RESEARCH ARTICLE

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Starting New Populations of Longleaf Pine Ground-layer Plants in the Outer Coastal Plain of South Carolina, USA

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ABSTRACT: Southeastern United States habitats dominated by longleaf pine (*Pinus palustris* Miller) and associated plant species have declined dangerously. Conservation of rare and common plants of longleaf pine habitats may be aided by starting new populations in the field. We review methods for initiating plant populations and integrate information from our studies of rare and common longleaf pine ground-layer plants of the outer South Carolina Coastal Plain. In our experience it is possible to start new populations of most longleaf pine ground-layer plants, including rare species if (1) seeds are collected from frequently burned sites with reasonably large populations of desired species; (2) appropriate media are used for seedling propagation; (3) outplanting of nursery grown seedlings or direct seeding is done during periods of sufficient soil moisture; and (4) introduction sites properly match habitat requirements (inferred from indicator plants) of desired species, and the sites can be managed with frequent prescribed fire.

Index terms: Longleaf pine, *Pinus palustris,* rare plants, reintroduction, southeastern United States

INTRODUCTION

Longleaf pine (*Pinus palustris* Miller) savannas and woodlands are characterized by a sparse tree canopy and a very rich ground layer usually dominated by herbs (Bridges and Orzell 1989, Peet and Allard 1993). Decline of these biologically rich habitats, which once encompassed vast areas of the southeastern United States, is well documented (Frost 1993, Harcombe et al. 1993). Only about 3% of an estimated 37 million ha remains. Contributing factors include logging, clearing, intensive forestry, and, perhaps most important, fire exclusion. Although precise data are not available for many species, most herbaceous plants in longleaf pine dominated habitats apparently require frequent (i.e., mean fire return intervals less than 5 years), low-intensity fires for population maintenance (Lemon 1949, Platt et al. 1991, Waldrop et al. 1992). (Plant nomenclature follows Kartesz [1994] unless otherwise indicated.)

Given the continuing loss and endangerment of high quality longleaf pine habitats (e.g., Porcher et al. 1999), many of their characteristic plants could, or should, be considered rare or endangered. Two groups of species may be at greatest risk. The first group includes species that fit the traditional definition of rarity-species with small population sizes, few populations, or very limited geographic or ecological ranges (see Morse 1996, Gaston 1997 and references therein). These species typically appear on federal or state rare lists, and receive low G-ranks from The Nature Conservancy. Hardin and White (1989) and Walker (1993) compiled and published lists of longleaf pine associated species that meet these traditional criteria for rarity. Walker's (1993) list included 389 species, 187 of which were considered rare range-wide and vulnerable to extinction (G-ranks = 1-3). Most are herbaceous perennials that depend on frequent natural fire. More than half (65%) occur in moist longleaf pine habitats (i.e., seasonally flooded flatwoods and savannas, depressions, shrub bog ecotones, seepage slopes, pond margins), although many (45 species, 24.2% of the total) occur in typical mesic-dry upland habitats (Walker 1993). An update of Walker's (1993) list, available online at http://www.talltimbers.org/research.html, includes 256 additional species. This large increase reflects, in part, the endangerment of ever-larger numbers of ground-layer plants of longleaf pine habitats.

The second group of at-risk species includes formerly dominant, but still often locally abundant, "climax" grasses of North American prairies and savannas. These grasses tend to be shallow-rooted and are highly susceptible to even light to moderate disturbance of upper soil horizons such as mechanical site preparation for artificial regeneration of pine stands (e.g., Schultz 1976).

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Wind-pollinated and limited in dispersal, these plants may also be particularly vulnerable to habitat fragmentation and declining population size (Tilman et al. 1997).

Ecologists generally agree that conservation is a more effective tool for protecting and maintaining biodiversity than restoration (Falk et al. 1996). Fortunately, some large tracts of properly managed, high quality longleaf pine habitat remain on private and public lands. Nevertheless, to counteract continuing loss of biodiversity, it may be necessary to start new populations of the most threatened species (Falk et al. 1996, Pavlik 1996). There are three basic strategies for starting plant populations: translocation (i.e., moving individuals or parts of individuals directly from field populations), outplanting of nursery grown seedlings or cuttings, and direct seeding (Guerrant 1996). Each strategy involves several procedural issues. For example, to successfully grow and outplant seedlings one must collect and process the seed, germinate it, select a growth medium, choose a planting site, and manage the new population. Direct seeding also involves seed collection and germination and requires information on the environmental and biotic conditions needed to maximize germination and establishment under field conditions. Translocation may be the easiest initiation technique, although it is often hard to justify ethically, and choice of planting site and transplant conditions are critical concerns (Hall 1986).

This paper reviews methods for starting populations of ground-layer plants of longleafpine savannas and woodlands, and includes some of our own unpublished data. We emphasize species additions to relatively intact communities. In contrast, Pfaff and Gonter (1996) discussed community restoration on badly degraded or reclaimed land. We discuss results from our studies of both rare and common longleaf pine ground-layer plants because (1) many rare plant species have not been well studied, and studies of related common species might provide important hints about common biological characteristics and propagation strategies (e.g., Buchele et al. 1991); (2) the process of endangerment of longleaf pine ground-layer plants has been going on for centuries, and historical evidence suggests that many currently rare species were more common prior to recent antbropogenic declines (Elliott 18161824, Porcher 1848, Ravenel 1876, Weakley 1999); and (3) if current trends continue, today's common species may be rare in the near future. In the first section of this paper we discuss seed issues, including choice of collection sites and dates, seed processing and storage, and germination tests. The second section covers seedling issues and includes considerations of seedling propagation, planting sites, and seedling performance after outplanting. This section also contains results from a small translocation experiment we conducted with ***Agrimonia incisa***, a globally rare forb of subxeric longleaf pine habitats. The third section discusses direct seeding methods, and compares results from two of our own studies of direct seeding that varied with respect to competition control. Finally, we briefly discuss native plant gardens and the potential role of gardens as refuges and source populations. For each topic, we first provide a review of pertinent literature, and when appropriate, present our own unpublished data. We present data suggesting that it is not difficult to start new populations of longleaf pine ground-layer plants, including rare species, if the introduction site is located in an appropriate habitat and can be managed with frequent fire.

I: SEED ISSUES

Seed Collection Sites and Dates

Finding a quality seed collection site is usually the first step in starting a new plant population. Unfortunately, there is little information on collection site quality for longleaf pine ground-layer species. For rare species generally, seeds should be collected from large populations to adequately capture the range of genetic variability present in the population and to minimize inbreeding depression (Center for Plant Conservation 1991, Zettler and McInnis 1992). However some seeds also should be collected from small populations because interpopulation genetic variation can be high (Center for Plant Conservation 1991). For further recommendations on seed sampling for genetic diversity, see Center for Plant Conservation (1991).

Fire history is an important factor in site quality for ground-layer plants of longleaf pine habitats. Frequently burned sites have reduced competition from hardwood shrubs and sprouts (Waldrop et al. 1992), resulting in more vigorous ground-layer plants with larger inflorescences and greater seed production. On sites with a history of frequent fire, canopy density can have an influence on seed viability. Means (1997) found a negative correlation between density of overstory slash pine (***Pinus elliottii***) and seed viability of ***Aristida beyrichiana*** Trinius and Ruprecht. Fire history also influences seed predation, which can have a major impact on seed availability. Hiers et al. (2000) found that approximately 68% of ***Tephrosia virginiana*** pods in unburned control plots contained seed predators compared to only 23% in burned plots.

Seed production of most longleaf pine ground-layer species tends to decline with time since burning. Seeds are most abundant during the year of the bum, or, if the bum occurs late in the year, the following growing season. However, some species, such as ***Gymnopogon ambiguus***, ***Aristida purpurascens,*** and ***Muhlenbergia capillaris***, flower and produce abundant seed for several years following fire (Pfaff and Gonter 1996). It is not known whether seed quality in these species declines with time since fire.

Season of burning can affect seed production. Many pine savanna grasses, and some composites, flower more prolifically after growing-season bums (Streng et al. 1993). Efficiency of wind and insect pollination tends to increase with larger numbers of flowering stems (Kunin 1997), and it might be expected that growing-season bums would lead to increased seed production. However, Hiers et al. (2000) did not find a consistent, positive effect of growing-season burns on sexual reproduction (flower and fruit production) of legume species common in dry longleaf pine woodlands. Rather, species responded individualistically to burn season. Further, there appeared to be little overall effect of burn season on seed production in the three focal species.

We collected and tested (see "Germination Tests" for germination methods) seed of 42 ground-layer species from 15 longleaf pine sites (Table 1) in or near the Francis Marion National Forest (FMNF), northeast of Charleston, South Carolina. Except for two roadside sites that were maintained by mowing, all sites had a recent history of tire and a relatively open longleaf pine canopy. Although most collections had germination rates > 30% (Table 1, Figure 1), there was considerable variability in percent germination, even within the same species.

The literature suggests that information on bum season and time-since-bum can help predict quality seed collection sites. To test the effect of bum season, we selected 11 species for which we had collected seed from both dormant-season bum sites and growing-season bum sites. Data were compared using a paired t-test. Consistent with Hiers et al. (2000), mean seed germination for the two treatments were similar (growing season = 36.7% germination; dormant season = 30.4%) and there was no significant effect of bum season (t = df = 10, ***P = 0.37***). To test effects of time-since-bum, we collected seed of *Eupatorium rotundifolium* and *E. leucolepis* from a site that had been burned approximately 2 years previous and from sites burned earlier within the same year. Germination rates were similar regardless of the time elapsed since burning. It appears that for these species, quantities of viable seed may be obtained from sites not burned for at least 2 years, assuming that competition from shrubs is not excessive.

Our results suggest that quality of seed collection sites for longleaf ground-layer species cannot be entirely predicted by time-since-bum or bum-season. To maximize genetic diversity, it might be advisable to collect seed following a variety of different bum treatments or periods of time without burning.

Table 1. Results of germination tests 19961999. Letter code below species name is a collection site label. Collection dates are next to the site labels. Burn codes are as follows: D= dormant season burn, G = growing season burn, G -1 = growing season burn in the previous year; except for G - 1 all burns occurred less than 1 year prior to the date of seed collection. "Germ tray" indicates germination tests carried out in closed plastic germination boxes with seeds on moist blotting paper. Tests were performed on a bench placed next to a window at room temperature with no attempt to precisely control light or temperature. "Grow tray" is for outside germination tests carried out in standard horticultural trays filled with moist sand. For these latter tests seed was placed on top of cells within 1 month after it was collected from the field sites. Thus these seeds were exposed to a regime of natural light and temperature fluctuations. Numbers under column headings are germination percentages. If different from n=100, sample size is listed in parentheses after the germination result. For *Carphephorus tomentosus* stage of seed maturity is indicated after each line as follows: NE = pappus not expanded, E = pappus expanded, but heads not entirely opened, G = pappus expanded, heads opened, seeds arranged in a 360 degree pattern around the heads, thus appearing globose (• preceding name indicates that it is locally rare). Globally rare species (Walker 1993), *Parnassia caroliniana, Plantago sparsiflora, Rhexia aristosa, Tridens ambiguus* and *Sporobolus pinetorum* Weakley & P.M. Peterson are preceded by **. Results for *P. caroliniana* are given for covered (cov.) and uncovered (unc.) seeds (see also Figure 5).

	Collection Date	Burn Season	*Germ* Tray	*Grow* Tray
A. APIACEAE				
Oxypolis filiformis				
(AS)	10/05/99	G	75.3(150)	
B. ASTERACEAE				
Arnica acaulis				
(PL)	05/28/96	G	90.0	64.3(115)
(SO)	05/12/98	G	48.7(150)	
(SCTS)	05/24/99	D	57.3(150)	
Aster concolor				
(MS)	01/24/97	G	10.3(107)	1.4(73)
Aster dumosus				
(HC)	01/21/97	D	14.0	12.5(96)
(MS)	01/24/97	G	50.0(128)	47.4(97)
Aster linariifolius L.				
(HC)	01/21/97	D	5.0(80)	0.0(26)
(MS)	01/24/97	G	46.8(79)	48.0(25)
Aster tortifolius				
(HC)	01/21/97	D	20.7(29)	33.3(10)
Aster walteri				
(HC)	01/21/97	D	78.7(61)	66.7(15)
(MS)	01/24/97	G	63.7(104)	74.7
Bigelowia nudata				
(HC)	11/27/96	D	52.0	51.0
(HC)	01/21/97	D	29.8(57)	
(HC)	01/21/97	D	0.0(60) (ABORTED SEED?)	
Carphephorus paniculatus				
(HC)	10/26/96	D	1.8(57)	5.0(20)
(HC)	11/27/96	D	35.0	30.4(92)
(HC)	01/21/97	D	42.2(90)	42.0(88)
(MS)	01/24/97	G	21.8(101)	19.0
• *Carphephorus tomentosus*				
(PL)	10/28/96	G	29.6(142)	45.0(80) NE
(PL)	10/28/96	G		44.4(36)E
(PL)	11/27/96	G	17.0(53)	41.6(36) NE
(PL)	11/27/96	G	21.0	30.9(81) E
(PL)	11/27/96	G	35.3(68)	72.2(54) G

continued

Seed Collecting Technique

To maintain appropriate levels of genetic diversity in new plant populations, it is important that collection methods ensure genetic diversity (Center for Plant Conservation 1991, Guerrant 1996). Random or systematic sampling can avoid biasing the sample toward large, vigorous, or easily accessible plants (Huenneke 1991). At a minimum, effort should be made to collect seeds from all areas of a donor population's habitat and from all plant morphological types.

A goal of seed collecting is to obtain mature or hardened seed rather than immature "soft" seed. A time-honored method of assessing maturity is to bite the seed. Generally, ripe seed cannot be bitten in two. Apfelbaum et al. (1997) list four additional cues to guide seed collection of tallgrass prairie species: (1) seeds are full size, (2) seeds have changed color (i.e., from green to a darker hue), (3) seed-bearing stalks have dried, and (4) seed has begun to drop. We disagree somewhat with cue 3. In the southeastern United States, plant stem and leaf tissue often remains green into the winter, thus plants dispersing seed may have green stems. Also longleaf pine savannas contain many spring-flowering plants that stay green in the summer after flowering.

Another good cue for detecting ripe seeds in many plant families (e.g., Melastomataceae, Onagraceae, Saxifragaceae) is the presence of dehiscent capsules. Many capsules act as "salt and pepper shakers" that continue to disperse viable seeds for many months after opening. Another cue is the ease with which the seeds can be removed from the plant: ripe seeds can typically be dislodged with minimal effort; unripe seeds are much harder to remove. Young and Young (1986) suggested a more quantitative indicator: monitoring seed moisture content. Moisture content is high in immature seeds, but declines to approximately 10% as seeds mature. Philips (1985), Clinebell (1997), and Zettler (1997) provided numerous suggestions for collecting seeds of more specialized groups of plants such as prairie genera and Orchidaceae (a notoriously challenging family).

Table 1, ***continued***

	Collection Date	Burn Season	Germ Tray	Grow Tray
Chaptalia tomentosa				
(WH)	04/14/98	-	88.7(150)	
(SIM)	04/16/99	-	64.0(150)	
Chrysopsis gossypina				
(C169)	01/19/99	G	32.7(150)	
Chrysopsis mariana				
(MS)	01/24/97	G	28.3(99)	40.0(90)
Coreopsis oniscicarpa Fern.				
(MS)	01/24/97	G	30.1(83)	28.9(45)
Erigeron vernus				
(C195)	06/07/98	G	10.0(150)	
(SCTS)	05/24/99	D	1.2(80)	
Eupatorium leucolepis				
(MS)	01/24/97	G	43.0	27.1(96)
(SO)	01/14/99	G-l	32.0(150)	
Eupatorium rotundifolium				
(HC)	01/21/97	D	24.0(121)	26.3(99)
(MS)	01/24/97	G	15.0	7.4(94)
(SO)	10/14/99	G-l	46.7(150)	
Liatris squarrosa				
(C195)	12/01/98	G	62.0(150)	
Pityopsis graminifolia				
(HC)	01/21/97	D	2.6(115)	2.0(99)
Pterocaulon pycnostachyum (Michx.) Ell.				
(HAC)	06/23/96	D	31.0	21.7(115)
(HAC)	06/29/96	D	42.0(115)	20.0
(HC)	07/02/99	D	44.7(150)	
Solidago fistulosa				
(MS)	01/23/97	G	49.1(57)	
Solidago odora				
(HC)	01/21/97	D	0.0(29)	0.0(20)
Vemonia angustifolia				
(C195)	10/24/98	G	35.3(150)	
C. FABACEAE				
Desmodium tenuifolium				
(HC)	01/21/97	D	59.6(57)	53.8(26)
Lespedeza capitata				
(HC)	10/06/96	D	11.4(35)	
(MS)	01/23/97	G	7.3(41)	
Rhynchosia reniformis				
(HAC)	06/15/96	D	94.9(59)	42.4(59)
(HAC)	06/23/96	D	32.8(61)	13.3(60)
(HAC)	06/29/96	D	0.0(59)	0.0(60)
(C184)	06/22/98	D	48.7(150)	
Tephrosia virginiana				
(C195)	08/03/98	G	70.0(150)	
D. HYPERICACEAE				
Hypericum setosum				
(HC)	01/21/97	D	13.4(120)	8.3(108)
(HC)	01/21/97	D	46.7(120)	

NOTE: top line is after 4 months, bottom line is germination after 1.5 years.

continued

One method to determine the best time to collect seeds of a particular species is to resample the same population over time as seeds mature (e.g., Seamon et al. 1989). We employed this technique for representative species of four major plant families of longleaf pine ground-layer plants as part of the germination study mentioned above. To avoid bias, we established transects at two sites (PL and HC in Table 1) and selected different random locations for each collection date.

Germination tests of these various collections (see "Germination Tests" for methods) indicated substantial changes in seed germination rates among collection dates for most species (Figure 2). Furthermore, the changes were systematic, rather than entirely random, so that it was possible to determine an optimal collection period. We recommend collecting ***Rhynchosia reniformis*** seeds in mid-June, ***Rhexia alifanus*** in late November (despite the fact that this species flowers in mid-summer and capsules appear to open by early September), and ***Carphephorus paniculatus*** seeds in mid-December. ***Ctenium aromaticum***, a dominant grass of wet savannas in South Carolina, did not display a discrete germination maximum across the range of collection dates. For this species it appears that viable seed can be collected over a broad period from early October through early February.

Prior results such as those presented above can provide guidance as to when to collect seeds of particular species. Because maturation dates can vary among years for a variety of reasons, it is also important to evaluate seed maturity cues when deciding when to collect seed. For example, seeds of ***Carphephorus tomentosus*** (a fall-flowering composite at the southern edge of its range in the FMNF and consequently locally rare) collected from site PL on two dates in the autumn of 1996 (Table 1) showed best germination from seed collected in late November and classified as "globose" (i.e., pappus fully expanded and seed arranged in a 360° pattern around the peduncle attachment point; Figure 3). Typically, globose Asteraceae inflorescences contain seeds that have good germination rates unless the seed is damaged in some fashion. In another example, a striking

Table 1, *continued*

	Collection Date	Burn Season	Germ Tray	Grow Tray
E. MELASTOMATACEAE				
** *Rhexia aristosu*				
(HC)	10/06/96	D	3.6(55)	0.0(55)
(HC)	10/28/96	D	1.1(90)	6.2(81)
Rhexia nashii				
(HC)	10/06/96	D	56.7(60)	63.3(60)
(HC)	10/28/96	D	2.5(80)	60.0(80)
Rhexia alifanus				
(HC)	10/06/96	D	12.0	2.0
(HC)	10/26/96	D	9.0(95)	6.3(95)
(HC)	11/27/96	D	22.1(68)	20.0(115)
(HC)	01/21/97	D	13.4(98)	2.4(85)
(C195)	09/13/98	G	4.7(150)	
F. ONAGRACEAE				
Ludwigia virgata				
(HC)	01/21/97	D	6.1(115)	11.0
G. PAFWASSIACEAE				
** *Parnassia caroliniana*				
(BH)	12/19/94	D		34.0 (Cov)
(BH)	12/19/94	D		20.0 (Unc)
H. PLANTAGINACEAE				
** *Plantago sparsijlora*				
(WH)	6/15/98	Mowed	17.6(228)	
I. POACEAE				
Aristida virgata Trin.				
(HC)	01/21/97	D	48.4(93)	43.1(65)
(MS)	01/23/97	G	58.3(103)	66.2(74)
Ctenium aromaticum				
(HC)	10/06/96	D	27.0	25.8(89)
(HC)	10/28/96	D	30.0	23.1(91)
(HC)	11/27/98	D	21.0	21.0
(HC)	01/23/97	D	19.4(98)	29.8(94)
(MS)	01/24/97	G	36.4(110)	20.9(110)
(C195)	12/02/98	G	3.0(150)	
Muhlenbergia expansa (Poir) Trin.				
(PL)	10/29/96	G	12.0	13.0
Panicum virgatum				
(MS)	01/23/97	G	9.9(91)	1.3(80)
Schizachyrium scoparium				
(PL)	10/24/96	G	5.0	11.0
(C196)	11/23/98	G	55.3(150)	
** *Sporobolus pinetorum* Weakley & P.M. Peterson				
(PL)	10/29/96	G	51.0	23.3(30)
** *Tridens ambiguus*				
(PL)	10/28/96	G	88.0	68.0
J. POLYGALACEAE				
Polygala lutea				
(SO)	07/07/98	G	28.7(150)	

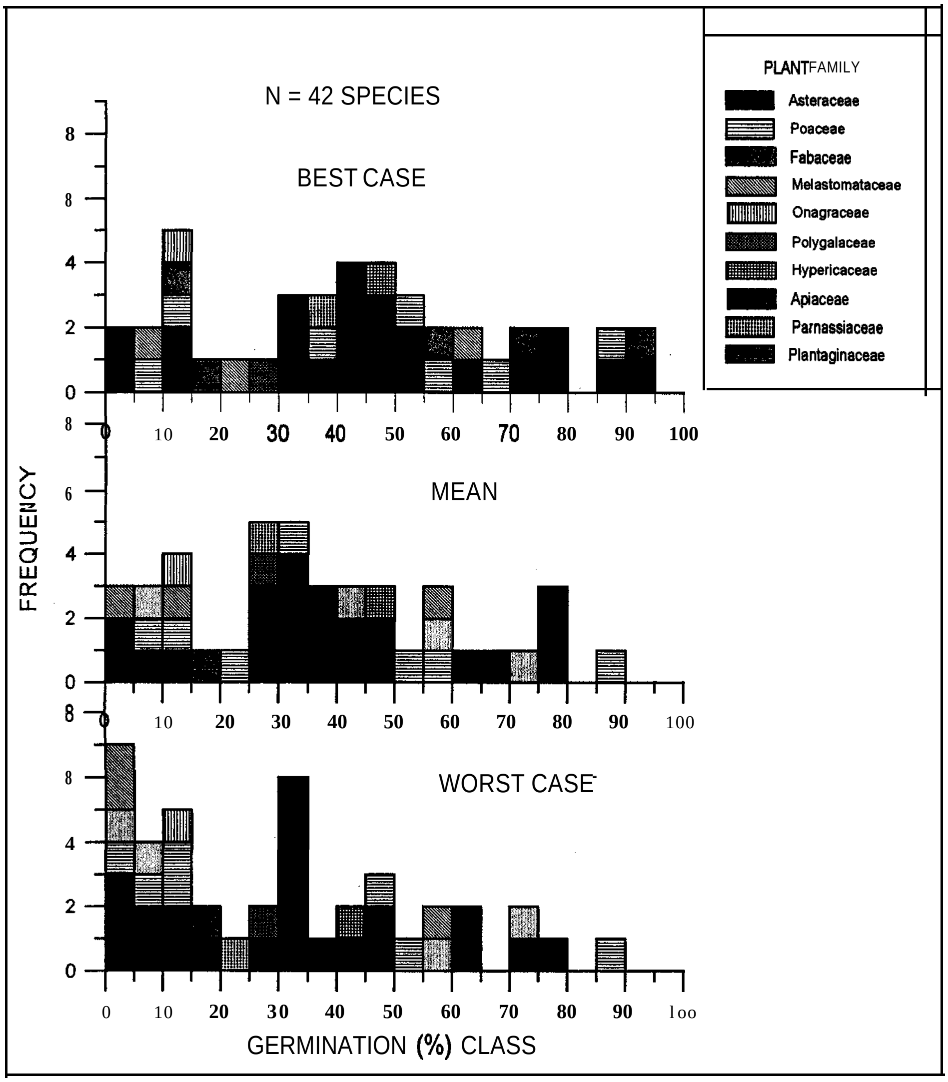

Figure 1. Germination results summarized according to plant family. Top graph ("best case" includes the best germination results for each species; middle graph ("mean") includes mean of all tests; bottom graph ("worst case") includes the single poorest result for each species.

decline in germination rates was observed among seed collections of ***Rhynchosia reniformis*** (a species of dry sites in the Fabaceae) made during June 1996 (Figure 2). This probably indicated hardening of the seed coat and development of induced dormancy, typical of seed maturation in this family (Fenner 1985, Pfaff and Gonter 1996).To successfully germinate legume seed, it appears best to collect shortly before complete maturity and to germinate seeds as soon as possible after collection; otherwise mechanical or chemical scarification may be required to promote germination (Young and Young 1986; R.J. Mitchell, scientist, Joseph W. Jones Ecological Research Center, Newton, Ga., pers. corn.).

Seed Processing and Storage

Generally, there are four stages in seed processing: seed drying, seed threshing, seed scalping, and seed cleaning (Young and Young 1986, Band and Hendry 1993, Apfelbaum et al. 1997). Processing is required if seeds are to be stored or if seed purification is desirable.

Seeds can be dried by: (1) placing them on wire mesh trays and circulating air around them (Apfelbaum et al. 1997), (2) placing seed trays in a warm greenhouse (Apfelbaum et al. 1997) or ventilated room with low humidity (Philips 1985), or (3) placing seeds in paper bags in a ventilated greenhouse (Young and Young 1986) or drying room where relative humidity can be controlled (Apfelbaum et al. 1997). Some species may require special handling. For example, orchid capsules should be dried thoroughly (i.e., to around 5% moisture content) within 24 hours of collection using a desiccant (such as Drierite, $CaSO_4$) to minimize damage by bacteria and fungi (Zettler 1997).

Threshing, which is the process of separating seed from the inflorescence, occurs naturally as capsules or pods dry and split apart. Vigorously shaking capsules in a paper bag may be all that is required (Philips 1985). For recalcitrant species several techniques are available for hand threshing: rubbing fruits against a coarse screen, using rolling pins, or rubbing between paddles. For the screening technique (our preference), Apfelbaum et al. (1997) and Clinebell (1997) recommend 0.25-inch mesh for "most species," and 0.5-inch for very large seed (e.g., *Silphium* spp.). Hand threshing can be tedious, and the use of a mechanical hammermill is recommended for processing large amounts of seed (Young and Young 1986, Apfelbaum et al. 1997).

Scalping, or coarse cleaning, can be done with the same size screen used for threshing (Young and Young 1986, Apfelbaum et al. 1997, Clinebell1997). Seed can then be cleaned more thoroughly by using progressively finer screens (Philips 1985, Apfelbaum et al. 1997; see Clinebell 1997 for recommendations on screen sizes). Mechanical cleaning can involve a fanning mill or several other types of equipment (Young and Young 1986, Apfelbaum et al. 1997). After cleaning seed, Band and Hendry (1993: 9) recommended additional drying in a "dehumidifying chamber maintained at a constant relative humidity of 25% and temperature of 19-23" C until the moisture content has fallen to 5–7%." Harrington (1972, 1973), cited in Apfelbaum et al. (1997), recommended a moisture content of 5–14% for nonaquatic herbaceous seeds.

Seed moisture is an important consideration in seed storage. Drying times and storage conditions vary with the length of

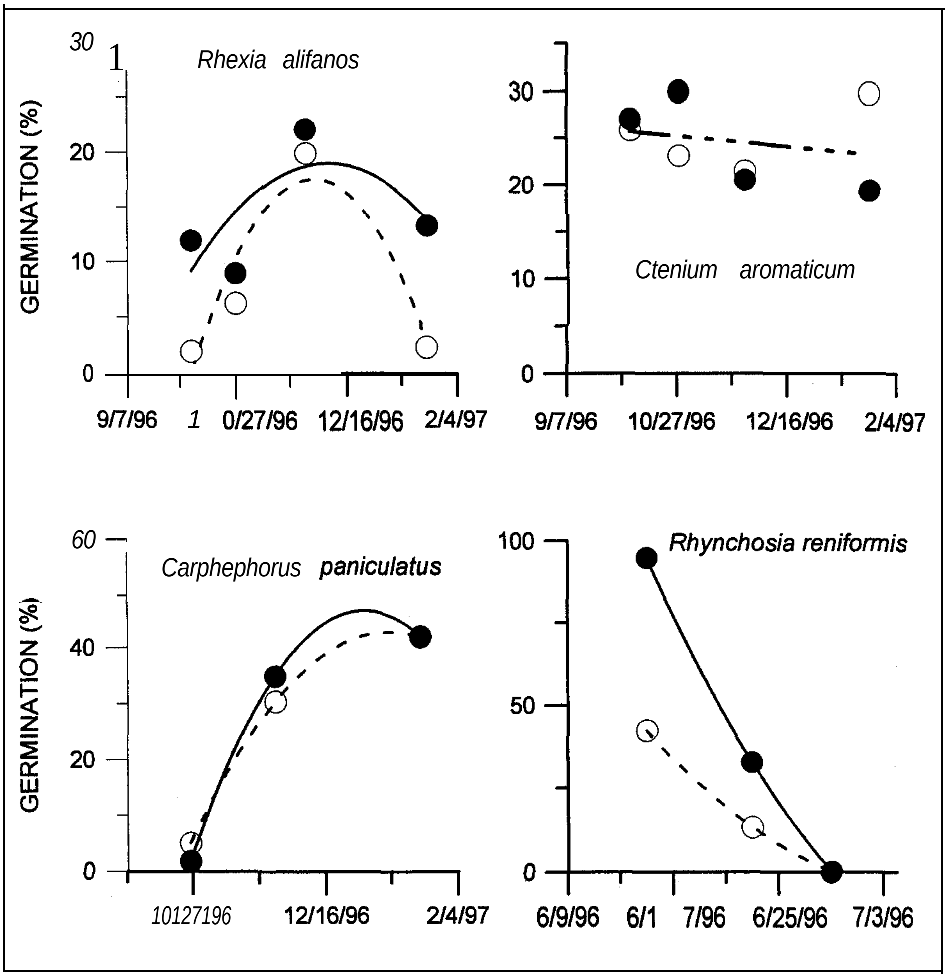

Figure 2. Germination test results plotted according to date of seed collection for four "representative" species of different plant families. Curves are for best fit polynomials. Solid circle = germination tray; open circle = growing tray.

time that seeds must be stored. There are three basic rules of thumb in seed storage (Harrington 1972, 1973; Young and Young 1986; Apfelbaum et al. 1997): (1) each 1% reduction in seed moisture doubles seed life, (2) each reduction of 5° C in seed temperature doubles seed life, and (3) the sum of the relative humidity (%) and temperature ("F) should not exceed 100%. For long-term storage, Band and Hendry (1993) suggested refrigeration of sealed polyester/15-µm aluminum foil/polyethylene packets at -18" C, an optimal technique for seeds of rare plants. Apfelbaum et al. (1997) listed three seed storage techniques: (1) in unsealed containers placed in a controlled environment room or chamber where temperature and humidity are set to specified levels, (2) in gasketed containers with silica gel dessicant refrigerated at 1.7–4.4° C, and (3) in paper or burlap bags in an unheated building. Zettler (1997) reported that seeds of the orchid *Platanthera clavellata* remain viable for > 5 years if stored at 0% relative humidity and -7°C; furthermore orchid seeds should be stored in complete and continuous darkness because embryos are light sensitive.

We have found that seeds of most longleaf pine ground-layer species can be stored in paper bags for several months under normal indoor conditions without a serious decline in germination. For example, *Aristida beyrichiana* Trinius & Ruprecht seed collected from South Carolina mesic savannas in December 1992 had a germination rate of 52.0% when tested in April 1993 (n=1 00). One year later (April 1994) the germination rate was nearly identical at 52.4%. However, after 2 years of storage under these same conditions, the germination rate dropped to 16%, and germinants were malformed and chlorotic. Seeds of wiregrass ***(Aristida beyrichiana)*** and other longleaf pine ground-layer species are adapted to a high humidity and high temperature environment (even during the winter), and seed dispersal often takes place over several months. Seeds of these species may have evolved internal mechanisms that allow persistence of seed viability under less than optimal humidity and temperature conditions.

Germination Tests

Germination tests may be performed prior to seed collection to determine if seed is worth collecting (Pfaff and Gonter 1996) or before planting to determine how much seed to place in each cell of a seedling tray for later outplanting (Booth and Hendry 1993). Seeds (we commonly use n=100) can be placed in suitable containers in an appropriate environment. Seeds are counted as they germinate, and a germination percentage is then calculated.

Germination containers can be Petri dishes lined with filter paper, although these tend to dry out. A better alternative is a small plastic germination tray with a removable top (available from Tii-Star Plastics, Henderson, Ky.) lined with crepe cellulose paper wadding (i.e., Kimpak) covered with a single thickness of steel blue blotter. This technique, recommended by the federal Seed Testing Laboratory in Dry Branch, Georgia, was used in our studies. Alternative germination media include washed silica sand, compost, and polyethylene beads (Booth et al. 1993). Gordon-Reedy (1997) used a mixture of perlite, vermiculite, peat, and sand in seed flats to successfully germinate *Dodecahema leptoceras* (slender-homed spineflower), an endangered plant in California. A controlled environment chamber (many are available commercially at reasonable prices) may be required to satisfy particular humidity, temperature (Thompson and Band 1993), and photoperiod (Thanos 1993) requirements for germination. Alternatively, a germination chamber can be constructed out of an old refrigerator by installing a fluorescent light source (Young and Young 1986).

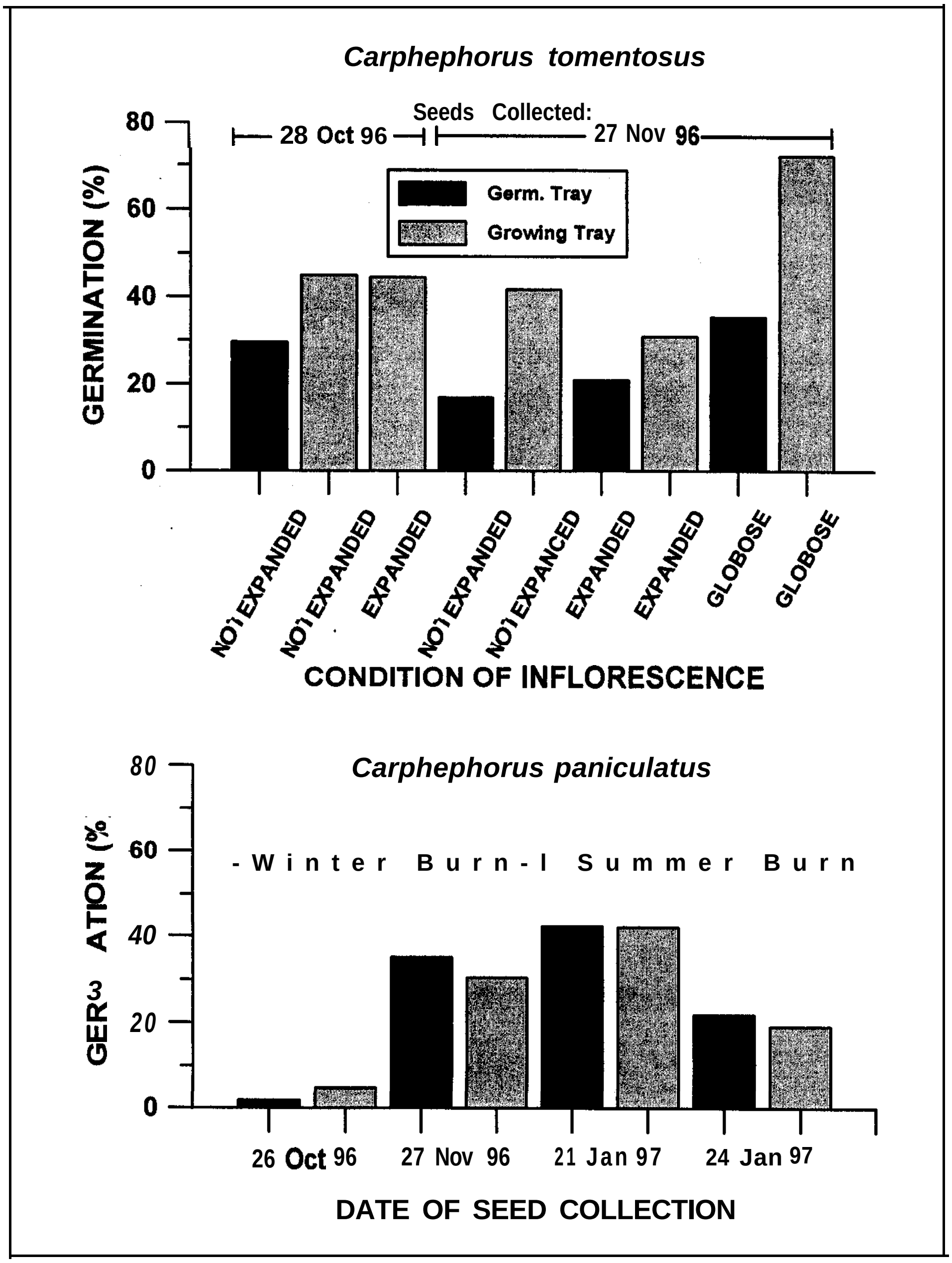

Figure 3. Germination teat results for *Carphephorus tomentosus* for different dates and stages of seed maturity. Results for C. *paniculatus* are shown for comparison.

In some instances seeds remain dormant even when exposed to favorable germination conditions and require treatments to stimulate germination. One simple treatment is after-ripening, accomplished simply by leaving seeds in storage at room temperature for up to 3 months. According to Booth et al. (1993) winter annuals, fall-fruiting perennial grasses, and small-seeded species that seed bank are among the species most likely to demonstrate improved germination following after-ripening. An apparent example of an after-ripening effect on seed germination in *Schizachyrium scoparium* is discussed below in "Seedling Issues: Seedling Cultivation."

Other treatments useful in breaking seed dormancy include cold stratification (dry and moist), scarification, moist heat, alternating temperatures, water-soluble inhibitors, avoidance of high irradiation, non-water-soluble inhibitors, hydrogen peroxide, variable light regimes, sulphydryl compounds, and ethylene (Young and Young 1986, Jones and Foote 1990, Thompson 1993, Thompson and Booth 1993, Thanos 1993 and references therein, Gordon-Reedy 1997, Steffan 1997, Zettler 1997). Detailed discussion of these various procedures is beyond the scope of this paper, and the reader is referred to the above publications (see also Fenner 1985: Chap. 5). We note that in our experience (also B. van Eerden, The Nature Conservancy, Charlottesville, Va., pers. corn.), prolonged stratification in moist vermiculite in a cold storage room does appear to substantially enhance germination of a variety of perennial pine savanna grasses including *Andropogon gerardii, Schizachyrium scoparium, Ctenium aromaticum,* and *Erianthus giganteus* (Walt.) P. Beauv.

Several publications provide recommendations for germinating seeds of native North American plant taxa (e.g., Young and Young 1986, Wiesner 1991, Steffen 1997 and references therein). With few exceptions (e.g., generally widespread grasses and some legumes that also occur in tallgrass prairie and oak woodland habitats in the midwestem United States), these publications do not list longleaf pine ground-layer species. A potential problem in applying these recommendations to pine savanna plants is that significant geographical variation can exist in germination cues. Thus, seeds of a particular species or genus collected from a Wisconsin prairie might require cold stratification to germinate but this treatment may be unnecessary when the same species is collected from a South Carolina pine savanna. As an example, we report (Table 1) a high rate of germination for *Sporobolus pinetorum* Weakley & P.M. Peterson, a rare pine savanna grass, without pretreatment.

We conducted two germination tests on each seed collection (see "Seed Collection Sites and Dates" and "Seed Collecting Technique," above). For the first test, seeds (n= 50 to 100, see Table 1) were placed in plastic germination trays on moist blotting paper as described above. Trays were placed on a bench near a window at room temperature. No attempt was made to control for light or temperature regime. Seed germination was tracked for ≥ 3 months.

For the second test, seedling trays (hereafter, "growing trays") with 38 cells/tray were filled with fine sand and placed in an outdoor nursery at the Santee Experiment Station, FMNF, under a light shade-cloth covering. Seeds were pressed flat on the sand, with n=5 or 10 seeds/cell depending on seed availability (see Table 1 for overall sample sizes). Germination was tracked for 2 months. Fresh seed (i.e., seed collected not more than 3 weeks prior to the start of the test) was used in both tests. Germination conditions for the outdoor test took advantage of natural germination cues typically experienced by seeds of the test species. The goal of our germination study was not to understand germination cues, but to determine whether it was possible, using relatively unsophisticated methods, to obtain an acceptable seed germination rate for a variety of different longleaf pine ground-layer plants, including some rare species. Very little is known about seed germination rates for most of the study species (Young and Young 1986, but see Whelan 1985, Pfaff and Gonter 1996).

Results of the germination studies were encouraging. Of the 42 species, 32 had germination rates greater than 20% in at least one test (Figure 1, top). This translates into what we might term a "best case scenario" success ratio of 78% if a successful seed collection is defined as one with at least 20% germination. If species response is based on mean germination, the success ratio is 74%, still quite good (Figure 1, middle). Finally, even in a worst case scenario (i.e., results for a species summarized according to its poorest test result), the success ratio is a respectable 57% (24 of 42 species). This includes tests from collections known to be suboptimal due to excessively early or late collecting.

In practical terms our results suggest that it should be possible to fill a seedling tray by placing five seeds into each partition, an operation that is not inordinately difficult. In addition to practical issues, several other interesting observations can be made from the germination test results (Table 1, Figure 1). First, there was no clear difference in germination rates among the different plant families studied. Germination results within families were quite variable: some species in each family germinated well and other species germinated poorly. When germination data for the different families are plotted by species, results for the two germination techniques appear highly correlated (Figure 4). This is expected if seed quality is the major limitation to germination. When data are plotted so that growing tray germination is the y-axis and germination tray germination is the x-axis, the slope of the regression line relating the two variables is generally less than one. This indicates that germination in the germination trays was generally greater than that in the growing trays. Again, this result is not surprising given the more favorable substrate and higher humidity in the germination trays. More interesting is the observation that substantial deviations from the various regression lines tended to be positive (i.e., above the line) rather than negative (i.e., below the line) (see Figure 4). This suggests that certain species received stimulatory germination cues in the outdoor treatment that were lacking in the indoor treatment. This appeared to be particularly true for some fall-seeding composites that, like the grasses mentioned earlier, most likely received cold stratification prior to germination. Another striking example was the much higher germination of ***Rhexia nashii*** seeds collected in late October 1996 in the outdoor tray (60%) vs. in the indoor tray (2.5%) (Table 1). This difference was particularly striking because the results of the two techniques were quite similar for another collection made at the same site earlier in the same month. It appears that ***R. nashii*** had developed some form of innate dormancy (sensu Fenner 1985) over less than a month, which was overcome by some unknown aspect of the outdoor environment.

Four of the species in our germination tests appear on Walker's (1993) list of rare longleaf pine plants: ***Pamassia caroliniana, Plantago sparsiflora, Rhexia aristosa,*** and ***Sporobolus pinetorum*** (this last species, recently described by Weakley and Peterson [1998], is listed as ***Sporobolus*** spp. by Walker [1993]). A fifth species, ***Tridens ambiguus,*** did not appear on Walker's (1993) original list but is considered rare by Weakley (1999). ***Parnassia caroliniana*** and ***Plantago sparsiflora*** are forbs of wet pine savannas; ***Rhexia aristosa,*** another forb, inhabits cypress savannas and other wet depressions; and ***Tridens ambiguus*** is a grass that lives in wet pine savannas and other types of depressional wetlands. ***Sporobolus pinetorum*** is a locally dominant grass in pristine wet savanna habitats over a very small area of southeastern North Carolina. It was not known from South Carolina until very recently. We discovered it in the FMNF while collecting seed at PL in 1996 and have since found it at a few other locations as well. The FMNF populations represent the currently known southern range limit for the species.

Except for ***Rhexia aristosa,*** which essentially failed to germinate in both indoor and outdoor tests, germination results for these five rare species were encouraging (Table 1). The two grasses in particular had high germination rates in the indoor test ***(5 1%*** for ***T. ambiguus, 80%*** for S. ***pinetorum),*** suggesting that they lack a cold stratification requirement. ***Pamassia caroliniana*** tests were done as part of an experiment to investigate seed density effects on germination. Fenner (1985) stated that positive or negative density effects are not uncommon in herbaceous plant populations. Additional factors in the experiment involved seed spacing (aggregated vs. dispersed) and whether or not seeds were covered with a thin layer of soil. Details of the experimental design are in Glitzenstein et al. (1998a). Results indicated little effect of seed density or spacing (Figure 5). However, covering seeds with soil did produce a significant enhancement of germination (i.e., ca. 14 %; see Figure 5). This may indicate a negative effect of light (see Fenner 1985) or improved moisture uptake by covered seeds.

II: SEEDLING ISSUES

Seedling Cultivation

Germinating seed is the first step in seedling cultivation. The second step is to ensure adequate growth and survival prior to outplanting. However, cultivation conditions should not be so favorable as to alter

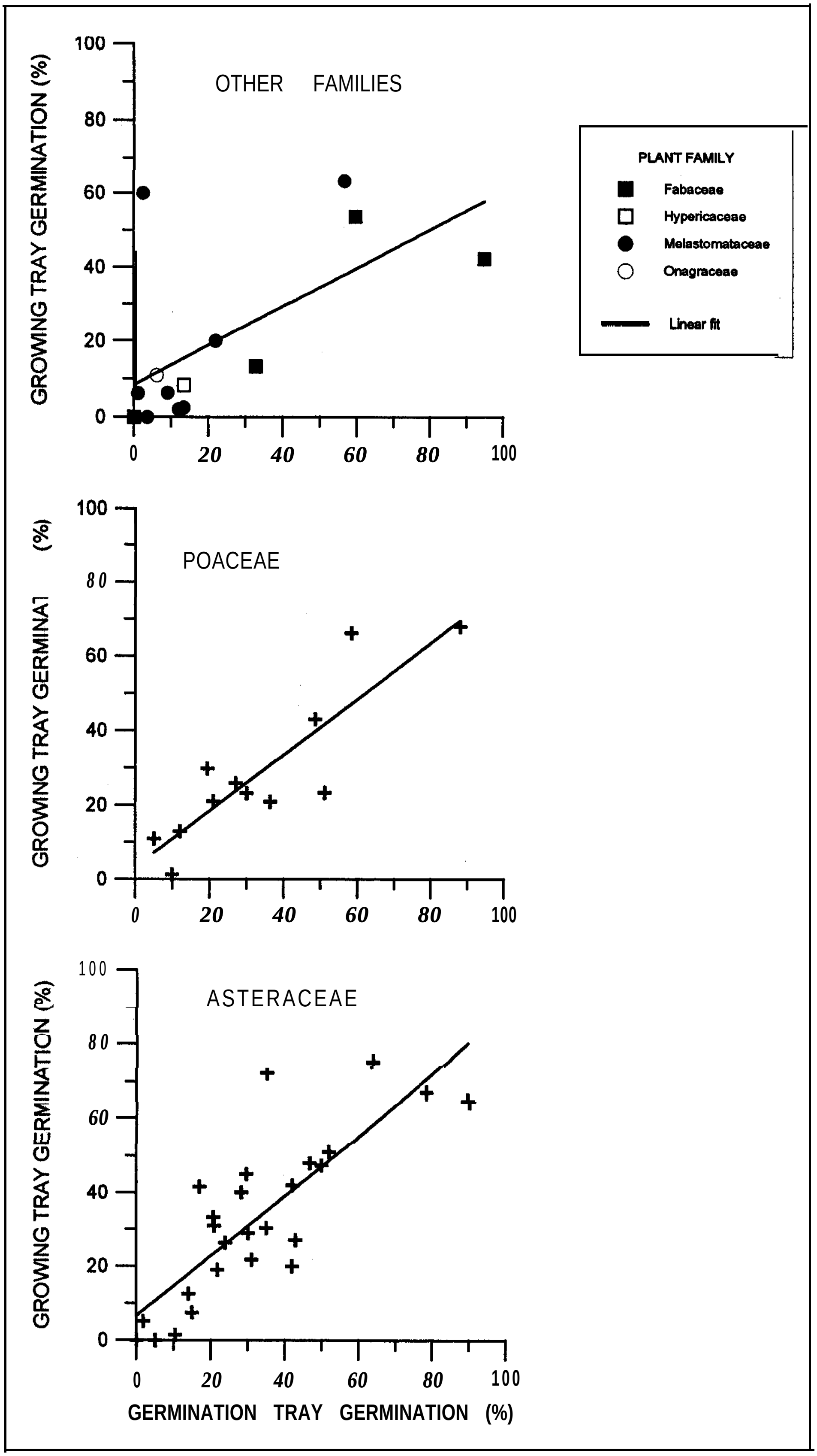

Figure 4. Relationship between indoor (germination tray) and outdoor (growing tray) germination. See text for descriptions of the two germination techniques.

the natural balance between root and shoot development or to select against slow-growing stress-tolerant genotypes that can comprise an important component of natural populations.

Choice of substrate or growth media can be critical for seedling cultivation. Numerous growth media are noted in the ecological and horticultural literature. For example, Booth et al. (1993), Jones and Foote (1990), Schramm (1997), Thompson (1992), and Gordon-Reedy (1997) discussed media ranging from amended available soil to commercial mixes. We employed two different strategies to cultivate rare plant species of longleaf pine habitats. We (JSG, DRS, DDW) have primarily used a conservative approach with unmodified soil taken from the A-horizon of the restoration/reintroduction site and mixed with a small quantity of soil from the seed donor site. Adding donor site soil is potentially important to provide mycorrhizal inoculum (Seamon et al. 1989). By using unmodified soil we hoped to select genotypes capable of survival and growth under field conditions. This approach has been tried with some success for two very rare plants of wet sandy pine savannas, ***Pamassia caroliniana*** and ***Plantago sparsiflora*** (see Glitzenstein et al. 1998a and results below in “Gutplanting and Translocation”) as well as various dry-site forbs ***(e.g., Liatris squat-rosa, Chrysopsis gossypina).*** In contrast, JB uses an artificial soil mix that has proven effective for cultivating orchids and a wide variety of other rare plants of bogs, seepage slope habitats, and wet savannas (Table 2). The mixture consists of 5 parts perlite, 3 parts vermiculite, and 2 parts chopped or milled sphagnum. The mixture provides pore space and an oxygen supply to roots, and promotes the wet, highly acid conditions required by bog species. To cultivate native grasses, we use a medium composed of 75% soil and 25% vermiculite (or perlite). These latter media are sterile; in other words, they do not alter soil fertility but improve drainage and water and nutrient retention.

Steffen (1997) provides a helpful discussion of propagation techniques. He advocates outdoor germination methods that

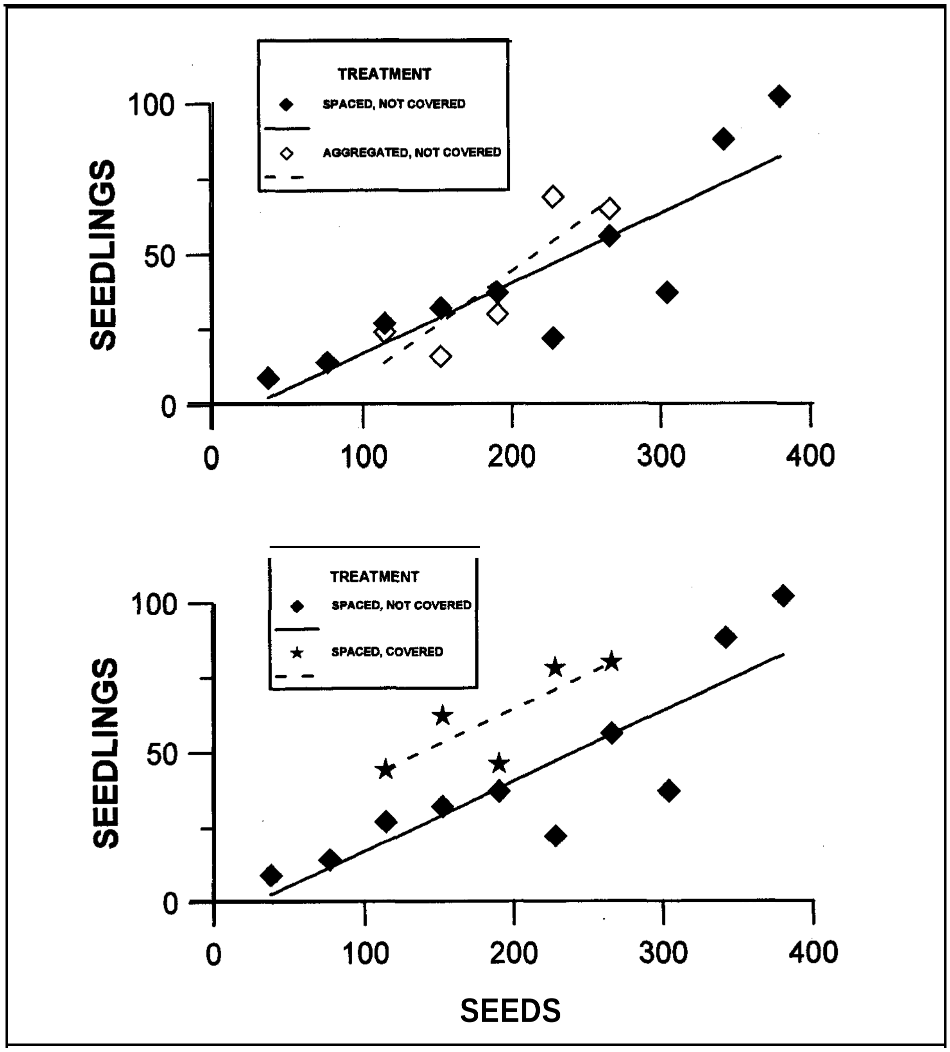

Figure 5. Relationship of *Parnassia caroliniana* germination to seed density. Also shown are effects of seed spacing and germination differences between covered (i.e., with a thin soil layer) and uncovered seeds.

take advantage of natural germination cues. Among his useful suggestions are the following: (1) cover seeds lightly with a thin layer of vermiculite; this material not only holds moisture but also transmits light and therefore does not interfere with germination of light-requiring seeds; (2) cover unsheltered trays with window screening to prevent seeds from washing out during heavy rain; and (3) place over-wintering flats in a cold-frame or Quonset hut to prevent excessive freeze-thaw cycles; alternatively, flats can be covered with a tarp and a layer of bark or mulch (in the southeastern United States it is necessary to protect newly germinated seedlings from frost).

An important aspect of plant cultivation that has received little experimental attention is watering regime. By varying watering frequency, species characteristic of both dry and wet habitats can be maintained in the same soil. For native grasses, soils should be kept continuously moist during seed germination and early seedling establishment. After this stage, grasses characteristic of mesic-dry sites (e.g., *Schizachyrium scoparium, Aristida beyrichiana, A. virgata* Trin.) tolerate, or even prefer, relatively infrequent watering (e.g., refilling irrigation trays every 1-2 weeks) whereas wet savanna species ***(e.g., Ctenium aromaticum, Erianthus giganteus)*** prefer continuously wet soils.

We conducted an experiment using ***Schizachyrium scoparium*** to evaluation growth media and propagation techniques. The experiment was a randomized block-split plot design with a seed storage treatment (i.e., room temperature vs. cool outdoors) as the main plot factor and three ratios of soil to vermiculite (100:0, 75:25, and 50:50) as the split-plot factor. Results indicated a significant effect ($P \leq 0.1$) of the split-plot factor ($F = 4.56$, $P = 0.06$, $df = 2,6$) with fewest seedlings in the soil trays without vermiculite (mean = 13.8) and almost three times as many seedlings in the trays with the 75:25 soil:vermiculite mixture (mean = 34.3). Intermediate numbers of seedlings were counted in the 50:50 trays (mean = 24.8). The main plot contrast was not statistically significant ($F = 3.71$, $P = 0.3$, $df = 1,1$). However, the apparent difference in seedling emergence (30.8 indoors vs. 17.7 outdoors) may represent an effect of after-ripening, as discussed above.

Outplanting and Translocation

Site Selection

Suitable introduction sites should encompass habitat requirements and be within the historic range of the species (Falk et al. 1996). However, given the sporadic distribution of many rare plants and recent range contractions, historic range might not be easily determined. For example, ***Parnassia caroliniana*** is one of several wet savanna species with a distribution focus in southeastern North Carolina and another in north Florida-southeast Georgia (Peet and Allard 1993). Furthermore, it occurs sporadically through northern and central South Carolina, with a local maximum in the vicinity of Plantersville, about 20.3 km north of Georgetown. Recent discovery of a new population extends this distribution about 12.6 km southward (Porcher et al. 1999). Our introduced population in the FMNF occupies a similar habitat to the new population. However, the reintroduction site is another 44.4 km farther south, still outside of the currently documented southern limit of the northern section of the range of ***P. caroliniana.*** Is this a suitable outplanting site? Only time will tell. We would argue, however, that the apparent advantages of this site (i.e.,

Table 2. Plants in John **Brubaker's** bog garden, **Awendaw,** SC. (E = endangered; SC= Species of Concern; R = rare.)

Species	G-Rank	Federal List	SC State List
	4		R
Calopogon pallidus	*4*		
Calopogon tuberosus			
Dionaea muscipula	*3*	*SC*	R
Eriocaulon decangulare			
Habenaria repens			
Lachnocaulon anceps			
Macbridea caroliniana	*2*	*SC*	
Pamassia caroliniana	*2*	*SC*	R
Pinguicula caerulea			
Platanthera blephariglottis	***4***		
Platanthera ciliaris			
Platanthera cristata	*5*		
Platanthera flava			
Platanthera integra	*3*		R
Rhexia alifanus			
Rhexia lutea			
Rhexia mariana			
Rhynchospora colorata			
Sarracenia jlava			
Sarracenia leucophylla	*3*		
Sarracenia minor			
Sarracenia purpurea	*4*		
Sarracenia rubra	3		R
Spiranthes cemua			
Thalictrum cooleyi	1	E	
Xyris platylepis			

remote location, apparently suitable habitat, and a high probability of continued appropriate management by frequent prescribed burning) outweigh the minor uncertainty about range boundaries (see also Fiedler and Laven 1996). This argument is supported by recent suggestions that stochastic and historical effects are considerably more important than has been appreciated in determining population distributions and range boundaries of rare plant species (P. White, unpubl. data). Furthermore, Primack (1996) argued that introducing a species slightly outside of its current range is justified because the act simulates the process of gradual dispersal that has probably always been part of the ecology of the species.

The above arguments aside, known extirpation sites are among the best candidates for rare plant reintroduction, but only if the site can be managed properly (Fiedler and Laven 1996). Implicit in the use of extinction sites is that the reason for the initial loss of the species is known and can be remedied. In longleaf pine-dominated habitats, the most common factor causing local extinction of rare plants is tire exclusion or reduced fire frequency. For example, populations of the federally endangered longleafpine ground-layer forb *Schwalbea* ***americana*** (American chaffseed) in the FMNF declined catastrophically with a few years of fire exclusion (Figure 6). Enhancing these populations with new seedlings would probably not be effective unless regular burning was resumed. Furthermore, mechanical treatments to remove loblolly pine (***Pinus taeda***) saplings that have invaded due to lack of burning may also be required.

Outplanting Techniques

A discussion of outplanting techniques is found in Schramm (1997). The author advocated several site preparation methods that should be done prior to outplanting. Besides fire, we feel that such methods are generally unnecessary for outplanting seedlings in longleafpine habitats (see results below). Examples of successful outplanting projects using a variety of propagation methods are presented in Guerrant (1996).

Over the last 8 years we have outplanted nursery grown seedlings of seven perennial grasses ***(Andropogon gerardii, Aristida beyrichiana, A. virgata, Ctenium** aromaticum,* ***Erianthus giganteus, Schizachyrium scoparium, Sorghastrum nutans*** *???????)* and two rare forbs ***(Pamassia caroliniana, Plantago sparsiflora).*** We have also done a small translocation experiment for ***Agrimonia incisa,*** a rare forb. Three of the grasses (***Aristida beyrichiana, Ctenium aromaticum, Sorghastrum nutans)*** and the three forbs were outplanted, or transplanted, in the case of the ***Agrimonia,*** into experimental fire research plots in the FMNF (see Table 3 for planting dates for each species). These plots occurred at three sites that are typical of different longleaf pine dominated habitats. The "dry" site is subxeric longleaf pine woodland (sensu Peet and Allard 1993) on Chipley loamy fine sand (thermic coated Aquic Quartzipsamments). The "mesic" site is mesic longleaf pine woodland with occasional ***Quercus marilandica*** and ***Q. stellata.*** Moist savanna patches are also present but these are now mostly closed woodlands dominated by ***Pinus taeda, Liquidambar styraciflua, Nyssa sylvatica,*** and ***Q. phellos. The*** soil is a Craven fine sandy loam (clayey mixed thermic Aquic Hapludult). The "wet" site is moist flatwoods intermixed with wet savanna (see Peet and Allard 1993 for typical wet savanna dominants). F'latwoods patches are dominated by ***Ilex glabra, Clethra alnifolia,*** and ***Arundinaria tecta*** (Walt.) Muhl. Soils are Quitman loamy sands (fine loamy siliceous thermic Aeric Paleaquult) (soils information is from Long 1980 and Soil Conservation Service, Charleston, S.C., pers. corn.).

Of the six species planted into the experimental fire plots, three ***(Aristidu beyrichiana, Pamassia caroliniana,*** and ***Plantago sparsiflora),*** are true introductions, because they were not previously found in the plots. ***Plantago sparsiflora*** and ***A. beyrichiana*** do, however, occur elsewhere in the FMNF. In fact, extant populations of these two species were found very recently (Porcher et al. 1999), confirming historical observations (Elliott 18 16-1824, Porcher 1848). ***Aristidu beyrichiana*** is a dominant grass of original pine savannas over much of its range, but it is rare in central South Carolina where it is at the northern limit of its range (see Peet 1993). In the FMNF there is only a single population (Porcher et al. 1999). ***Plantago sparsiflora*** presently occurs in three roadside

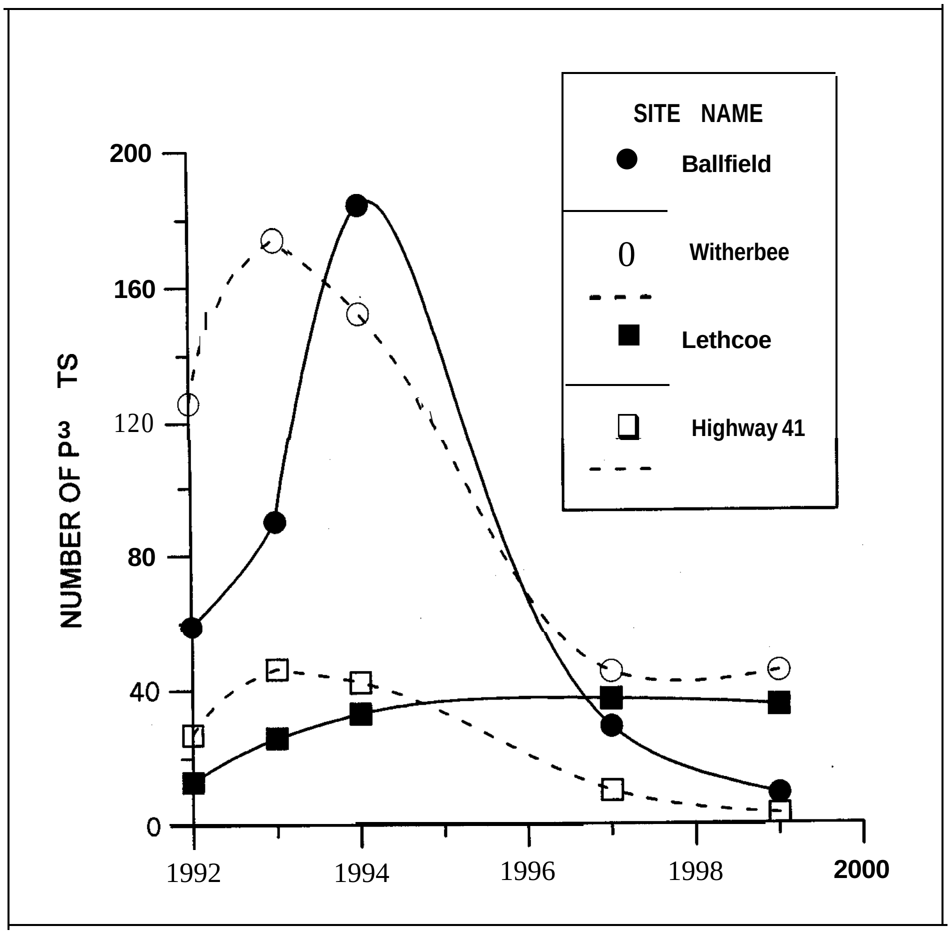

Figure 6. Population size changes in four FMNF populations of *Schwalbea americana* with differing burn histories. All populations were burned annually from 1992 to 1994. The Witherbee Rd population also burned in 1998 and Lethcoe Rd was burned in 1996 and 1998. The Ballfield and Highway 41 populations have not burned since 1994.

populations maintained by mowing and susceptible to severe disturbances from road grading operations (Porcher et al. 1999).

Three other outplanted species, *Agrimonia incisa, Ctenium aromaticum,* and *Sorghastrum nutans,* were already present in the fire research plots prior to the start of the study. On a standwide scale, plantings of these species constitute enhancements, rather than introductions per se. *Agrimonia incisa* is a state endangered (federal species of concern) forb found in dry longleafpine forests, particularly along oak-hickory ecotones and in other subxeric situations (Weakley 1999). Three known populations occur in the FMNF. One of these, a population consisting of approximately 250 individuals, spans two plots in our "dry" study site. On 30 January 1998 we attempted to start another *A. incisa* population in a different research plot at the same site by moving 16 newly germinated seedlings and three nongerminated seeds. The new site is on the edge of a large canopy opening in the vicinity of a patch of *Carya alba.*

Ctenium aromaticum is a common component of wet savannas throughout its range (Peet and Allard 1993) and is the dominant grass of these habitats in the outer South Carolina Coastal Plain (Porcher 1995). It is abundant in high quality savannas in the FMNF, but occurs patchily in the wet site. In the mesic site it occurs as scattered plants in the savanna patches now dominated by gums and pine. We hypothesized that the species was formerly more abundant at both sites.

Sorghastrum nutans, the last of the outplanted species, is a characteristic component of the mesic woodland portions of the mesic site. It also occurs rarely at the wet site. Presumably it also has been reduced in abundance by past episodes of fire exclusion.

The fire experiment was initiated in 1992 and terminated in 2000. It consisted of 63 fire treatment plots, each 1 ha in area (100 m x 100 m on a side) arranged into three blocks (i.e., the different study sites described above) of 21 plots apiece. Judging from the condition of the vegetation at the start of the study, all the sites had a history of at least occasional fire with more frequent burning over the last decade. Each of the sites burned in 1991, 1 year prior to the start of the study. Experimental burns were originally to be administered at mean intervals of 2, 4, or 6 years with additional treatments incorporating variability in burning season and randomness (i.e., burns occurring at regular intervals vs. burns with random inter-fire intervals but the same mean tire return time). Plots were not burned as scheduled, particularly during the latter part of the study. Results presented herein are summarized according to number of fires that actually occurred at particular outplanting locations during the period 1991-1997 regardless of the assigned burn treatment.

Planting locations within plots were randomly selected for the grasses. However, rare forbs were planted into microsites that appeared particularly favorable (i.e., canopy gaps, wet savanna patches for *Parnassia caroliniana* and *Plantago sparsiflora;* oak-hickory transition for *Agrimonia incisa).* Thus the grass data represent an unbiased estimate of bum history effects on planting success within each habitat, whereas forb data cannot be extrapolated beyond the selected microhabitats. Seedlings (plugs from growing trays) were outplanted following fires using a small bulb planter. No additional site preparation was employed, except in one *Plantago sparsijlora* plot where the seedlings were planted into small (20 cm x 20 cm) soil disturbances created by shallow spading. Additional details of the experimental treatments and outplanting arrangements can be found in Glitzenstein et al. (1998b).

Table 3. Survival percentages of seedlings (i.e., plugs from growing trays) planted out or (in the case of *Agrimonia incisa*) transplanted into the fire treatment plots. Number of fires refers to experimental burns during the period 1991-1998; in parentheses are listed the number of burns actually survived by the planted seedlings. Abbreviations are as follows. Site: D = dry study plot; M = mesic study plot; W = wet study plot. Dates: W = winter; Sp. = Spring; Su = summer.

Species	Site	Planted out	No. Plants	No. fires	Last Census	Survival (%)
A. GRASSES						
Aristida beyrichiana	D	w 93-94	73	4(2)	Jan. 98	32.9
	D	W 93-94	72	3(1)	Jan. 98	55.6
	D	W 93-94	24	2(1)	Jan. 98	54.2
	D	W-Sp. 97	24	5(1)	Jan. 98	45.8
	D	W-Sp. 97	72	4(0)	Jan. 98	100.0
	D	W-Sp. 97	48	3(0)	Jan. 98	95.8
	D	W-Sp. 97	24	2(0)	Jan. 98	100.0
	M	w 93-94	49	4(2)	Jan. 98	81.6
	M	w 93-94	90	3(1)	Jan. 98	61.5
	M	W 93-94	32	2(1)	Jan. 98	90.6
	M	W-Sp. 97	25	5(0[a])	Jan. 98	100.0
	M	w-sp. 97	73	4(0)	Jan. 98	100.0
	M	W-Sp. 97	48	3(0)	Jan. 98	97.9
	M	W-Sp. 97	24	2(0)	Jan. 98	100.0
	W	W 93-94	72	4(2)	Su. 98	87.5
	W	W 93-94	72	3(1)	Su. 98	69.4
	W	W 93-94	24	2(1)	Su. 98	75.0
	W	W-Sp. 97	24	5(1)	Su. 98	87.5
	W	w-sp. 97	88	4(0)	Su. 98	96.6
	W	W-Sp. 97	24	3(0)	Su. 98	100.0
	W	W-Sp. 97	24	2(0)	Su. 98	91.7
Ctenium aromaticum	M	W 93-94	48	4(2)	Jan. 98	43.8
	M	W 93-94	87	3(1)	Jan. 98	55.2
	M	W 93-94	32	2(1)	Jan. 98	53.1
	M	W-Sp. 97	24	5(0[a])	Jan. 98	100.0
	M	W-Sp. 97	72	4(0)	Jan. 98	98.6
	M	W-Sp. 97	48	3(0)	Jan. 98	100.0
	M	W-Sp. 97	24	2(0)	Jan. 98	100.0
	W	W 93-94	72	4(2)	Su. 98	77.8
	W	W 93-94	72	3(1)	Su. 98	51.4
	W	W 93-94	24	2(1)	Su. 98	33.3
	W	W-Sp. 97	25	5(1)	Su. 98	84.0
	W	w-sp. 97	88	4(0)	Su. 98	98.9
	W	W-Sp. 97	24	3(0)	Su. 98	100.0
	W	W-Sp. 97	24	2(0)	Su. 98	100.0
Sorghastrum nutans	M	W-Sp. 97	25	5(0[a])	Jan. 98	92.0
	M	W-Sp. 97	72	4(0)	Jan. 98	95.8
	M	w-sp. 97	47	3(0)	Jan. 98	95.7
	M	W-Sp. 97	24	2(0)	Jan. 98	95.8

continued

Ultimately, an introduction project can be considered successful only when it results in a self-maintaining population with sufficient genetic diversity for long-term persistence (Pavlik 1996). In practice, few introduced populations are monitored long enough or with sufficient rigor to determine whether these goals are actually attained (Pavlik 1996, Sutter 1996). Over the short term, success criteria for perennial plants typically include survival and growth of the outplanted individuals along with information on fecundity. Based on these modest criteria, results of our outplanting experiments are encouraging. Almost all species had initially high survival (i.e., > 90%) during the first year after outplanting (Table 3). Furthermore, in all but a few cases, survival remained high (> 60%) for several years afterwards and most plants have now survived at least one fire (Table 3). Further, many plants are growing into larger size classes (results available online at http://www.talltimbers.org/research.html).

Another criterion for the success of plant introductions is persistence (Pavlik 1996). Pavlik (1996: 139) cites a review by Birkinshaw (1991) concerning introduction attempts in Britain. Of 144 attempts, 29% did not persist, 15% were less than 5 years old and could not be evaluated, and 22% were more than 5 years old and were deemed persistent. There were also a few examples of introduced populations that had persisted over the long term (i.e., up to *83 years* in the case of ***Arabis stricta*** Huds., a limestone outcrop plant). Of the six species outplanted into our fire plots, three (*Aristida beyrichiana, Ctenium aromaticum,* and *Parnassia caroliniana)* have reached or exceeded the 5-year threshold for persistence. The other three species cannot yet be evaluated, but results to date indicate these populations should survive at least 5 years. None of the introductions has thus far failed.

Of all the introductions, the *Parnassia caroliniana* plantings are closest to achieving true population status. Some flowering has occurred for this species in each of the last 4 years. Seeds collected from one capsule were planted into a "peat-plug" type germination tray and abundant seedlings

Table

Species	Site	Planted out	No. Plants	No. fires	Last Census	Survival (%)
	W	w-sp. 97	25	5(1)	su. 98	44.4
	W	w-sp. 97	88	4(0)	su. 98	80.0
	W	W-Sp. 97	24	3(0)	Su. 98	94.4
	W	W-Sp. 97	24	2(0)	Su. 98	100.0
B. RARE! FORBS						
Agrimonia incisa	D	Jan. 98	19	3(0)	Apr. 00	*26.3*
Pamassia caroliniana	W	Nov. 95	228	4(1)	Fall 98	66.7
	W	Nov. 95[b]	47	3(0)	Fall 98	*78.7*
Plantago sparsiflora	W	Aug. 98	21	4(0)	Apr. 00	66.7
	W	Apr. 99	18	4(1)	Apr. 00	83.3

[a] Fire was patchy and planted grass plots did not bum.

[b] Includes a few individuals planted out the prior November.

germinated (germination percentages were not determined). If any "wild" seedlings were produced, they most likely did not survive, because all *Parnassia caroliniana* plots were burned early in spring 2000 as part of a FMNF prescribed burn of the surrounding compartment. Seedling establishment is a relatively rare phenomenon in most perennial species (Sutter 1996), and this may be the case in longleaf pine savannas where all but the most vigorous seedlings are likely to be eliminated by fires within l-2 years after germination. We can say that, given the precarious condition of *Parnassia caroliniana* in South Carolina (i.e., most populations threatened by fire exclusion, intensive forestry, drainage, or some combination thereof; see Porcher et al. 1999), our introduced population appears as likely to survive over the long term as most of the original populations.

A detailed analysis of site and fire regime effects on dynamics of the introduced populations will be left to subsequent publications. However, we would like to emphasize two key points. First, plantings at the dry study site (i.e., *Aristida beyrichianu* and *Agrimoniu incisa*) were among the least successful in terms of survival (Table 3). We hypothesize that this is because moisture stress at this site provides a strong limitation to initial establishment, a finding supported by results of direct seeding trials (see below). Because of the additional stress associated with moisture limitation, it may be advisable to wait longer (i.e., up to 2 years) for plants to establish before administering the first fire. In fact, very low first-year survival rates (< 45%) for *A. beyrichiunu* in the five-bum treatments (i.e., plots burned five times between 1991 and 1998; see Table 3) appeared to be due mostly to effects of burning too soon after outplanting. Second, except for *Ctenium uromuticum* at the wet site, grasses planted into infrequently burned plots (i.e., two fires during 1991-1998, 6 years between fires) had unexpectedly high survival (Table 3), although the surviving plants had little or no growth (results online at http://www.talltimbers.org/research.html) More frequent fire after establishment may be necessary for functioning populations of these grasses.

III: DIRECT SEEDING

Fire Plot Introductions

A second approach to beginning new populations is through direct seeding (Primack and Miao 1992, Pavlik 1996, Primack 1996, Pfaff and Gonter 1996, Packard 1997, Tilman 1997). We have experimented with this approach but not with rare plants. During October-December 1992 we collected mixed ground-layer seed from a variety of high quality dry, mesic and wet longleaf pine sites using a Woodward-Flail Vac mechanical seed stripper (available from Ag Renewal Inc., Weatherford, Okla.; shown in use in Pfaff and Gonter 1996). Seeds from the various collection sites were mixed together and introduced into seed-addition subplots (n = 3 per main plot) randomly located within FMNF fire treatment plots. Seeds were introduced immediately after experimental fires in winter or spring 1993. The subplots are 1.5 m x 2.0 m and were subdivided, using plot-frames, into 48 25-cm x 25-cm cells. We tallied all species present in each cell of every subplot, both before and 2 years after the seed introductions. The same procedure was followed in control subplots (also n = 3 per main plot). Multivariate analysis of the dataset was done using CANOCO (ter Braak 1987-1992). There was no significant effect of seed introduction at the dry site (F = 1.07; $P = 0.22$), but significant effects were observed at the mesic and wet sites (F's = 1.54,1.27 respectively; $P = 0.01$). However, these significant results were due almost entirely to one species, *Aristidu beyrichianu*. When this species was excluded, the analysis was no longer significant for either site (F's = 1.01, 0.92; $P =$ 0.13, 0.70).

Our results suggest that with the exception of a few competition-tolerant species (see also Tilman 1997 for a similar study involving oak savanna plants), establishment from seed is rare in undisturbed longleaf pine habitats. These habitats are typically dominated by perennial plants that appear to inhibit establishment of new seedlings (Brewer et al. 1996, Primack 1996, Tilman 1997). Thus, seed introduction may not be a particularly effective method for starting new plant populations. We should emphasize, however, that conclusions from our small-scale experiment may not be relevant to large-scale restorations (see Pfaff and Gonter 1996). Seed introductions that involve seed drills or other machinery may be successful in locating the occasional safe-site and initiating the occasional population. This technique is also likely to provide strong initial selection for appropriate genotypes, so that, once established, populations have a strong likelihood of ultimate success. For most rare plants the limit to such an approach is seed availability. With at most a few hundred seeds, the probability of successful establishment by direct seeding would be too low to justify the approach (see also Reinartz 1997). An agricultural plot technique might work, wherein numbers of seeds are first increased by several orders of magnitude and then introduced to the restoration site. Artificial site preparation, either mechanical or chemical, might also enhance the probability of success by creating additional space for seedling establishment (see Morgan 1997). However, such treatments are inappropriate when the goal is to establish new rare plant populations in existing quality longleaf pine ground-layer.

Gradient Study

A common gardening technique is to cultivate plants in competition-free beds (Jones and Foote 1990). We have used this technique in an experimental context to examine establishment from seed of longleaf pine ground-layer species in the absence of competition. Beds were specially constructed so that we could also explore effects of important environmental gradients (i.e., soil texture and distance to B-horizon) on establishment processes and community composition of longleaf pine ground-layer communities. Three beds were constructed at the FMNF seed orchard in an area occupied by natural longleaf pine ground-layer (wet-mesic savanna) but free of canopy trees. Soils in the area are of the Lenoir series, a sandy loam with a drainage-resistant clay subsoil at approximately 18 cm (Long 1980).

For each bed, a l-m x 3-m area was established and existing vegetation and surface soil were removed to expose the subsoil. Beds were then leveled to a uniform depth approximately 17 cm below the soil surface, varying by l-2 cm among beds. Absolute elevation of each bed was 14 cm above the water table on 14 April 1998, the day the beds were constructed. Surface soil was replaced in each bed, but with soil textures randomly assigned: bed 1 was back-filled with the sandy loam surface soil that had been removed during the process of excavating the beds; bed 2 was filled with Lakeland sand surface soil; and bed 3 received a surface soil taken from a site mapped as Bonneau loamy sand. Each bed was reconstructed so that the filled soil formed a micro-elevation/drainage gradient with the highest end at 55 cm above the clay subsoil and the lowest end at 5 cm, with a constant slope in between. A PVC pipe well (2-inch inner diameter, 5 feet long, 4 feet deep) was installed in each bed to monitor water level fluctuations.

To reduce edge effects, a small buffer of 5 cm was left on both sides of each bed. Beds were then subdivided into sections of 90 cm x 50 cm. Each section was further subdivided into 2-cm rows, with each row consisting of a l-cm-wide planting strip and a l-cm-wide buffer. Within the planting strip, potential planting locations were limited to increments of 2 cm beginning at 0 cm. As seeds of different species became available, they were planted into the bed by randomly selecting one planting location for each of the 25 rows. The same planting arrangement was used for each of the 18 sections (i.e., 3 beds x 6 sections/bed) to avoid confounding bed or gradient position with seed arrangement. The planting technique was to press seeds flat and then cover with a thin layer of soil. Seeds were covered with soil in part to keep them from moving away from their assigned gradient positions.

The experiment was initiated in early May 1998 and terminated in late November 1999. Sixteen species were planted onto the beds as seeds became available. We selected plant species characteristic of a range of different longleaf pine habitats, from xeric to hydric. Germination was monitored approximately weekly throughout the study, except during late winter–early spring when up to 3 weeks were required between censuses to tally all emerging seedlings. In addition to monitoring seedling emergence, we monitored seedling growth and mortality for planted species, and seedling mortality for weeds that died before they could be pulled. These variables were monitored weekly during 1998. During 1999 growth and mortality were checked in May and September. In the September census we also recorded flowering and various measures of plant and inflorescence size.

Water levels in the wells were monitored on a weekly basis. We also measured soil moisture (i.e., matric potential) using a QuikDraw tensiometer (Soil Moisture Equipment Corp., Goleta, CA, USA). These two variables were strongly related (Figure 7), suggesting that hydrological variations strongly determine droughtiness in Coastal Plain environments.

In contrast to the results of the fire plot introduction study described above, numerous seedlings of a variety of species successfully germinated (Table 4) and became established on the experimental gradients (Table 5). Germination was strongly related to hydrology/drought, with peak periods of germination strongly correlating with prolonged periods of high water tables and moist soils (Figure 7). There were interesting differences among species (Figure 7). Fall-fruiting grasses and composites tended to appear in late winter or early spring. In contrast, spring and summer fruiting species had two germination peaks, a minor peak in late spring shortly after seeds were placed, and a major peak in autumn (Figure 7). Legumes, which in our study included the summer-fruiting species ***Rhynchosia reniformis*** and ***Tephrosia virginiana,*** were distinctive in that they tended to appear throughout the year and were apparently able to take advantage of relatively brief periods of favorable soil moisture. These differences in seedling germination patterns within longleaf pine ground-layer species are reminiscent of similar differences within floodplain trees that are related to seed size and time of seed deposition (Streng et al. 1989).

By September 1999 many of the plants

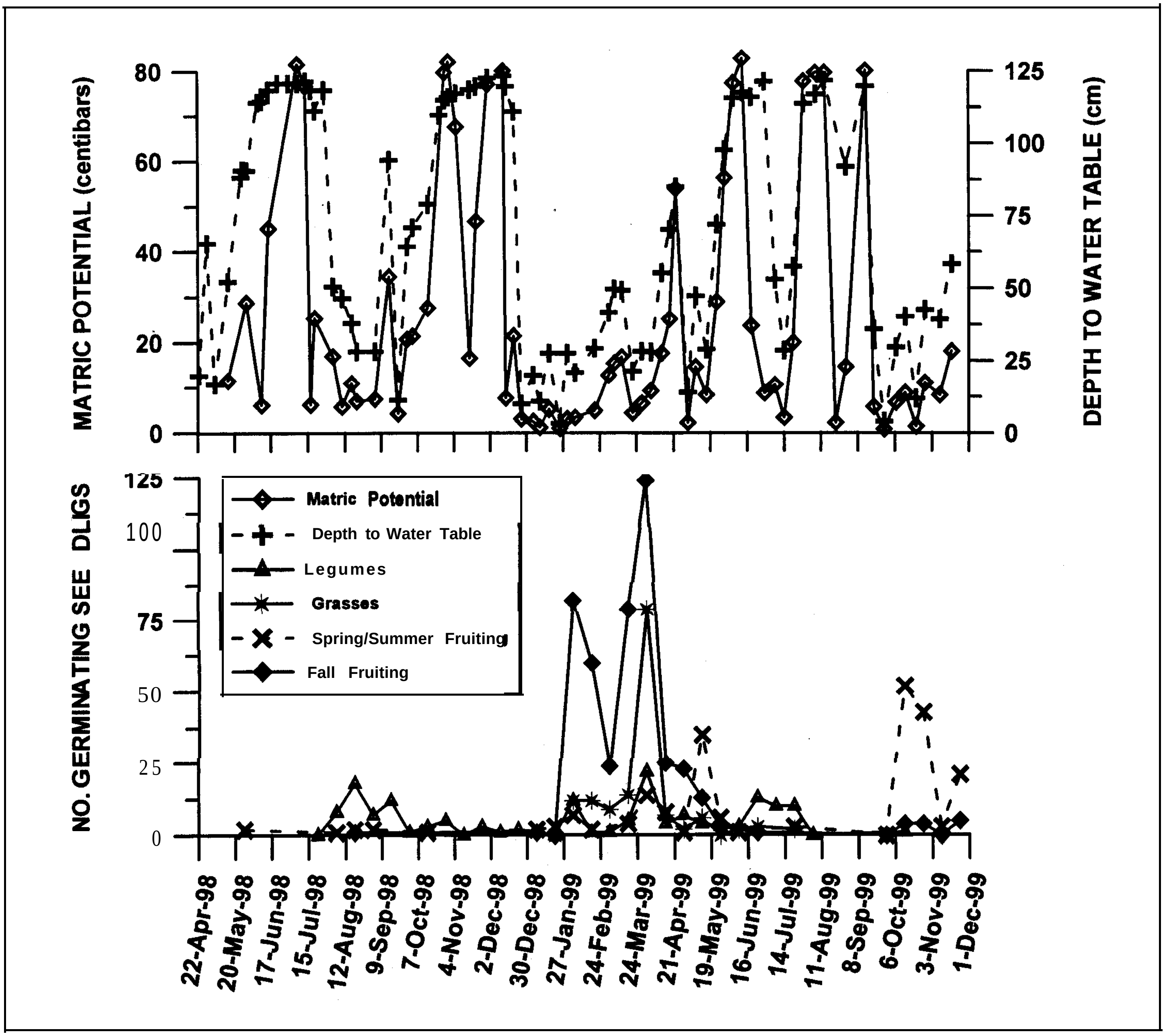

Figure 7. Seedling appearance patterns on the experimental gradients as a function of hydrology and matric potential, a measure of soil moisture availability.

recruited onto the experimental gradients during summer 1998 through spring 1999 had grown to maturity and flowered (Table 5). Detailed discussion of soil texture and gradient influences on vegetation development and compositional patterns will be deferred to future publications. For now we merely state that such effects were evident and results provided experimental evidence that the two variables included in the study do in fact control much of the vegetation pattern in longleaf pine ground-layer. For the present discussion, the important point is that starting populations of longleaf pine ground-layer species from seed is feasible if gradient effects are considered and competition is reduced or eliminated. Another point is that a successful introduction from seed requires a certain degree of good luck in the form of favorable climatic conditions. Even if an appropriate microhabitat is found and competition is reduced, the introduction may fail if rainfall is inadequate. Study results for *Arnica acuulis*, a spring-fruiting composite, provided a good example of this sort of variability. Seeds of this species, previously determined to be highly viable (Table 1), were introduced onto the experimental gradients in spring 1998 and again in spring 1999. Due to prolonged drought during 1998 that lasted into autumn (Figure 7), virtually no seeds of this species germinated in the first year of the study. However, as a consequence of more favorable climate, numerous *A. acaulis* seedlings were

Table 4. Seedlings germinating on the three experimental gradients from May 1998 through November 1999. Seed number refers to number of seeds added during the experiment. Seedlings are individuals observed to originate from cotyledons or otherwise determined to be new germinants. Note that the few observed seedlings of *Oxypolis* and *Eupatorium rotundifolium* may be explained mainly by the inadequate observation period for these species (i.e., about 1 month between planting and the end of the experiment).

Species	No. Seeds	Date Added	No. Seedlings	Appearance (%)
Arnica acaulis (1998)	900	5/12–29/98	7	0.8
Arnica acaulis (1999)	450	6/16–21/99	65	14.4
Chaptalia tomentosa (1998)	450	5/12–15/98	7	1.6
Chaptalia tomentosa (1999)	450	4/18–29/99	44	9.8
Chrysopsis gossypina	450	1/29–2/8/99	94	20.9
Ctenium aromaticum	450	1/9–11/99	30	6.7
Erigeron vemus (1998)	450	6/15–16/98	12	2.7
Erigeron vemus (1999)	450	6/16–21/99	5	1.1
Eupatorium leucolepis	450	1/29–2/8/99	171	38.0
Eupatorium rotundifolium	450	10/14–29/99	7	1.6
Liatris squarrosa	450	1/9–11/99	111	24.7
Oxypolis filiformis	450	10/14–29/99	4	0.9
Polygala lutea	450	7/13–14/98	15	3.3
Pterocaulon pycnostachyum (Michx.Ell)	450	7/14–15/99	31	6.9
Rhexia alifanus	450	9/22–23/98	27	6.0
Rhynchosia reniformis	450	6/23–25/98	44	9.8
Schizachyrium scoparium	450	11/30-12/14/98	118	26.2
Tephrosia virginiana	450	8/4/98	112	24.9
Vemonia angustifolia	450	10/24–28/98	74	16.4

observed in fall 1999. The lesson of this study is that multiple trials may be necessary if direct seeding is used to start populations.

SYNTHESIS AND CONCLUSIONS

Our results to date are consistent with a theory of longleaf pine plant community dynamics in which frequent fires reduce but do not entirely eliminate competition (Peet et al. 1983). The implication of this theory for conservation is that unlimited opportunities exist for starting new populations of rare and other longleaf pine ground-layer plants in sites managed appropriately with frequent prescribed burning. As we have discussed, starting populations from seed can often be difficult due to interactive effects of limited competition and frequent fire on seedling establishment. However, starting new populations may not be particularly difficult if this "bottleneck" is bypassed by outplanting seedlings or cuttings (see Gordon 1996, Ledbetter 1997 for two more case studies). Of course, considerable effort may be needed to grow and outplant sufficient numbers of individuals to ensure appropriate levels of genetic diversity, but this is a logistical rather than a biological challenge.

Another recent hypothesis supported by our results is that many plant species can be more limited by dispersal than intrinsic site factors (Primack and Miao 1992, Matlack 1994). This is not surprising in a landscape in which anthropogenic impacts have led to large declines in biodiversity, and habitat fragmentation inhibits natural immigration processes (Matlack 1994, Tilman et al. 1997). The consequence is that large areas of potentially suitable but unoccupied habitat may exist for many species (Primack and Miao 1992, Matlack 1994). In longleaf pine habitats, reinitiating frequent prescribed burning provides a necessary framework to support high levels of plant diversity, but dispersal limitation could prevent a site from accumulating species that would otherwise occur there. The idea that large areas of suitable habitat may exist for rare longleaf pine plants argues for a "Johnny Appleseed" approach, emphasizing initiation of multiple new populations instead of expending scarce resources on exhaustive studies of habitat factors. Recent findings point to the importance of stochasticity in plant population initiation and persistence (Menges 1992). These findings also support the strategy of starting many new populations, since some populations will fail due to random and unpredictable phenomena including continued anthropogenic impacts. According to Guerrant (1996: 198) "the single most effective design feature for reducing overall risk of failure is to reintroduce multiple populations as a standard procedure." In the FMNF and other national forests this strategy has been employed successfully for red-cockaded woodpeckers (*Picoides borealis* Vieillot); we suggest that a similar strategy can work equally well for many rare plant species.

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Table 5. Additional results from the experimental gradients: survival, size, and reproduction in September 1999 of plants originating from seeds germinated prior to that date. Sample size (n) indicates the number of germinated seeds. Note that for some species (e.g., spring-summer fruiting species *Arnica* and *Pterocaulon*), most of the germination occurred after the September 1999 census and sample sizes shown below are consequently not as large for these species as they are in Table 4. Flowering is given as a percentage of living plants. Numbers under **Ht/Len** are mean values for plant height in cm unless followed by an L which indicates that leaf length measurements are given instead (this was for species with basal rosettes only). For species with a mixture of bolting and non-bolting stems, mean heights were calculated by assigning a height of 1 cm to individuals present only as rosettes.

	Bed 1 (sandy loam)				Bed #2 (sand)				Bed #3 (loamy sand)			
Species	n	% alive	% flower	Ht/ Len	n	% alive	% flower	Ht/ Len	n	% alive	% flower	Ht/ Len
	4	0.0	—	—	2	0.0	—	—	3	0.0	—	—
Chaptalia tomentosa	7	0.0	—	—	22	0.0	—	—	19	2.1	0.0	0.8L
Chrysopsis gossypina	28	10.7	—	1.0	33	78.8	50.0	17.2	29	58.6	0.0	1.0
Ctenium aromaticum	12	0.0	—	—	7	0.0	—	—	11	33.3	0.0	6.7L
Erigeron vernus	4	0.0	—	—	3	0.0	—	—	12	0.0	—	—
Eupatorium leucolepis	53	17.0	44.4	20.9	42	67.3	81.5	34.2	68	61.8	52.4	25.5
Liatris squarrosa	34	52.9	5.6	2.2	43	51.2	50.0	15.0	34	82.4	14.3	4.1
Polygala lutea	4	0.0	—	—	3	33.3	100.0	15.0	4	25.0	0.0	1.9
Pterocaulon pycnostachyum (Michx. Ell)	1	0.0	—	—	—	—	—	—	—	—	—	—
Rhexia alifanus	9	0.0		—	1	0.0	—	—	3	0.0	—	—
Rhynchosia reniformis	11	27.3	0.0	0.7	10	10.0	0.0	0.9	22	63.6	0.0	0.9
Schizachyrium scoparium	59	49.2	31.0	25.8	25	72.0	72.2	49.0	34	55.9	31.6	23.5
Tephrosia virginiana	36	19.4	0.0	20.1	34	32.4	0.0	24.0	42	21.4	0.0	18.6
Vernonia angustifolia	25	16.0	0.0	10.2	22	50.0	18.2	12.2	26	38.5	0.0	8.3

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