
Patterns of Differentiation in Wiregrass (*Aristida beyrichiana*): Implications for Restoration Efforts

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Abstract

Aristida beyrichiana (wiregrass) is increasingly being planted in restoration projects across the southeastern coastal plain, with little focus on genetic differences among populations across the region. Local and regional population differentiation for establishment and growth traits were examined in common garden and reciprocal transplant experiments. Seeds from up to 20 plants from each of seven populations were collected in northern and central Florida sites that encompassed gradients of soils, hydrology, and temperature. Reciprocal seed transplants using three of the common garden populations were conducted in two consecutive years. In the common garden, significant population differences were seen in seed weight, seedling emergence and survival, tiller height, number of tillers, the relationship between tiller number and tiller height, and flowering. Variation among maternal families was seen in tiller number and in the relationship between tiller number and tiller height. The reciprocal transplant study did not detect either local adaptation to sites of origin or consistent superiority of one source population or planting site in seedling establishment. These results suggest that the

probability of seedling establishment is primarily dependent on environmental conditions rather than genetic differences. Genetic variation for traits related to fitness (e.g., tiller number) may be retained within populations because phenotypically plastic growth responses of seedlings to environmental variation buffer genetic variation against the action of selection. But despite the lack of evidence for genetic influences on initial establishment in wiregrass, our common garden study suggests genetic differences among populations. This result, when combined with previous results indicating local adaptation in later life stages of wiregrass, suggests that restoration efforts involving this species should use local seed sources from sites with similar soil and hydrological conditions.

Introduction

In recently restored ecosystems, the adaptive capacity and genetic potential of the few dominant species planted on a site may strongly affect restoration success (Smith & Bradshaw 1979; Bradshaw & McNeilly 1981). Unfortunately, maintenance of the genetic structure within a species usually is not considered in plant restoration projects (Gordon 1994; Knapp & Rice 1994, 1996). But differentiation among populations resulting from local or regional selection (McMillan 1959; Aston & Bradshaw 1966; Antonovics & Bradshaw 1970; Robertson & Ward 1970; Clary 1975), genetic drift, or founder effects (Rapson & Wilson 1988; Clay & Levin 1989; Knapp & Rice 1996) is well documented. This differentiation represents an important component of genetic diversity that may influence both the initial establishment and the subsequent persistence of restored plant populations (Millar & Libby 1989; Gordon 1994; Knapp & Rice 1994). Because the genetic mixing and translocation associated with plant propagule movement during restoration is essentially irreversible, the consequences of such manipulations need to be understood.

Aristida beyrichiana Trin. & Rupr. (wiregrass) is a species currently under development for large-scale restoration efforts. (The nomenclature for this species south of North Carolina has been revised from *Aristida stricta* Michx. to *A. beyrichiana* Trin. & Rupr. [Peet 1993].) This perennial bunchgrass is a dominant understory species in ecosystems of *Pinus palustris* Mill. (longleaf pine) across much of the southeastern coastal plain. Several organizations have started propagating wiregrass for restoration because wiregrass can be reintroduced to sites through both direct seeding and transplanting (Duever 1989; Seamon et al. 1989; Seamon & Myers 1992). The majority of the restoration research for longleaf pine systems has focused on wiregrass because of its original dominance as an understory species and because it maintains dead leaves and tillers within

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bunches that contribute substantially to the fine fuels integral to these pyrogenic systems (Platt et al. 1988; Clewell 1989).

Interest in restoring longleaf pine sandhill communities has increased because of their decline in area by 88% across the southeast, and by 98% in Florida (Kautz 1990). These communities are dominated by longleaf pine, *Quercus Laevis* Walt. (turkey oak), and wiregrass. Conversion to forest plantations and improved pasture has caused much of the decline in the areal extent of this community type. Degradation of these communities has also resulted from several decades of fire suppression. The focus on restoration has increased both because of concern for federally listed species that rely on sandhill habitats (e.g., Red-cockaded Woodpecker) and because degraded or converted areas have been acquired as buffers around more pristine sandhill communities.

Despite the broad geographic range of wiregrass (North Carolina to south Florida and eastern Mississippi) that spans several different climatic regimes as well as soil and community types (Clewell 1989), relatively little is known about intraspecific variation in this species. Significant regional genetic differentiation has been demonstrated in other wide-ranging perennial grasses (Clay & Antonovics 1985; Billington et al. 1988; Knapp & Rice 1994), so among-population genetic variation would be expected in *A. beyrichiana*. Population differentiation in wiregrass has been hypothesized based on preliminary experimental work (Parrott 1967). Electrophoretic analysis of a few populations across the range showed among-population genetic variability in isozyme markers (Walters et al. 1994). Also, Kindell et al. (1996) found evidence for localized adaptation within wiregrass populations in a reciprocal transplant experiment between nearby mesic (flatwoods) and xeric (sandhills) longleaf pine communities.

Increasing our understanding of potential population differentiation is critical prior to initiation of large-scale reintroduction and augmentation efforts. For example, if populations have become locally adapted to soil and environmental characteristics, then planting propagules in new locations may result in reduced survival, growth, or reproduction relative to locally adapted material (Fahsel 1988; Millar & Libby 1989; Bacchus 1992). If different populations have different levels of tolerance to infection by pathogens or other conditions, then mixing populations may result in significant shifts in tolerance over time (Conway 1988). Overall, inadvertent modification of natural patterns of genetic variability and diversity may have long-term, negative consequences for this species.

To understand the overall genetic architecture of a species undergoing restoration, it is important to measure genetic variation both among and within populations. While differences among populations may reflect the past action of selection in shaping locally adapted

populations, the within-population variation indicates the capacity of the population to evolve in response to selective pressures (Falconer 1989).

We initiated a common garden experiment, using populations that had been characterized electrophoretically (Walters et al. 1994), to look for population differences in wiregrass. We collected seeds from populations located in north and central Florida to examine whether plants from geographically proximate or environmentally similar sites are more similar than plants from geographically separated sites or contrasting environments. Seeds from individual plants within each of the populations were collected and planted separately so that the potential amount of genetic variation within populations could be compared (Falconer 1989).

Following the common garden experiment, we conducted a reciprocal transplant experiment in both 1992 and 1993 across three xeric sandhill sites to determine whether or not the among-population differences represent adaptation at a regional scale. Because of the local adaptation found by Kindell et al. (1996) across xeric sandhill to mesic flatwoods habitats, we hypothesized that populations originating within the xeric sandhill habitat type would exhibit large-scale patterns of differentiation in response to selective forces that reflect regional gradients in climate and soils.

Methods

Common Garden Experiment

In November 1990 we collected seed from 11–20 individual plants in each of seven populations in five different sites (Fig. 1). Seeds collected from each plant constituted a maternal family: although the pollen parent of each seed within a maternal family is unknown, all seeds collected from a plant share the same mother. The sites encompassed north and central Florida and included several soil series and moisture gradients. The two northernmost sites were at Torreya State Park (population 1) and the Apalachicola Bluffs and Ravines Preserve (ABRP, population 2) in Liberty County; the central site was at the Katharine Ordway–Swisher Memorial Preserve (population 3) in Putnam County; and the southern populations were from Wekiwa Springs State Park (populations 4 and 5) and Rock Springs Run State Park (populations 6 and 7) in Orange County. These sites spanned a distance of roughly 440 km. Populations 1 and 2, 4 and 5, and 6 and 7 were separated by 8, 1.6, and 0.4 km, respectively. All populations except those from Rock Springs Run (populations 6 and 7) were in xeric sandhill communities dominated by longleaf pine, turkey oak, and a diverse, primarily perennial, herbaceous understory that included wiregrass. Populations 6 and 7 were from a more mesic flatwoods com-

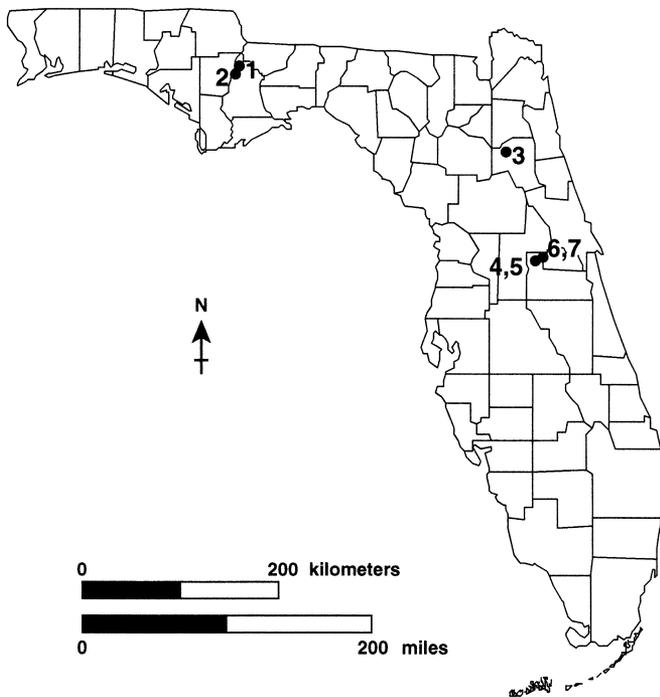


Figure 1. Sites within Florida from which wiregrass seed were collected for the common garden experiment and used for the reciprocal transplant experiment (populations 2, 3, and 4). Population 1: Torreya State Park, Liberty County; population 2: Apalachicola Bluffs and Ravines Preserve, Liberty County; population 3: Ordway-Swisher Memorial Preserve, Putnam County; populations 4 and 5: Wekiwa Springs State Park, Orange County; populations 6 and 7: Rock Springs Run State Park, Orange County.

munity dominated by longleaf pine, *Ilex glabra* Gray (gallberry), and a denser but similarly diverse understory (Myers 1990). By collecting from a flatwoods site as well as from multiple sandhill sites, we hoped to examine differences between wiregrass populations in hydrologically contrasting community types (sandhill versus flatwoods) as well as regional variation of wiregrass populations found within a particular community type (i.e., sandhill habitats). All sites are prescribe-burned at 3–5-year intervals.

Seeds from each plant (i.e., family) were stored separately. Ten to fifteen randomly selected families from each population were established in the common garden. Plants were grown under shade-cloth on the campus of the University of Florida (Alachua County), within 65 km of the population 3 site. Seeds from each of the families were sown into C cells (6.4 × 25.4 cm) in February 1991. Several seeds from an individual family were sown into each of five replicate pots. The soil medium used was two-thirds sand, one-third peat. Because wiregrass is mycorrhizal (D. Gordon, unpub-

lished data), soil from the site from which population 2 was collected (but without wiregrass seed present) was mixed into the upper 2 cm of each pot and was used to shallowly cover the seeds after sowing. A slow release 14–14–14 fertilizer (Osmocote®) was applied (1.5 g/pot) to the soil surface in each pot in late August.

The average weight of seeds from 10 families per population was measured. Averages were calculated from the composite weight of 10 seeds/family. Seeds were then placed in petri dishes on saturated filter paper and checked weekly for radicle emergence. Percent germination per family was not calculated because some spikelets may have shattered prior to seed collection from the plants.

Pots were watered to field capacity every other day. The date of first emergence of any plant in a pot was recorded. Shoot emergence started early in March and continued through June. On 1 May 1991, plants were thinned so that two robust, centrally located plants remained in each pot. Height, number of leaves, and number of tillers of one randomly selected marked plant per pot were recorded monthly. Presence of flowering culms was also recorded for each plant. The plants grew in the pots for one year.

In early June 1991, plants were thinned to the one marked individual per pot. The maximum height and shoot dry weight of the plants removed during thinning were measured to determine whether plant height could be used as a nondestructive measure of plant weight. This correlation was strong and positive overall ($r = 0.92$; $p < 0.0001$) and ranged from 0.82 to 0.96 across the populations (log-transformed data).

Differences among populations in mean seed weight were examined with one-way analysis of variance. The effects of population and family (nested within population) on the timing of seedling emergence and flowering were tested by a hierarchical analysis of variance. Growth responses of plant height, tiller number, and number of leaves to population and family differences were compared with repeated-measures analysis of variance. Pillai's trace statistic was used to determine significance at an alpha level of $p = 0.05$ because of its power and relative insensitivity to violations of model assumptions (SAS Institute 1995). Distributional properties of the data for plant height, tiller number, and number of leaves satisfied parametric assumptions; time to emergence data required log transformation in order to homogenize variances. Specific differences among populations were identified by means of a priori orthogonal contrasts.

Reciprocal Transplant Experiments

Three fire-managed xeric sandhill sites (ABRP, population 2; Ordway-Swisher, population 3; and Wekiwa

Springs, populations 4 and 5) were selected for this reciprocal transplant experiment because these populations encompassed both the range of growth and the flowering responses observed and the geographical range of the earlier common garden experiment (Fig. 1). All sites had an open overstory of longleaf pine and turkey oak and a relatively low cover understory. All soils were excessively drained sands—Lakeland sand (thermic coated typic quartzipsamment) at ABRP and Candler fine sand (hyperthermic uncoated typic quartzipsamment) at both Ordway-Swisher and Wekiwa Springs. All sites had 0–5% slope. Planting sites were in units not burned the previous growing season and near the seed collection populations in each location. The experiment was conducted in the same locations in both 1992 and 1993.

In late November of each year, seed was hand-collected from each of the three populations. A minimum of 30 plants growing at least 2 m apart were sampled, and the seed within each population were bulked. All seed collection sites had been burned during the previous growing season. In 1993, seeds were sorted by means of a dissecting microscope to increase the probability that only filled seeds were used. Average seed weight of these seeds was determined for each source population for use as a covariate in the analyses if necessary. Seed germination tests were conducted in petri dishes in the laboratory. Five dishes of 10 seeds each were tested for each population in both years.

Using a randomized complete block design, we established 20 experimental planting blocks in fairly open areas in each of the three sites. We created four 10 × 10 cm plots in each block by removing litter, lightly scraping the soil surface, and removing any small plants present. A 25 cm buffer was left around each plot, resulting in 95 × 95 cm blocks. Each plot was marked with a plastic pot-marker to identify the population seed source. Seeds from each of the three populations were sown separately in three of the plots, while the fourth plot was left empty as control for local seed contamination. In 1992, 50 seeds from each population were sown per block and lightly covered with soil. In 1993, 25 seeds were sown per plot, attached by their awns with wood glue to a 10 × 10 cm piece of nylon window screening. This design modification increased the probability that seeds would remain in the plots. Blocks were sown on three consecutive days in February of 1992 and 1993.

In both years, severe storms occurred within two weeks of sowing. The heavy rain likely washed significant numbers of seeds from the plots. For example, as an indirect indication of storm intensity, no glue was evident on the screens following the 1993 storm. In the analyses, seed loss during these storms is assumed to have occurred with equal probability at all blocks.

Timing of seedling emergence was examined on a weekly basis. Plots were weeded of other species as needed. In November of each year we intended to remove and measure surviving plants to preclude leaving individuals from nonlocal populations in the field, but low seedling survival prevented collection of these data.

Weather data for 1992 and 1993 were obtained from the weather station nearest to each of the three sites. Using monthly means, we examined correlations (Spearman rho) among the sites in total and average rainfall as well as minimum and maximum temperatures. Data for seed germination and weight analyses were collected in the same manner as the common garden experiment. Seed source, population, and year effects on the number of seedlings emerging and number of plots with seedlings were analyzed by chi-square tests. Timing of emergence in different sites was analyzed by the non-parametric Friedman's test.

Results

Common Garden Experiment

Analysis of variance showed that the average seed weight per family was significantly dependent on the population or origin ($df = 6, F = 3.12, p < 0.005$). Tukey tests revealed that seeds from population 3 were significantly lighter ($p < 0.05$) than those from populations 1, 5, and 7 (Fig. 2). For both sets of experiments, it should be noted that environmental differences among seed

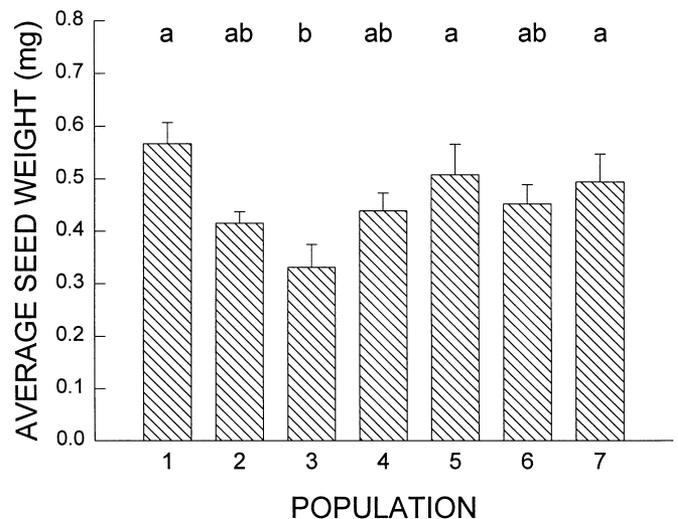


Figure 2. Mean seed weight from groups of 10 seeds each for wiregrass families from seven populations in Florida. Populations are geographically ordered from north (1) to south (7). Populations sharing the same lower case letters are not significantly different ($p > 0.05$), as indicated by Tukey tests.

collection sites may have influenced seed size during seed maturation and cannot be differentiated from genetic differences among the populations.

The date of seedling emergence differed significantly among populations ($df = 6$, $F = 2.52$, $p = 0.025$) but not among families within populations. Orthogonal contrasts showed significant differences ($p < 0.05$) between populations 3 and 7 and the other populations. Seedlings emerged later in population 3 than in 1, 4, 5, 6, and 7 (Fig. 3). The percentage of families and number of pots within families producing seedlings (Table 1) suggest lower seed viability or germinability in populations 2 and 3. Further, these populations showed the highest seedling mortality through the first 7 months of growth.

Seedling height initially followed patterns of emergence of the smaller plants in later emerging populations, but over time seedlings from the flatwoods site (populations 6 and 7) became larger than those from the sandhill populations. By October 1991, the height increment in all plants had slowed considerably. Repeated-measures analysis of height data indicated significant effects of population ($df = 6$, $F = 4.04$, $p = 0.0007$), sampling date ($df = 8$, $F = 136.35$, $p < 0.0001$), and their interaction ($df = 48$, $F = 1.76$, $p = 0.0012$) but no main effect of family within a population ($p > 0.40$) or interaction of family with sampling date ($p > 0.10$). Contrasts among populations indicated that average plant height within the flatwoods populations (populations 6 and 7) was significantly greater than in the sandhill populations.

Differences in the numbers of leaves and tillers initially increased over time, resulting in a trend of smaller

Table 1. Seedling emergence and survival in the common garden experiment by population of origin.

Population	% of Maternal Families Producing Seedlings	% Seedling Mortality	# Pots Per Family with Seedlings (n = 5)	
			Mean	SD
1	100	0	4.18	0.75
2	77	9.5	2.33	1.00
3	87	17.4	1.77	0.93
4	100	3	4.47	0.74
5	93	1.8	3.86	1.46
6	93	0	3.54	1.26
7	100	6.2	3.2	1.15

plants from sandhill population 3 than from the flatwoods populations (populations 6 and 7; Fig. 4). The number of tillers per plant was dependent only on the effects of family within a population ($df = 83$, $F = 1.37$, $p = 0.04$) and sampling date ($df = 5$, $F = 179.45$, $p < 0.0001$). For individual sampling dates, significant ($p < 0.05$) differences existed among the populations; after a year in the pots, these differences were no longer significant. Convergence of plant size at the end of the experiment may indicate that plant growth was eventually constrained by pot volume.

Analysis of covariance of the effect of population, maternal family, tiller number, and the interaction between population and tiller number with tiller height at each sampling date revealed population differences in the relationship between increases in plant size (as measured by tiller number) and tiller size (as measured by tiller height) ($df = 6$, $p < 0.05$). Although tiller size al-

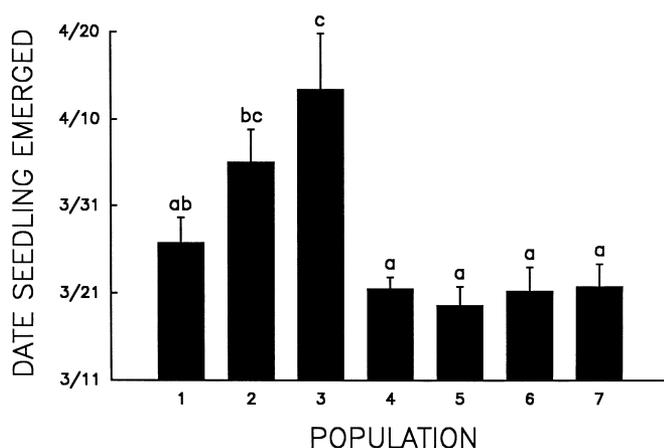


Figure 3. Mean (± 1 SE) date of first leaf emergence of wiregrass plants from seven populations grown in a common garden. Populations are geographically ordered from north (1) to south (7) in Florida. Populations sharing the same lower-case letters are not significantly different ($p > 0.05$), as indicated by Tukey tests.

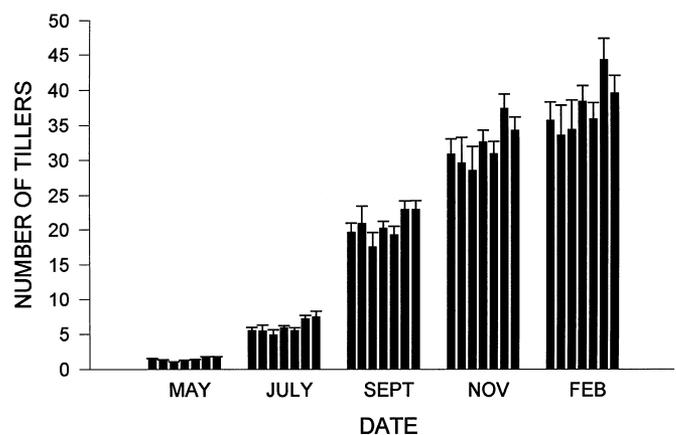


Figure 4. Mean (± 1 SE) numbers of tillers per plant by sampling date of wiregrass plants from seven populations grown in a common garden experiment. Bars represent means for populations, which are geographically ordered from north (left) to south (right) in Florida.

ways increased with plant size ($df = 1, p < 0.0001$), one of the flatwoods populations (population 6) was distinctive in that increases in tiller size were less correlated to increasing plant size than in the other populations. While population 6 plants usually had more tillers at a given height than did plants from the other populations, by the end of the experiment population 2 plants had more tillers at a given height. Interactions between population and tiller number were significant ($df = 6, p < 0.003$) in over half of the sampling dates.

Although few of the plants flowered during the experiment, those that did were all from the four southernmost populations (populations 4, 5, 6, and 7; 20–40% of the plants within those populations flowered). Population source significantly influenced the probability of flowering ($df = 6, F = 3.19, p = 0.006$). Although sample sizes were small, production of inflorescences did not appear to be determined exclusively by plant size.

Reciprocal Transplant Experiments

Average daily maximum and minimum temperatures were highly correlated among the transplant sites in both years (Spearman rho $> 0.91, p = 0.0002$). Temperature ranges were from a low of 5.6°C at ABRP to a high of 36.2°C at Ordway-Swisher. In contrast, total monthly rainfall and average daily rainfall were significantly correlated only between the Ordway-Swisher and Wekiwa Springs sites (Spearman rho = 0.89 and 0.93, $p = 0.0005$ and 0.0001 , respectively) in 1992, in part because ABRP received 30% more rain than the other sites that year. In 1993, no significant correlations existed for rainfall parameters among any of the sites ($p > 0.15$). Even when associated with regional cold fronts, variation among sites in average daily rainfall indicates that precipitation is locally patchy. Rainfall was consistently lower in 1993 than in 1992, with February through November totals (January and December not available for all sites) of 982, 1011, and 1033 mm at Wekiwa Springs, Ordway-Swisher and ABRP, respectively.

On average, seeds from population 3 (mean \pm SD = 8.93 ± 0.52) were significantly heavier ($df = 2, F = 11.25, p < 0.0001$) than seeds from the other two populations (population 2: mean = 8.07 ± 0.60 ; population 4: mean = 8.15 ± 0.53) in 1993. These differences were not correlated with either germination success or seedling survival ($p > 0.05$). Seed germination trials in petri dishes revealed no significant differences in either the percentage or timing of germination across the populations in either year.

For the different site-by-source treatment combinations, chi-square tests were used to examine differences among source populations in the number of plots containing at least one seedling. In 1992, the southernmost sites (Wekiwa Springs; $p < 0.05$) and northernmost sites

Table 2. Chi-square tests of the effects of planting site and seed source population on the probability of wiregrass seedling emergence by year and across the 2 years of the reciprocal transplant experiment.*

Factor	1992	1993	1992–1993
Site	A > W, O***	W > O, A***	—
Population	W > O, A**	—	W > O > A**
Site \times Pop	—	—	—

*Sites are abbreviated: A = Apalachicola Bluffs and Ravines Preserve, O = Ordway-Swisher Memorial Preserve, W = Wekiwa Springs State Park.

** $p < 0.01$.

*** $p < 0.001$.

(ABRP; $p < 0.01$) contained significantly more plots with seedlings from population 4 than from either of the other two populations. The total number of plots with seedlings from any source increased from south to north in 1992 and from north to south in 1993, paralleling results for the total number of seedlings (see below). Although both planting site and source population were significant ($p < 0.05$), their interaction was not significant when data from the two years were examined separately (Table 2). Across all sources, more plots contained seedlings in 1992 than in 1993.

When the total number of plants that emerged from each of the source populations was examined, there were also significant main and interactive effects of planting site and seed source (Fig. 5). Total germination in 1992 was highest at ABRP; in 1993, germination was highest at Wekiwa Springs ($p < 0.05$). Overall, in 1992 seed from population 4 germinated with higher frequency, while in 1993 seed from population 2 showed the lowest germination rate ($p < 0.05$). In 1993 and

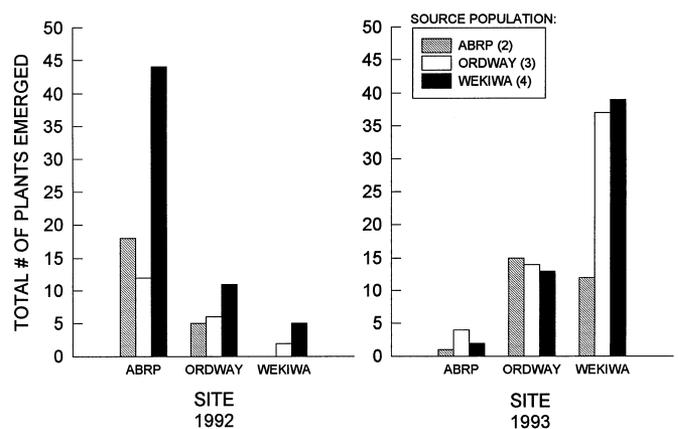


Figure 5. Total number of wiregrass seedlings emerging at each reciprocal transplant site by seed source population and year. Significant site and population effects follow Table 2. In both 1993 and when the 1992 and 1993 data are combined, chi-square tests revealed significant interactions between population and site ($p < 0.05$)

when data from both years were combined, however, a significant site-by-population interaction was detected. Thus, while some source populations appear to have greater viability than others, no clear patterns with site were evident over both years of this experiment.

Analysis of covariance on ranked data (Friedman's test) was used to evaluate the main and interactive effects of site and population on the timing of seedling emergence (Fig. 6). Despite apparent differences in germination timing of the 1992 cohort, the trends are not significant. During 1993, site significantly ($p = 0.01$) affected the timing of wiregrass germination. Seeds sown at Wekiwa Springs germinated earlier than those at Ordway-Swisher, which in turn germinated earlier than cohorts at ABRP. The indication of a site effect ($p = 0.06$) over the two years reflects earlier germination at Ordway-Swisher than at ABRP. When 1992 and 1993 data were combined, significant source effects ($p = 0.02$) reflected the overall slower germination of the northernmost seed (population 2) compared to the southern seed populations (populations 3 and 4).

Discussion

We found significant intraspecific phenotypic variation for several traits associated with wiregrass growth and

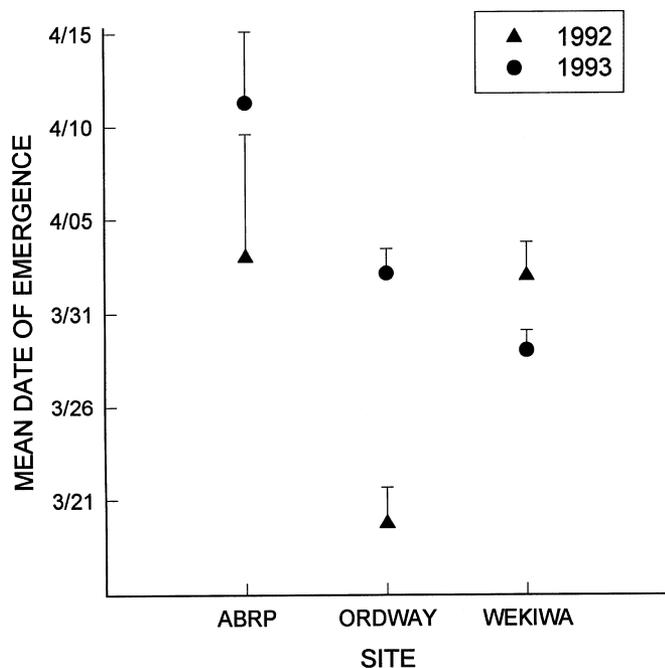


Figure 6. Mean date at which wiregrass seedlings emerged at each of the reciprocal transplant sites in 1992 (triangles) and 1993 (circles). Data reflect the mean (± 1 SE) across all three seed source populations at each site. Data designated with different letters indicate significant differences ($p < 0.05$), as indicated by Tukey tests (no significant differences in 1992).

phenology in both the common garden and reciprocal transplant experiments. Results from the common garden further suggest that for some traits there is significant genetic variation within populations. These different scales of variation have distinct implications for wiregrass restoration efforts. Differences among populations in demographically important traits such as seedling survival or age of first reproduction may indicate the action of natural selection in the past and thus reflect local adaptation (McMillan 1959; Bradshaw 1984; Rice & Mack 1991). Although the reciprocal transplant experiment did not provide evidence for local adaptation (see below), the variation detected among seed source populations indicates that, at minimum, restoration efforts need to consider the source of planting material of wiregrass populations. This evidence for regional differentiation among wiregrass populations from sandhill and flatwoods habitats is in addition to previous evidence for localized differentiation of populations between xeric sandhill and mesic flatwoods habitat types in northern Florida (Kindell et al. 1996).

In our study, significant among-family differences detected in the common garden suggest that there may be significant genetic variation within the flatwoods populations for traits such as tiller number. Given that the often severe physical conditions of sites under restoration may result in the creation of strong selective regimes, genetic variation within populations represents an evolutionary potential that may be critical for the long-term success of a restoration project. The fact that the populations varied in the degree of differentiation at the family level further suggests that the amount of within-population variation, and thus the ability to respond to natural selection, may be population-dependent.

We can only speculate as to the processes that may maintain genetic variation in tiller number, a trait that might be expected to be highly correlated with plant fitness. The habitat differences in within-population variation may indicate that stabilizing selection for tiller size is stronger within the sandhill sites, or that variable selection for tiller number is more pronounced in the flatwoods site, or both. Alternatively, within-population genetic variation for tiller number in wiregrass may persist in spite of rather than because of selection. Both our reciprocal transplant experiment and that of Kindell et al. (1996) indicate that temporal and spatial environmental variation may be much more important than genetic variation in determining seedling survival during establishment. Chance dispersal of genotypes into favorable microhabitats, coupled with plastic growth responses on the part of the young seedlings, may act to reduce the ability of selection to eliminate less-fit genotypes. In a very real sense, phenotypic plasticity buffers the genetic variation of the population against the effects of selection (Sultan 1987).

It is possible that a number of microevolutionary processes, and not just natural selection, contribute to the hierarchical structure of variation in wiregrass populations. Especially at the regional level, processes such as founder effects and genetic drift can be important in creating among-population differences (Levin 1988). But results from an electrophoretic survey of these populations by Walters et al. (1994) provide evidence against the importance of founder effects and drift. The survey included eight enzyme systems and 15 loci. Nei's genetic identity values for the populations were all above 0.97. Although a phenogram of genetic distances was able to discriminate among regional populations, these high genetic identity values indicated that the populations were very similar in terms of electrophoretic markers. If one assumes that these allozyme loci are largely neutral to selection, then they are good markers for detecting the influence of gene flow and drift in creating genetic differences among populations (Slatkin & Barton 1989; Knapp & Rice 1996). The percent of polymorphic loci ranged from 67% to 80% across populations, suggesting potentially high gene flow. The minimal differences among these wiregrass populations in allozyme variation would suggest that genetic drift has not been an important factor in creating regional genetic structure or that gene flow among populations is high, or both.

If genetic drift is relatively unimportant in causing the differences among populations observed in the common garden, then natural selection is the most likely explanation. In the reciprocal transplant experiments, seed source population did influence the probability and timing of seedling emergence. But we observed no consistent "home site" advantage in seedling establishment, which would imply local adaptation to sites of origin.

Several factors associated with the relative vulnerability of seedlings to environmental stress may explain our inability to detect local adaptation at a regional scale. Previous studies suggest that the probability of seedling establishment is much more dependent on local environmental conditions than on genetic differences (Kindell et al. 1996). Survival of naturally establishing seedlings may depend on relatively regular precipitation through late winter and spring (P. Seamon, personal communication). High rainfall events caused soil removal and exposure of seedling roots, however, which resulted in desiccation of virtually all of the seedlings in the reciprocal transplant experiments (D. Gordon, personal observation). Kindell et al. (1996) similarly found low survival rates among 1-week-old transplanted wiregrass seedlings and, more important, no indication of local adaptation in this early age class. This negative result contrasted with their detection of significant local adaptation for older (4- and 8-week-

old) transplanted wiregrass plants. To explain this transplant age effect, Kindell et al. (1996) hypothesized that environmental conditions are relatively harsher for younger seedlings. These environmental effects are suggested to reduce the phenotypic expression of genetic variation in 1-week-old seedlings, resulting in high phenotypic similarity among individuals in the population.

Recommendations

Our experiments suggest that the material used for restoration of this species in conservation areas should be collected from many parent plants from sites of similar hydrology near the re-introduction sites. This approach will not necessarily increase the probability of seedling establishment, which appears to be variable and environmentally dependent over time, but it would conserve patterns in genetic variation and expression that may affect survival and fitness characters in adults. Further, it is important to remember that our studies examined plant traits only during very early stages of seedling growth and establishment. As suggested by the results of Kindell et al. (1996), local adaptation may manifest itself in wiregrass primarily in older seedlings or adult plants. The clearest results indicate that seed should not be moved between xeric sandhill and mesic flatwoods habitats. Understanding the consequences for restoration success of moving populations within those habitat types will require further investigation of the fitness implications of within-population variation. But the complex pattern of differentiation within and among populations suggests that local adaptation to both climatic and microsite conditions may influence species establishment and long-term persistence.

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