Wiregrass

GROWN FROM SEEDS OBTAINED ON
FLORIDA FLATWOOD AND SANDHILL SITES

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ABSTRACT

The results of our 2 long-term studies indicate that while it may be best to restore a site with wiregrass (*Aristida beyrichinia* Trin. & Rupr. [Poaceae]) obtained from a similar site, it does not seem to be essential. In the first study, after 12 y, plants grown on a flatwood site in south-central Florida from seeds collected at a sandhill site (2 locations) in north-central Florida had 83% survival and average aboveground dry mass was 39 g/plant (1.4 oz) with basal diameter of 11.6 cm (4.6 in). In a second study, wiregrass plants from seeds collected at 8 locations (8 entries) across Florida were grown on a flatwood site in central Florida. Four of these entries were also grown on a sandhill site in north Florida. After 4 y on the flatwood site, one entry originating from a nearby flatwood survived better (88%) than the 7 other entries. One entry from a sandhill was notably inferior in survival (3%), but for the remaining 6 entries survival was similar (average 32%). On the sandhill site, the same entry of flatwood origin that had 88% survival on a flatwood had 92% survival, while the other 3 entries averaged 7% survival. Plant dry mass and diameter were not strongly associated with plant origin. Mass averaged 14.8 and 3.1 g/plant (0.52 and 0.11 oz) and diameter averaged 63 and 30 mm/plant (2.5 and 1.8 in) on the flatwood and sandhill sites, respectively.

KEY WORDS
Aristida beyrichinia, restoration, native plants, genotype x environment interaction, Beyrich threeawn

NOMENCLATURE
USDA NRCS (2004)

Wiregrass (*Aristida beyrichinia* Trin. & Rupr. [Poaceae]) plays an active role in maintaining fire-adapted longleaf (*Pinus palustris* P. Mill. [Pinaceae]) and slash pine (*P. elliottii* Englm. [Pinaceae]) communities in the southeastern US and is considered to be a key species in the system (Clewell 1989; Noss 1989). Restoration of wiregrass ecosystems is important (Clewell and Cleckley 1994) because of the extensive loss of this plant community across the southeastern US (Frost 1993; Ware and others 1993). The longleaf pine–wiregrass ecosystem has declined to < 5% of its original range (Ware and others 1993; Landers and others 1995), with much of that remaining area in poor condition (Noss 1989). Reintroduction of wiregrass where it had been exterminated is done by either direct seeding or outplanting of container stock (Seamon and others 1989). At issue is whether seeds collected from a given location produces individuals that will be adapted to an ecologically different location. Burton and Burton (2002) and Jones (2003) provide thoughtful insight into both sides of this debate. With respect to wiregrass, Kindell and others (1996) feel that propagules should be collected on-site or from nearby areas with environmental conditions similar to the restoration site. They found survival and biomass of 2 reciprocally planted wiregrass populations from sandhill (xeric) and flatwood (mesic) environments were generally greater after 6 mo when grown on the site of their origin.

The purpose of our investigation was to determine if origin of wiregrass seeds affected plant survival and growth when outplanted on a markedly different site. In the first of 2 studies, seeds from a Wekiwa Springs sandhill site were grown on a flatwood site, and in the second, seeds from sandhill and flatwood sites across Florida were grown on sandhill and flatwood sites in north and central Florida, respectively.

METHODS AND MATERIALS

Wekiwa Springs Collection

We collected wiregrass seeds at Wekiwa Springs State Park in November 1989 from 2 sandhill areas (referred to as WS-21 and WS-22 entries; Table 1) burned in May 1989. Containers (Multi-Pot #3-96, Stuewe & Sons Inc, Corvallis, Oregon) were filled with 5:3:2 Canadian sphagnum moss: polystyrene: vermiculite (v:v:v) and were amended with Osmocote fertilizer (17 N:6 P_2O_5:10 K_2O; Belco Resources Inc, Hampstead, North Carolina) at 2.4 kg/m^3 (2.4 oz/ft^3) and flaked S at 1.15 kg/m^3 (1.15 oz/ft^3). In February 1990, we broadcast seeds over each container, thinned germinants to 1 plant/cavity, and grew them in full sun with overhead irrigation. In August 1990, seedlings were transplanted to the field at Ona, Florida (Hardee County) (27° 26' N, 81° 55' W). Soil was an unlimed, unfertilized Myakka fine sand (sandy siliceous, hyperthermic Aeric Alaquod). Understory vegetation was typical of flatwood (Abrahamson and Hartnett 1990), of which wiregrass was a part, and the overstory was scattered south-Florida slash pine (*P. elliottii* var. *densa* [Pinaceae]). One outplanting had 35 plants each of WS-21 and WS-22 on 60-cm (approximately 2-ft) centers (7 x 10 plants) and was set in an area free of shrubs and local wiregrass. The outplanting area consisted mainly of *Dichanthelium* spp. (Poaceae) and various forbs that were mowed (5-cm [2-in] stubble) once prior to planting.

Six years later in July 1996, wiregrass was backfire burned, and in November we determined survival, noted plants with inflorescences, and harvested inflorescences from those individuals that flowered. About 100 florets of each plant were selected at random and examined for presence of caryopses under a binocular microscope (6X). Wiregrass was burned again in December 2000, and survival, biomass, and basal diameter were determined in December 2002. We compared entries for aboveground dry mass and basal diameter using Wilcoxon signed-ranks test (Wilcoxon 1945) as performed by the univariate procedure of SAS (1999).

Statewide Collection

Seeds of 8 wiregrass entries were collected in 1996 (Table 1), sown in containers in April 1997, and grown as described previously. In October 1997, we outplanted all 8 entries on a Myakka fine sand (same location as above and referred to as flatwoods), and 4 entries (Avon Park, Blackwater, Old Jennings, and Wekiwa Springs) were outplanted on a sandhill in Washington County (approximately 30° 10' N, 84° 10' W) on a

TABLE 1

Locations listed north to south for the 1996 statewide wiregrass seed collections.

Location (entry)	Coordinates [a]	Site	Soil	Date burned/collected
Blackwater	30° 40' N, 86° 50' W	Upland	Ultisol	Jun/Nov
Old Jennings	30° N, 81° 55' W	Mixture [b]	Entisol	May/Nov
Pt Washington	29° 45' N, 82° 45' W	Sandhill	Entisol	May/Nov
Ocala	29° 25' N, 81° 40' W	Sandhill	Entisol	Jun/Nov
Wekiwa Springs [c]	28° 50' N, 81° 30' W	Sandhill	Entisol	Jul/Nov
Rock Springs	28° 50' N, 81° 30' W	Flatwood	Spodosol	May/Nov
Withlachochee	28° 25' N, 82° 40' W	Sandhill	Entisol	Jun/Oct
Avon Park [d]	27° 30' N, 81° 25' W	Flatwood	Spodosol	May/Nov

[a] Approximate.

[b] Old Jennings was rolling terrain with a mixture of flatwood and sandhill sites interspersed.

[c] Wekiwa Springs is where WS-21 and WS-22 seeds were collected in 1989.

[d] Accession No. 9060362 (USDA NRCS, Plant Materials Center, Brooksville, Florida).

Eustis fine sand (siliceous, thermic Psammentic Paleudults). The sandhill was non-forested with vegetation characteristic to the region (Platt and others 1988; Myers 1990). On the flatwood site, we outplanted 64 plants (8 x 8) on 25-cm (approximately 1-ft) centers for each entry (8 contiguous plantations). On the sandhill site, a single plantation containing 70 to 96 plants of each entry was planted with random placement of the plants on 25-cm (approximately 1-ft) centers.

The flatwood site was backfire burned in December 1998 and 2000. No burning occurred on the sandhill. Plant survival was determined in December 1998 (before burning) and December 2001 at the flatwood site and October 1998 and December 2001 at the sandhill site. Basal diameter and biomass were determined at both locations in December 2001.

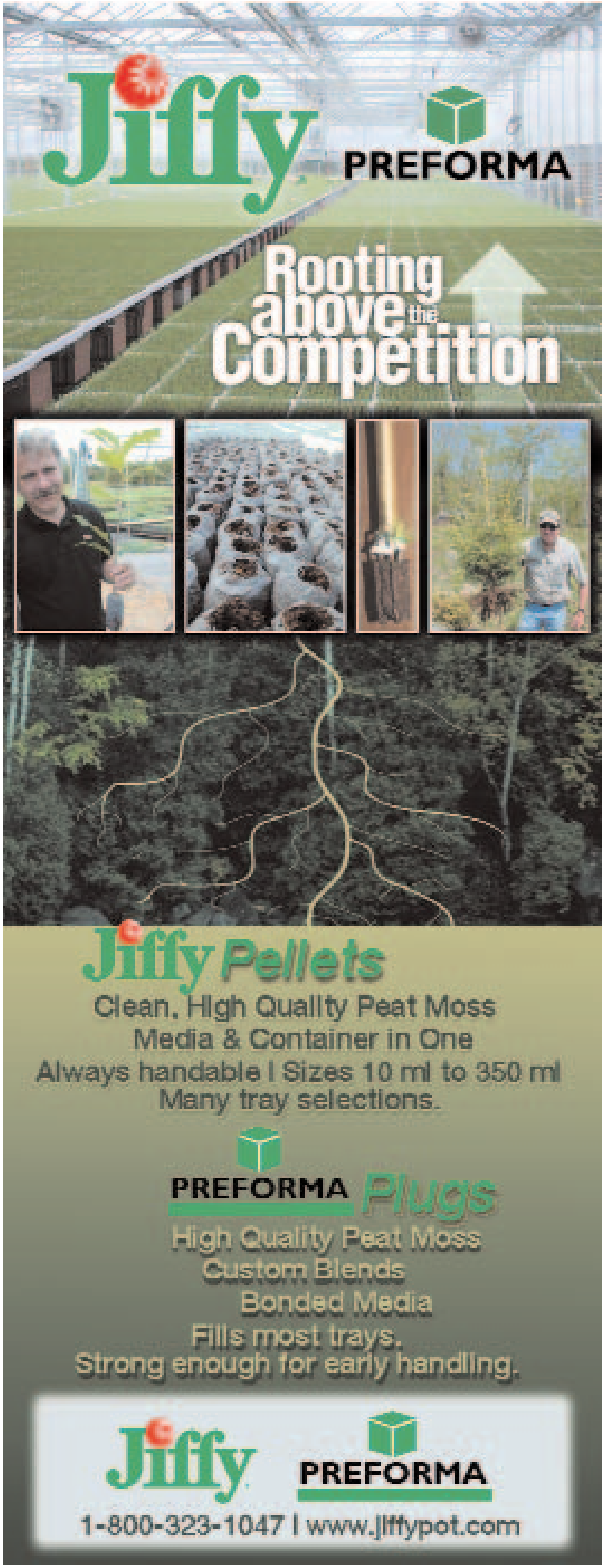
Plant survival was analyzed separately by site with the CATMOD procedure (SAS 1999). This procedure uses chi-square to analyze categorical data by portioning the variation in survival percentage into various sources (Forthofer and Koch 1973). For our data the sources included entry, date (1998 and 2001), and their interaction. Differences among entries were determined by linear contrasts. For the flatwood site, pair-wise comparisons of entries were made for plant diameter and mass using the Wilcoxon signed-ranks test (Wilcoxon 1945). For the sandhill site, plant diameter and mass were analyzed in a general linear model (SAS 1999) for a completely random design, and Duncan's multiple range test was used to separate means.

RESULTS AND DISCUSSION

Wekiwa Springs Collection

In November 1996, 6 y after planting, survival for WS-21 and WS-22 was 100% (data not shown). Although WS-21 and WS-22 came from the same locale, individual plants differed in response to burning with no floral induction on 29% of WS-21 and 37% of WS-22 plants. Considerable variation existed for seed production within plants that did flower. Of the total plants of WS-21 and WS-22, 26% and 31% had florets containing no caryopses; and 14% and 11% were weak with < 25% of their florets containing caryopses, respectively. In 20% of both entries, 26% to 50% of florets contained a caryopsis, and good caryopsis content (51% to 75%) was found only in 11% of WS-21 plants. Neither entry was rated very good for caryopsis content (> 75%). Outcalt (1994) also noted great variability in seed production traits within and between localized sites.

Because good seed production was found in a small portion of the WS collection, plant selection based only on seed production could narrow the gene pool, which may limit other traits that may confer the ability to survive in a broad range of environments. Recurrent selection for specific traits tends to decrease genetic diversity unless stringent measures are fol-



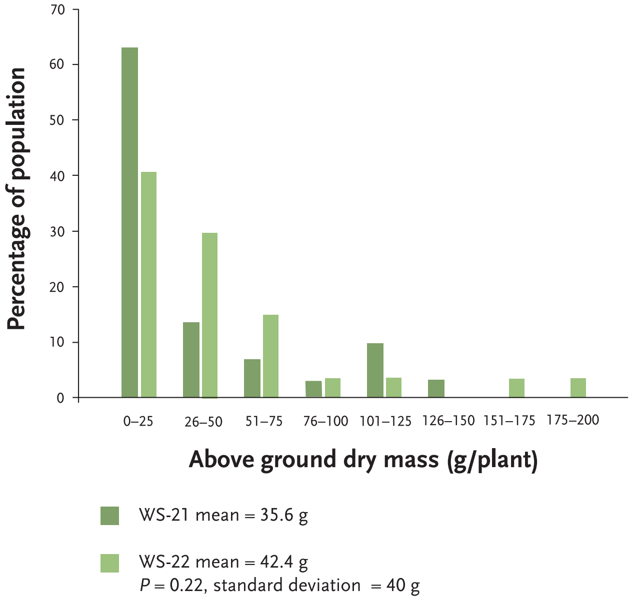


Figure 1. Above ground dry mass of 2 wiregrass entries from seeds collected at Wekiwa Springs (sandhill site) and grown for 12 y at Ona, Florida (flatwood site). Plants were burned in December 2000 and were sampled for mass in December 2002. (g • 0.035 = oz)

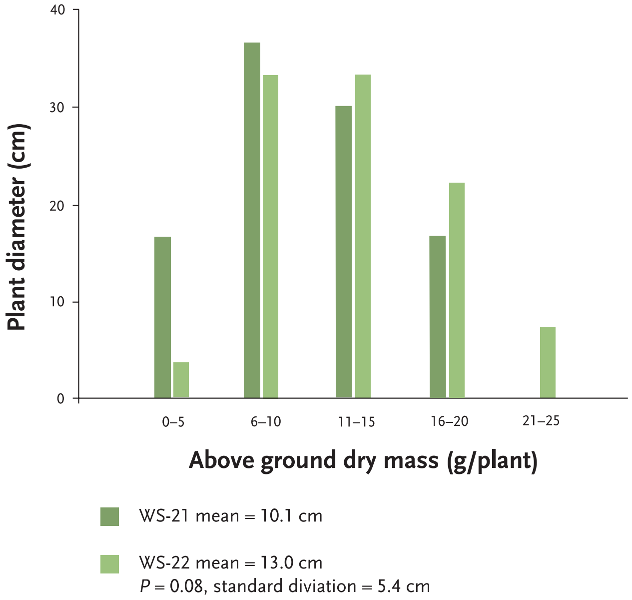


Figure 2. Plant diameters of 2 wiregrass entries from seeds collected at Wekiwa Springs (sandhill site) and grown for 12 y at Ona, Florida (flatwood site). (mm • 0.0039 = in)

lowed to ensure maintenance of diversity in correlated traits. Although genes of plants that produce more seeds are better represented in such a selection, it is important that many other genotypes are represented to increase diversity.

After 12 y, survival was 86% for WS-21 and 80% for WS-22 (data not shown). Without a summer burn in 2002, all plants remained vegetative. Therefore, aboveground mass represented 2-year's growth that was highly variable (standard deviation [s] = 40 g [1.4 oz]), and biomass was similar ($P = 0.22$) for both entries (35.6 g [1.3 oz] for WS-21 and 42.4 g [1.5 oz] for WS-22) (Figure 1). There was a tendency for WS-21 plants, however, to be lower in mass as 64% of these plants were < 25 g (0.9 oz) each compared with 40% of WS-22 plants in this category. The trend was that more WS-22 and fewer WS-21 plants occurred in larger size categories.

Although there was much variation in basal diameter (s = 5.4 cm), WS-22 plants had greater ($P = 0.08$) diameter (13.0 cm [5.1 in]) than WS-21 plants (10.1 cm [3.4 in]) (Figure 2). On average, our plants expanded in diameter about 1 cm (0.4 in)/y. As plant diameter increased, a greater portion of plants with large diameters was found in WS-22 compared with WS-21. As a point of reference, Clewell (1989) describes "mature" wiregrass plants on Florida Panhandle sandhills with 1.2- to 7-cm (0.5- to 2.8-in) diameters. Outcalt (1994) indicated plants averaged 23 cm (9 in) on a central Florida sandhill.

Plant diameter and mass were not always related because tillers of large-diameter plants were often diffuse (data not shown). In some cases, tillers formed a ring around the one-time center of the original plant, which is the "donut" characteristic noted by Clewell (1989). Our plants had not reached the point of fragmentation (about 15 cm in diameter), which begins after 15 y on Florida Panhandle sandhills (Clewell 1989).

Statewide Collection

Flatwood

An entry x sample date interaction ($P = 0.0001$) for plant survival was demonstrated at the flatwood site at Ona (Figure 3). In 1998, 1 y after planting, survival of Avon Park and Pt Washington entries was similar, and greater than that of all other entries. Survival of the Withlachochee entry was statistically lowest. Old Jennings and Blackwater entries had similar survival, both greater than that of Ocala, Wekiwa Springs, and Rock Springs, which were not different from each other. By 2001, however, 4 y after planting, survival of the Blackwater, Pt Washington, and Ocala entries had declined, with no change between years for other entries (Figure 3). Furthermore, entries from Avon Park, Old Jennings, Ocala, and Withlachochee all differed in survival, while entries from Blackwater, Pt Washington, Wekiwa Springs, and Rock Springs were similar to each other.

Site conditions may have been the key factor in the variation in survival among the entries between sampling years. In the 6 mo after planting at Ona, 1231 mm (48.5 in) of rain was received in this El Niño year. Normally (60-y mean), 384 mm (15.1 in) are received during this period. The flatwood site was continuously saturated and had occasional standing water (1 to 2 cm [0.4 to 0.8 in]) from fall to spring. With no reprieve from high water in winter, the site went into a typical wet summer. These wet conditions seemed to have a negative effect on

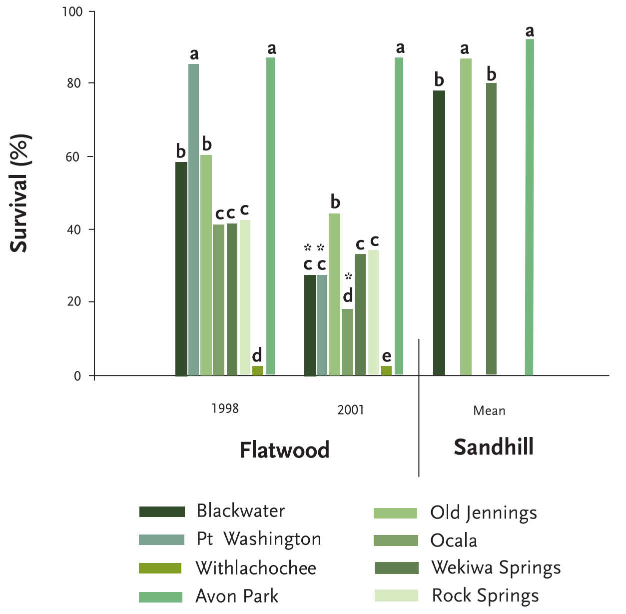


Figure 3. Sample date x entry means for plant survival of wiregrass grown on flatwood and entry main effect means for plants grown on sandhill. Bars within years on flatwood or on sandhill with the same letter are not different ($P > 0.05$). Asterisk (*) above bars in 2001 flatwood indicates a decline ($P < 0.05$) in survival from 1998 to 2001.

several entries, especially the one from Withlachochee. Parrott (1967) reported that 100% of outplanted wiregrass seedlings died within 200 d where the water table was 5 cm (2 in) below the soil surface. Kindell and others (1996) noted mortality of wiregrass seedlings on flatwoods in a wet summer.

We observed 83% survival of the 2 Wekiwa Springs entries after 12 y in the former study on this same flatwood site compared with 38% survival from the Wekiwa Springs entry after 4 y in the current study. Annual variation in environmental conditions can lead to different results with regard to adaptation on the same site. Kindell and others (1996) pointed out that evidence of population differentiation may not be apparent because of temporal variation in environment.

It is well known that wiregrass varies greatly in its range of adaptation to soil water from xeric upland sands to semi-hydric transitions and bogs (Wells and Shunk 1931). Wherever it is found, wiregrass has been noted to live indefinitely (Parrott 1967). Clewell (1989) mentions a wiregrass plantation in which "the rows were as straight as the day on which Stoddard planted them 40 years earlier." Because individual wiregrass plants are so long-lived, they must have tolerance to a wide range of environments, at least beyond the seedling stage. Any one plant may experience a wide variation in environmental conditions over a period of 40 y.

Other than the Avon Park entry, origin did not clearly confer any advantage in wiregrass survival on our flatwood site after 4 y. Conversely, Kindell and others (1996) found that, after 6 mo, wiregrass seedlings from flatwoods had survived better than seedlings from sandhills when both were planted on flatwoods.

Dry mass of plants from Rock Springs, Wekiwa Springs, and Avon Park tended to be greater than other entries (Table 2). Diameter of Rock Springs plants was greater than diameter of Avon Park plants, with values from Pt Washington and Wekiwa Springs plants intermediate and similar to the former. Diameters of plants from Old Jennings, Withlachochee, and Ocala were similar. Diameter of plants from Blackwater was lowest and similar to Withlachochee plants. While flatwood entries tended to have greater mass or basal diameter than sandhill entries grown on flatwood, there was no sharp separation of the 2 groups.

Sandhill

Wiregrass survival on the sandhill site depended on sampling date ($P = 0.004$) and entry ($P = 0.0002$) with no interaction (Figure 3). Mean survival was 90% in 1998 and 82% in 2001. Survival of Blackwater and Wekiwa Springs entries was similar and lower than the similar survival of the Old Jennings and Avon Park entries. Thus, flatwood entries survived better on the sandhill than entries from a sandhill. Kindell and others (1996) indicated that survival of seedlings from sandhill origin when planted on sandhill tended to be greater after 6 mo than that of plants of flatwood origin, but the difference was not significant.

Over all entries, survival on the sandhill (mean 85%) was very good as compared with that on flatwood (mean 35%). Recognizing the risk of attributing selective pressure to a single factor (Chapin and others 1987), we suggest that the greatest pressure for survival would be the trait that was most obviously different between the sites: extremes in soil moisture. Sandhills are xeric and soil water is not excessive even in the rainy summer months. While central Florida flatwoods are seasonally dry, they are saturated for many months, often continuously from June to October. Perhaps less genetic diversity exists for adaptation to wet, mesic sites than to xeric sites.

Differences in plant mass and diameter were apparent on the sandhill (Table 2). Both mass and diameter were lower for Blackwater plants compared with all other entries, which were similar. We observed no clear division in mass or diameter between plants of flatwood or sandhill origin, but plant mass on our sandhill was 3X to 7X less and plant diameter about half of that found on our flatwood. Kindell and others (1996) found little difference in mass between plants of flatwood or sandhill origin when grown on a flatwood site, but on sandhill sites, plants of sandhill origin were 2X to 3X greater in mass than those from flatwood sites.

Our 8 wiregrass populations originated on disjunctive sites and were genetically disconnected. They would be classified as a secondary restoration gene pool (RGP) in the concept proposed by Jones (2003). While it is most desirable to utilize wiregrass originating on a restoration site (primary RGP), it is not always possible. The occurrence of adaptive genotypes within plant populations from contrasting environments is

TABLE 2

Dry mass and diameter of wiregrass plants from seeds collected at 8 locations in Florida and grown on flatwood in Hardee County in south-central Florida and a sandhill in Washington County in north Florida. December 2001.

		Flatwood		**Sandhill**	
Entry	**Site**	**Mass** *(g)*	**Diameter** *(mm)*	**Mass** *(g)*	**Diameter** *(mm)*
Avon Park	Flatwood	21.9	69 bc [a]	3.4 a	31 a
Blackwater	Upland	3.3	43 d	1.2 b	25 b
Withlachochee	Sandhill	4.0	50 cd	— [b]	—
Ocala	Sandhill	4.7	45 c	—	—
Old Jennings	Mixture [c]	8.3	60 c	3.8 a	33 a
Pt Washington	Sandhill	17.1	77 ab	—	—
Wekiwa Springs	Sandhill	25.1	72 ab	3.8 a	30 a
Rock Springs	Flatwood	34.3	89 a	—	—
Mean		14.8	63	3.1	30

[a] Means within columns followed by the same letter are not different $P > 0.05$. For flatwood, plant diameter means were separated with pair-wise comparisons using the Wilcoxon signed-ranks test. For sandhill, means of both responses were separated with Duncan's multiple range test.

[b] Old Jennings was rolling terrain with a mixture of flatwood and sandhill sites interspersed.

[c] These entries were not planted on the sandhill site.

Conversions: g • 0.035 = oz; mm • 0.039 = in.

documented (Bradshaw 1984). Each population of wiregrass should contain individuals capable of adaptation to different sites within the entire range of the wiregrass. As Burton and Burton (2002) point out, "local environmental filters will select appropriate strains from the broader mix, so long as there is genetic diversity on which to draw."

Species that are long-lived, widespread, and cross-pollinated have more genetic variation within populations than between populations (Hamrick and others 1991). While we know about the longevity and distribution of wiregrass, its method of pollination is not known. Such knowledge would be helpful to estimate its potential for diversity and potential for adaptation.

The true test of adaptation is reproduction and recruitment. A plant might survive in an area for a very long time, even hundreds of years, but if it fails to reproduce, it eventually will cease to exist as part of the local flora (Baker 1959). We did not manage wiregrass to promote seed production because burning was done in winter, hence we observed no seedling recruitment in either of our studies. Mulligan and others (2002) showed that container wiregrass plants were capable of recruiting more wiregrass onto their site through seeds.

CONCLUSIONS

We believe that seeds collected at any location or site represent a new population of genotypes produced by their parents. Each combination of alleles in every crop of seeds possesses possible adaptation to many environments. Perhaps the greater the differences between contrasting sites, the lower the proportion of plants that survive. While it may be best to restore a site with wiregrass seeds obtained from a similar site, it may not be essential. The environment selects which combination of alleles will survive. As long as the environment is within the range acceptable to growth of wiregrass, some individuals will survive. While man's attempts are recent, Nature has always been a plant breeder.

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