currently represent 3% of the basal area per hectare, may become more dominant over time under the long fire intervals, particularly on these moist sites (Heyward 1939). The forb and grass layer of longleaf pine communities may be lost in 7-10 years under fire exclusion and a closed canopy (Frost 1990). The dominant herbaceous plants in the disturbed sites are adapted to and able to compete under the well-developed midstory, which provides almost complete understory shading. Ground line species, generally thought of as occurring in natural longleaf ecosystems, tended to occur in the few, small open areas in the disturbed sites.

Seed Bank Examination

Many factors contribute to the species differences observed in the greenhouse both between collection dates and between disturbed and non-disturbed sites.

The greater species differences between collection dates, versus disturbed and non-disturbed sites, may in part be due to seasonal variation in dormancy breaking requirements based on collection date (Whipple 1978). Soil collected pre-summer in May 1999 received

Table 4. Seed hank species, number of individuals, and classification

	Site		
	Non-Disturbed	*Disturbed*	*Classification*
August 1999 Collection			
Andropogon virginicus var. *virginicus*	1	0	Weedy
Clethra alnifolia	1	0	Indicative
Conyza canadensis	7	23	Greenhouse
Dichanthelium chamaelonche	41	281	Indicative
Dichanthelium laxifolium	12	22	Indicative
Drosera brevifolia	72	42	Indicative
Drosera capillaris	47	25	Indicative
*Eleusine indica**	1	1	Weedy
Eupatorium capillifolium	1	1	Weedy
Gnaphalium obtusifolium var. *obtusifolium*	0	1	Weedy
Hypericum reductum	4	6	Indicative
Juncus sp.	1	9	
Oxalis dillenii	8	8	Greenhouse
Pinguicula pumila	0	2	Indicative
Polygala lutea	5	16	Indicative
Rhexia petiolata	1	11	Indicative
Rhynchospora sp.	2	30	
*Sonchus asper**	0	2	Weedy
*Stellaria media**	1	0	Weedy
Vaccinium crassifolium	0	2	Indicative
Vaccinium tenellum	1	3	Indicative
Xyris ambigua	0	13	Indicative
Total	206	498	
May 2000 Collection			
Aronia arbutifolia	0	1	Indicative
Conyza canadensis	6	10	Greenhouse
Cyperus sp.	1	0	
Dichanthelium sp.	0	15	
Dichanthelium chamaelonche	4	37	Indicative
Dichanthelium dichotomum var. *nitidum*	4	27	Indicative
Dichanthelium mattamuskeetense	4	18	Indicative
Dichanthelium tenue	3	75	Indicative
Drosera hrevifolia	2	5	Indicative
Drosera capillaris	11	3	Indicative
Eupaforiurn capillifolium	2	9	Weedy
Eupatorium pilosum	0	7	Indicative
Gamochaeta purpurea	6	8	Weedy
Gnaphalium obtusifolium var. *obtusifolium*	1	1	Weedy
Hypericum crux-andreae	0	5	Indicative
Hypericum reductum	3	2	Indicative
Juncus canadensis	1	9	Weedy
Lachnanthes caroliana	0	1	Indicative
Lobelia nuttallii	2	0	Indicative
Ludwigia alternifolia	0	1	Weedy
Lysimachia loomisii	0	2	Indicative
Phytolacca americana 1 Greenhouse			
Pinguicula pumila	2	1	Indicative
Polygala lutea	3	9	Indicative
Rhexia petiolata	0	13	Indicative
Rhynchospora sp.	1	0	
Rhynchospora chapmanii	0	61	Indicative
Scleria muhlenbergii	0	3	Indicative
Solidago pulchra	4	0	Indicative
*Sonchus asper**	4	0	Greenhouse
Utricularia juncea	0	2	Indicative
Vaccinium tenellum	0	2	Indicative
Woodwardia virginica	0	1	Indicative
Xyris ambigua	0	29	Indicative

(*Continued*)

Table 4. *Continued*

	Site		
	Non-Disturbed	Disturbed	Classification
Xyris baldwiniana	0	2	Indicative
Xyris jupicai	0	1	Weedy
Total	65	360	

Collection dates are presented in separate lists. Each species is classified as indicative, weedy, or greenhouse. Unknown species arc omitted and those identified only to the level of genus arc not classified. Classification determinations are based on Weakley (2002), Radford (1964), Kartesz (1994). and LeBlond (North Carolina Natural Heritage Program, 1999, personal communication).
'Indicates a non-native species.

natural cold stratification just before placement in the greenhouse under conditions likely to prompt germination. Differences may be further compounded by uneven distribution of seed populations in the soil, which tend not to be homogenous or normally distributed. Seed distribution in the soil can have tremendous spatial variation even at the scale of a few meters (Benoit et al. 1989; van der Valk 1992). A less-common species like *Pinguicula pumila* would not be expected to be represented by many individuals; however, this was not the case with several species of ***Dichanthelium.*** Why these species were so well represented and a naturally abundant species such as ***Rhexia petiolata*** was not is uncertain.

In addition to uneven seed distribution, differences may also be due to one or more factors such as uneven predisturbance abundance or inadequate sampling of the soil. There is spatial variation of aboveground conditions and vegetation patterns over time. The spatial distribution of persistent seed banks can also vary with seed predation, seed pathogenesis, and seed viability, which themselves vary spatially (Hyatt & Casper 2000). The numerous factors potentially affecting spatial heterogeneity of seeds contribute to the difficulty of hypothesizing on why there are large differences in numbers not only between collection dates but also among the disturbed and non-disturbed sites.

There is often a lack of correspondence between standing vegetation of an area and the seed bank composition (Thompson & Grime 1979; Augusto et al. 2001), and this holds true for both the disturbed and undisturbed sites. This lack of correspondence is likely due to several factors. The vegetative structure of the disturbed sites with extensive shrub cover, complete shading, and heavy litter limits in situ germination of shade-intolerant species potentially present in the seed bank. The lack of shrub presence in the seed bank is likely due to both the inability of seedling emergence technique to detect tree and shrub species (Thompson & Grime 1979; Brown 1992) and the clonal nature of many of these species. The absence of dominant plants on the non-disturbed sites may in large part be due to season of burn, which may influence the flowering and seed production of many species, most notably wiregrass (Platt et al. 1988). Wiregrass abundance is critical for restoration because it is the primary species for carrying low-intensity fire. It can be considered a keystone species in the ecosystem (R. LeBlond, North Carolina Natural Heritage Program, 2000, personal communication; Weakley 2002). Additionally, some research suggests clonal reproduction is more prevalent in systems with regular, small-scale disturbance (Fenner 1985; Thompson 1992).

Conclusions

In spite of number and species differences among seed bank collection dates and disturbed and undisturbed

Table 5. The most frequently occurring species germinating in the greenhouse.

Disturbed Sites	Non-Disturbed Sites
August 1999	
Dichanthelium chamaelonche (60%)	*Drosera brevifolia* (37%)
Drosera brevifolia (9%)	***Drosera capillaris* (24%)**
Drosera capillaris (5%)	*Dichanthelium chamaelonche* (21%)
Dichanthelium laxiflorum (5%)	*Dichunthelium laxiflorum* (6%)
***Polygala lutea* (3%)**	***Polygala lutea* (2%)**
May 2000	
Dichanthelium tenue (21%)	***Drosera capillaris* (20%)**
Rhynchospora chapmanii (17%)	***Dichanthelium dichotomum* var. *nitidum* (7%)**
Dichunthelium chamaelonche (11%)	*Dichanthelium chamaelonche* (7%)
Xyris ambigua (8%)	*Dichunthelium mattamuskeetense* (7%)
***Dichanthelium dichotomum* var. *nitidum* (8%)**	***Solidago pulchra* (7%)**

The number in parentheses is the percent contribution of that species to the total number of individuals for that collection date and site type. Species shown in bold were also encountered in the vegetation survey.

sites, several conclusions can be made. Of primary importance is the detection of a viable and persistent seed bank in highly disturbed, former longleaf pine ecosystems. Not only are seed banks present, but they are of value with regard to species composition and may provide an additional tool for restoration in areas considered too disturbed for restoration. Many detected species are considered to be not only indicative, but rare to longleaf pine ecosystems. Seed dormancy is an adaptive trait of many plant species, and variation exists in the length of seed viability and the necessary cues for germination (Simpson 1990). It is possible that rare and other species of pristine longleaf ecosystems occur in the seedbed and that they might also germinate given the proper conditions. Considerable work needs to be conducted before a prescription can be developed for utilizing longleaf pine ecosystem seed banks in a restorative capacity. However, the confirmation of a viable seed bank is the first step toward realizing this potential.

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