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SEED BANK COMPOSITION ALONG A PHOSPHORUS GRADIENT IN THE NORTHERN FLORIDA EVERGLADES

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Abstract: Seed-bank samples were collected in the northern Everglades along a phosphorus gradient with three vegetation zones (cattail with the highest phosphorus levels, mixed cattail-sawgrass (transition), and sawgrass with the lowest phosphorus levels). The size and composition of the seed banks were estimated using both a direct seed separation (seed assay) and a seedling emergence technique (seedling assay). In the seedling assay, seed-bank samples were kept under two moisture regimes, saturated soil and shallowly flooded. In the seed assay, whole seed of 21 species were found, with a mean of about 8 species per sample in the cattail zone and about 5 in the transition and sawgrass zones. On the basis of their appearance, seeds of 18 species were judged to be intact, that is, probably viable. There were about 7 species per sample with intact seed in the cattail zone, and 3 and 4 in the transition and sawgrass zones, respectively. In the seedling assay, seedlings of only 11 species were found. All 11 were found in the saturated soil treatment, and 7 were also found in the shallowly flooded treatment. In the seed assay, the mean total number of whole and intact seeds in the cattail zone was estimated to be 78,400 and 44,400 seeds m^{-2}, respectively. The mean total number of whole and intact seeds in the transition zone was much lower, 14,200 and 10,500 seeds m^{-2}, respectively, and in the sawgrass zone, it was slightly higher at 20,900 and 14,700 seeds m^{-2}, respectively. In the seedling assay, seed densities were much lower and were estimated to be only 3,700, 800, and 1,300 seeds m^{-2}, respectively, in the cattail, transition, and sawgrass zones. The seedling assay results suggest that only about 1.3% of the intact seed had germinated. Overall, the composition of the seed banks of the transition and sawgrass zones were not significantly different from one another, but they were significantly different from that of the cattail zone. Seeds of several species were restricted primarily or exclusively to cattail-dominated areas, including seeds of *Typha* sp.

Key Words: dispersal, establishment, Everglades, Florida, plant invasion, seed bank, seed germination, wetlands

INTRODUCTION

Seed banks play a central role in vegetation dynamics of many wetlands. As environmental conditions change and established species are eliminated, species adapted to the new conditions often are recruited quickly from the seed bank (van der Valk and Davis 1978, van der Valk 1981, Pederson and van der Valk 1984). Consequently, seed bank data, because they can be used to predict seedling recruitment patterns, are an important component in many models of wetland vegetation dynamics (van der Valk 1981, Poiani and Johnson 1993, Stockey and Hunt 1994, Ellison and Bedford 1995).

Over the last 25 years, changes in the vegetation of the northern Everglades, especially the replacement of *Cladium jamaicensis* Crantz, sawgrass, by *Typha domingensis* Pers., cattail, have been hypothesized to be due to an increase in phosphorus inputs into the Everglades (Koch and Reddy 1992, Urban et al. 1993, Davis 1994, DeBusk et al. 1994, Jensen et al. 1995). This study was designed to examine the composition of the seed banks along the phosphorus gradient in Water Conservation Area 2A (WCA-2A) in the northern Everglades. Prior to this study, there was nothing known about the species composition and size (seeds m^{-2}) of the seed banks of different plant communities in the Everglades. The only previous studies had been of the seed germination characteristics of individual species, e.g., those of *Cladium jamaicensis* by Ponzio et al. (1995).

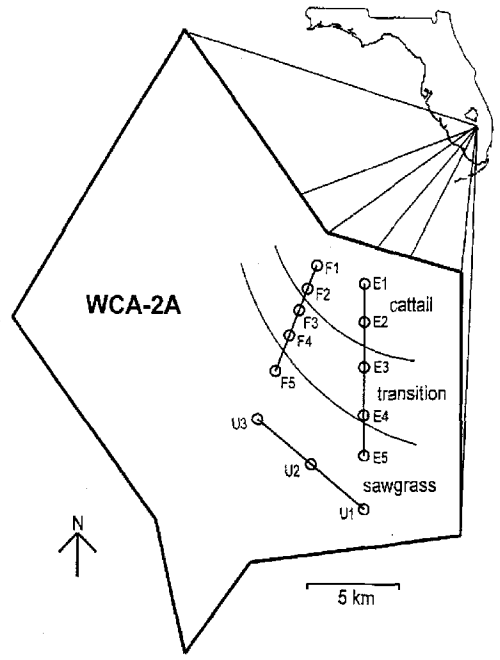

Figure 1. Location of sampling sites along transects E, F and U in Water Conservation Area 2A.

The primary objective of this study was to determine the species composition and size of seed banks at 13 sampling sites along three permanent transects (E, F, and U) in WCA-2A (Figure 1). These transects were established by the South Florida Water Management District to examine the effects of phosphorus enrichment in areas where canals carrying water from the Everglades Agricultural Area enter the northern Everglades. [For a description of the hydrology and recent changes in the vegetation of WCA-2A, primarily the spread of *Typha domingensis,* attributed to increased phosphorus inputs, see Urban et al. (1993) and Jensen et al. (1995)]. Two of these transects (E and F) begin in cattail-dominated areas with high phosphorus and end in sawgrass-dominated areas with low phosphorus levels. The effects of cattail invasion on the composition and size of the seed banks of the northern Everglades were the primary foci of this study. We specifically wanted to determine if seeds of *Typha* are found in the seed banks of areas currently not dominated by this species.

Two methods were used to estimate the composition and size of the seed banks: a direct seed separation technique, which is referred to as the seed assay, and a seedling emergence technique, which is referred to as the seedling assay. Previous studies with wetland and terrestrial seed banks that used both of these techniques indicate that they give similar, but not identical, results. The seed assay generally gives higher estimates of seed density, while the seedling assay tends to detect more species (e.g., Poiani and Johnson 1988). By using both methods, it is also possible to estimate the germinability of the seeds of different species in the seed bank, which provides a crude measure of the relative ability of species to become established.

METHODS

Seed Bank Collection

Seed-bank samples were collected in WCA-2A along transects E, F, and U between November 6 and 8, 1995. A clear plastic tube, 5 cm in diameter, was pushed into the substrate by hand to collect core samples. A number of small samples were collected and composited as recommended by Bigwood and Inouye (1988). Specifically, at each sampling site at a randomly chosen spot, five cores to a depth of 10 cm were collected more-or-less equally around the periphery of an air boat, and five more were collected in the same pattern 15 to 20 m from the first five. The ten cores collected at a site were composited as they were being collected, and the composite sample stored in a cooler on ice.

Test corings indicated that, because of the thickness of the flocculant layer in cattail-dominated areas, cores needed to be 10 cm deep to contain at least 2 cm of consolidated substrate, which was necessary for them to be collectable. All core samples in areas not dominated by cattail also were taken to a depth of 10 cm. Periphyton mats, although collected while coring in areas dominated by sawgrass, were not considered as part of seed-bank sample because they are seasonal in occurrence and vary in their position in the water column. In other words, these cores were taken to a depth of 10 cm in the substrate irrespective of the thickness of the periphyton layer.

Seed-bank samples were collected at 13 sites, 5 along transects E and F and 3 along transect U. This resulted in four samples in the cattail zone, four in the transition zone, and 5 in the sawgrass zone (Figure 1). At site F5, a second sample was collected in a nearby slough, i.e. an area free of emergent vegetation. Data from the slough site have not been included in the analysis of the composition of the seed banks in the three vegetation zones. They have been included in analyses of the overall characteristics of the seed banks of WCA-2A.

Seed-bank samples were kept in coolers on ice to prevent overheating and shipped in these coolers to Ames, Iowa by air. In Ames, the samples were stored in the dark in a cold room until processed. Seed-bank samples were first passed through a coarse sieve to remove rhizomes, roots, and other debris, and the sieved samples stored in plastic pails in the cold room. Water that accumulated above the surface of the sam-

ples while in storage was siphoned off through a fine sieve (0.125 mm) and any material that collected on the sieve was mixed back into the sample.

Seedling Assay

The seedling assay study was done by spreading subsamples of a seed-bank sediment over sterilized media in a plastic container (28 cm inside diameter and 25 cm high inside). The media consisted of three layers: a 1-cm layer of sand on the bottom, then 8–9 cm of potting soil (1 part peat/pearlite mix, 1 part sand, 2 parts mineral soil), and a 1-cm layer of fine sand on top. Containers with seed bank subsamples were exposed to two water regimes: saturated soil and flooded. The saturated soil regime was set up using a double container system. The container with the seed bank subsample, which had several holes in its bottom, was placed in a slightly wider plastic pail and the water level in the pail kept at the same level as the bottom of the seed bank subsample in the inner container. The flooded regime was established by keeping a layer of water about 6 cm deep above the surface of the seed bank subsample by watering the container daily.

Each of the 14 seed-bank samples had two duplicate subsamples in each water regime. Subsamples were randomly removed from the seed-bank sample from each site. They had a volume of 620 ml and were carefully spread over the top of the fine sand in the containers to form a layer whose mean depth was 1 cm. All containers were placed on heating mats to maintain a sediment temperature of at least 28°C, the mean maximum air temperature at nearby Belle Glade, FL, and were arranged in a randomized block design. They received 12 hrs of high-intensity light each day during the entire study.

Seedling emergence was monitored from November 1995 to April 1996. Seedlings that germinated on floating algal mats in the flooded treatment were removed and potted in separate containers. Individuals of *Lemna* sp. and *Chara* sp. were counted and removed as they appeared to prevent overcrowding. Graminoid stems that were obviously tillers also were removed as they were produced. At the end of the study, plants species were identified and the number of individuals of each species counted.

Seed Assay

After the seed-bank sample was thoroughly mixed, three 50-ml subsamples were randomly collected from each seed-bank sample. Each subsample was washed through a series of three sieves of decreasing size: 2 mm, 0.5 mm, and 0.125 mm. The material collected on each sieve was washed onto separate transparent trays and these trays placed in an oven (65 C) to evaporate the water. Each tray was placed on a grid under a dissecting scope and the entire tray systematically searched for seeds. Seeds and seed fragments were removed from the tray as found. As in other studies using this method (see Kropac 1966, Roberts 1981), seeds were separated into three groups that reflected their potential viability. The three groups were (1) seed fragments, i.e., only part of a seed was present—definitely non-viable seed; (2) entire seed, i.e., the whole seed coat was present, but the seed contents were either missing entirely or in part or the seed was clearly immature—probably non-viable seed; and (3) intact seed, i.e., whole seed that appeared to be full and in good condition on the basis of its size, shape, color, texture, etc.—probably viable seed. Only entire seed and intact seed data are considered in this report. Whole seed is defined as the sum of the entire and intact seeds found in a sample. The seed fragment data were too sparse to be interpretable.

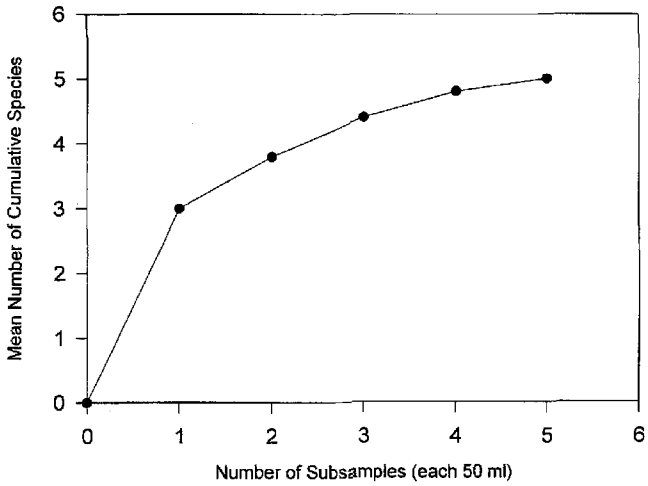

Figure 2. Mean number of cumulative species observed in all possible combinations of 5 subsamples from site E3 taken 1, 2, 3, 4, and 5 at a time.

The number of subsamples needed to obtain a representative sample was determined in a preliminary study in which a species-volume curve was constructed for the seed-bank sample from site E3. This curve (Figure 2) indicated that three 50-ml samples would be sufficient to detect the majority (ca. 90%) of the species. The 150 ml of seed-bank sample examined in this study are comparable or exceed the volume of soil used in previous studies of wetland seed banks, e.g., Poiani and Johnson (1988) examined only 100 g of soil.

Seed Identification

Seed and voucher specimens were collected for a number of wetland species in and around WCA-2A at

the same time the seed-bank samples were collected. Field seed collections were supplemented with seed collected from herbarium specimens in the Ada Hayden Herbarium at Iowa State University. Standard manuals for seed identification, especially Martin and Barkley (1961), and the reference seed collection were used to identify seeds. Plant nomenclature is based on Long and Lakela (1971).

Data Analyses

Seed counts from both the seed and seedling assays are expressed on an equal volume of sediment (1 m × 1m × 0.1 m or 0.1 m^3) basis to enable comparison of seed density between these two techniques. As is the custom in seed-bank studies (Leck 1989), seed density data given in the tables and text are given as the number of seeds m^{-2} to a depth of 10 cm. Estimates of the percent of seed that was viable (density of intact seed × 100/density of whole seed) in the seed assay and of the percent of seed that was germinable (density of seedlings × 100/density of intact seed) were calculated for each species. Wilcoxon Signed Rank tests were used to compare the median of the mean densities of whole seed, intact seed, and seedlings of all species among vegetation zones.

At the community level, Spearman rank order correlation coefficients were used to compare the composition of the seed banks within and among the cattail, transition, and sawgrass zones using whole and intact seed and seedling data. Similarities in community composition of seed banks from each site also were examined using an ordination technique, DECORANA (Hill 1979). Relative whole and intact seed and seedling densities were used to ordinate all 14 sites in a common species space.

RESULTS

Seedling Assay

Only 11 species occurred in the seedling assay study. One of these species, *Eleocharis elongata* Chapm., was found only at the slough site. All 11 were found in the saturated soil treatment, in which 51% of all seedlings occurred, while 7 species also were found in the flooded treatment (Table 1). Seeds of the *Typha* sp. germinated best in the flooded treatment (73%), while those of *Cladium jamaicensis* germinated best (84%) in the saturated-soil treatment. Seed densities were estimated to be about 3,700, 800, and 1,300 seed m^{-2} in the cattail, transition, and sawgrass zones, respectively. The most common taxa were a *Chara* sp., a *Lemna* sp., and a fern, *Acrostichum.* Species richness ranged from about 5 taxa per sample in the cattail tail zone to 2 in the transition and sawgrass zones. Species restricted to the cattail zone were *Amaranthus australis, Cyperus odoratus* Galingale, *Mikania scandens* (L.) Willd., and *Nymphaea odorata* Ait. (Table 2). *Typha* seed had the highest density in the cattail zone, but also was found in the other two zones. *Cladium* seed density was slightly higher than *Typha* seed density in the cattail zone and had a similar density in all three zones.

Table 1. The percentage of all the seeds from all 14 sites in WCA-2A that germinated in the saturated soil and flooded treatments in the seedling assay study.

	Saturated	Flooded
Acrostichum (danaeifolium) Lansd. & Fisch.	100	0
Amaranthus australis	100	0
Chara (fibrosa)	40	60
Cladium jamaicensis	84	16*
Cyperus odoratus	87	13*
Eleocharis elongata	100	0
Lemna sp.	21	79
Mikania scandens	100	0
Nymphaea odorata	67	33
Sagittaria lancifolia L.	67	33
Typha sp.	27	73

* Seedlings found only on algal mats floating on the surface.

Seed Assay

Altogether, seeds of 21 species were found in the seed banks of WCA-2A (Tables 2 and 3). Four species were found only at the slough site: *Eleocharis* sp., *Rhynchospora tracyi* Britt., and two unknowns. Seed banks from the cattail zone had the most species, around 8 per sample (Table 2). Seeds of several taxa were found primarily in the cattail zone: *Amaranthus australis, Cyperus odoratus, Fimbristylis* sp., and *Typha* sp. Although *Cladium jamaicensis* is no longer a significant component of the vegetation in the cattail zone, its intact seeds were still present at all four sites. Sites in the transition zone between cattail and sawgrass and in the sawgrass zone had generally about 5 species per sample (Table 2). Although *Typha* seed was found at two sites outside the cattail-dominated areas, it was not found at most of these sites. When *Typha* seed was found, seed density was very low.

The mean total number of whole and intact seeds in the cattail zone was 78,400 and 44,400 seeds m^{-2}, respectively (Table 2). The mean total number of whole and intact seeds in the transition zone was much lower, 14,200 and 10,500 seeds m^{-2}, respectively, and in the sawgrass zone was slightly higher at 20,900 and 14,700 seeds m^{-2}, respectively. *Typha* seed density

Table 2. The mean number of whole seeds, intact seeds, and seedlings per m^2 in the cattail (n = 4), transition (n = 4), and sawgrass (n = 5) zones.

	Cattail Zone			Transition Zone			Sawgrass Zone		
	Whole	Intact	Seedlings	Whole	Intact	Seed-lings	Whole	Intact	Seedlings
Acrostichum (danaeifolium)	0	0	1,088	0	0	464	0	0	0
Amaranthus australis	43,022	19,176	282	1,001	834	0	534	133	0
Carex sp. 1	167	167	0	0	0	0	0	0	0
Carex sp. 2	167	167	0	0	0	0	0	0	0
Chara (fibrosa)	0	0	282	0	0	81	0	0	1,016
Cladium jamaicensis	8,671	8,671	141	7,671	7,671	202	9,071	8,804	145
Cyperus odoratus	6,670	6,003	262	0	0	0	0	0	0
Fimbristylis sp.	4,502	4,502	0	0	0	0	0	0	0
Fuirena (squarrosa)	0	0	0	167	167	0	133	133	0
Lemna sp.	0	0	1,431	0	0	0	0	0	97
Ludwigia peruviana (L.) Hara	1,167	1,167	0	334	334	0	3,335	3,335	0
Mikania scandens	5,670	334	20	1,501	0	0	4,002	0	0
Nymphaea odorata	334	334	20	0	0	0	400	267	0
Polygonum densiflorum Meisn.	167	167	0	0	0	0	0	0	0
Polygonum punctatum Ell.	1,167	1,167	0	334	334	0	0	0	0
Rhynchospora sp. 1*	500	500	0	2,501	1,167	0	1,868	1,601	0
Rhynchospora sp. 2	0	0	0	500	0	0	133	0	0
Sagittaria lancifolia	167	0	20	0	0	20	0	0	16
Typha sp.	5,836	1,668	121	167	0	40	267	133	16
Unknown M	334	334	0	0	0	0	0	0	0
TOTAL	78,500	44,400	3,700	14,200	10,500	800	19,700	14,400	1,300
Species Richness	8.3	7.5	5.3	5.0	3.3	2.3	5.4	3.8	2.4

* *Rhynchospora microcarpa* or *miliacea.*

was relatively low even in the cattail zone. A Wilcoxon Signed Rank Test indicated that the median density of the mean whole and intact seed and seedling densities (Table 2) for species in the cattail zone was significantly different (one tailed test, $p < 0.05$) from those in the transition and sawgrass zones. The medians were not significantly different between the transition and sawgrass zones.

The most common seeds in the seed bank were those of *Amaranthus australis* and *Cladium jamaicensis.* They accounted for 38% and 24% of the total number of whole seeds found and 28% and 38%, respectively, of the intact seed. No other species accounted for more than 10%, including *Typha.* In most cases, the number of intact seeds was lower than the number of whole seeds (Table 3). The difference between the number of intact and whole seeds was greatest for *Amaranthus australis* and *Mikania scandens.* In the case of *Mikania,* intact seed was found at only one site in the cattail area along transect E, while whole seed was found at 11 sites. There was a very strong and significant ($p < 0.05$) correlation between the densities of whole and intact seeds in the three vegetation zones (Spearman rank order coefficients between 0.76 and 0.96) but no correlation between seed densities in the seed assay and seedling densities in the seedling assays (Spearman rank order coefficients between −0.03 and 0.08).

On the basis of appearance, about 62% of the whole seed was classified as intact (Table 3). Most of the *Cladium* seed (99%) was classified as intact, while only 29% of the *Typha* seed was. The percent of the intact seed that germinated in the seedling assay study was very low, 1.3% overall. Germinability of *Cladium* seeds was estimated to be only around 2% while that of *Typha* was around 10% (Table 3).

Community-Level Comparisons

The overall composition of the seed banks from the transition and sawgrass zones was fairly similar, with a mean Spearman rank order correlation coefficient of 0.74. Seed banks of the cattail zone, although they still had many species in common with those of the other two zones, were much less similar to them (Table 4). The mean Spearman rank order correlation coefficient was 0.50.

The results of the DECORANA ordination also indicated that the overall composition of the seed banks from the transition and sawgrass zones was very sim-

Table 3. Mean density of whole seeds, intact seeds, and seedlings per m^2 in the seed-bank samples collected (n = 14) in WCA-2A, and the estimated percent viability (percent of whole seeds that were intact) and germinability (percent of intact seeds that germinated) of the seeds of each species.

	Whole	Intact	Seed-lings	Via-bility	Ger-min-ability
*Acrostichum (danaeifolium)**	0	0	443	0	—
Amaranthus australis	12,768	5,765	81	45	1.4
Carex sp. 1	48	48	0	100	0.0
Carex sp. 2	48	48	0	100	0.0
*Chara (fibrosa)**	0	0	944	0	—
Cladium jamaicensis	8,290	8,195	150	99	1.8
Cyperus odoratus	1,906	1,715	75	90	4.4
Eleocharis elongata	429	429	12	100	2.7
Fimbristylis sp.	1,286	1,286	0	100	0.0
Lemna sp.*	0	0	443	0	—
Fuirena (squarrosa)	143	95	0	67	0.0
Ludwigia peruviana	1,620	1,620	0	100	0.0
Mikania scandens	3,526	95	6	3	6.1
Nymphaea odorata	334	286	17	86	6.0
Polygonum densiflorum	48	48	0	100	0.0
Polygonum punctatum	429	429	0	100	0.0
Rhynchospora tracyi	48	48	0	100	0.0
Rhynchospora sp. 1	1,572	1,096	0	70	0.0
Rhynchospora sp. 2	191	0	0	0	0.0
Sagittaria lancifolia	48	0	17	0	—
Typha sp.	1,810	524	52	29	9.9
Unknown M	95	95	0	100	0.0
Unknown S	95	0	0	0	0.0
Unknown T	48	48	0	100	0.0
MEAN	1,449	911	93	62	1.3

* Present in seed bank not as seeds but as either spores or turions.

Table 4. Spearman rank order correlations using whole seeds, intact seeds and seedlings among the three vegetation zones.

Zone	Cattail	Transition	Sawgrass
		Whole Seeds	
Cattail	—	0.46*	0.49*
Transition		—	0.83*
Sawgrass			—
		Intact Seeds	
Cattail	—	0.48*	0.46*
Transition		—	0.72*
Sawgrass			—
		Seedlings	
Cattail	—	0.56*	0.57*
Transition		—	0.68*
Sawgrass			—

* Significant correlation, $p < 0.05$.

ilar and distinct from that in the cattail zone (Figure 3), regardless of whether seed or seedling data were used to do the ordination. Variability in composition of the seed banks from different sites within a vegetation zone was greatest in the cattail zone. The one seed-bank sample collected from a slough site was very different in composition from other sites in the sawgrass, transition, and cattail zones (Figure 3).

DISCUSSION

On the basis of the seed assay, seed banks found in the northern Everglades are comparable in seed density to those found in other non-tidal freshwater wetlands and peatlands, but on the basis of the seedling assay, they are at the low end of the range reported by Leck (1989). The northern Everglades seed banks, however, had a comparable number of species to those in other peatlands (Leck 1989).

Seed banks of the cattail-dominated areas in WCA-2A were quite distinct from those in the sawgrass-dominated areas; they have more seeds and species and more variability in composition than those from the transition and sawgrass zones. However, seed banks of the cattail-dominated areas still contain most of the species found in the sawgrass zone and have acquired seed of a number of species not found in the sawgrass zone, including *Amaranthus, Fimbristylis,* and *Cyperus* seed. Other studies of wetland seed banks indicate that increased disturbance results in both more species, particularly annuals, and higher seed densities in disturbed than in nondisturbed wetlands (e.g., McIntyre et al. 1988). It seems likely that some of the species, e. g., *Amaranthus australis,* whose seeds were found only in the cattail zone, originally reached WCA-2A by means of the canal system from the agricultural areas to the north. Some of the species, e. g., the vine *Mikania scandens,* in the cattail seed banks can become very abundant locally in WCA-2A (Urban et al. 1993).

Because their seeds had to have been deposited prior to these areas being taken over by cattail, the continued presence in the cattail zone of *Cladium* seeds and of other wetland species that are found only in the *Cladium*-dominated areas suggests that seeds of these species were in the lower layers of the seed-bank cores. If this is the case, the *Cladium* seeds and the seeds of other species associated with it could be buried too deeply to be of any utility for restoration of the cattail zone to sawgrass unless the upper layer of cattail sediment is removed mechanically or by burning. Recruitment of species occurs normally only from seed in the upper 5 cm or less of the substrate (Jurik et al. 1994). *Typha* seed at the cattail-dominated sites in WCA-2A was found at densities comparable to those in other freshwater wetlands, e.g., in prairie pot-

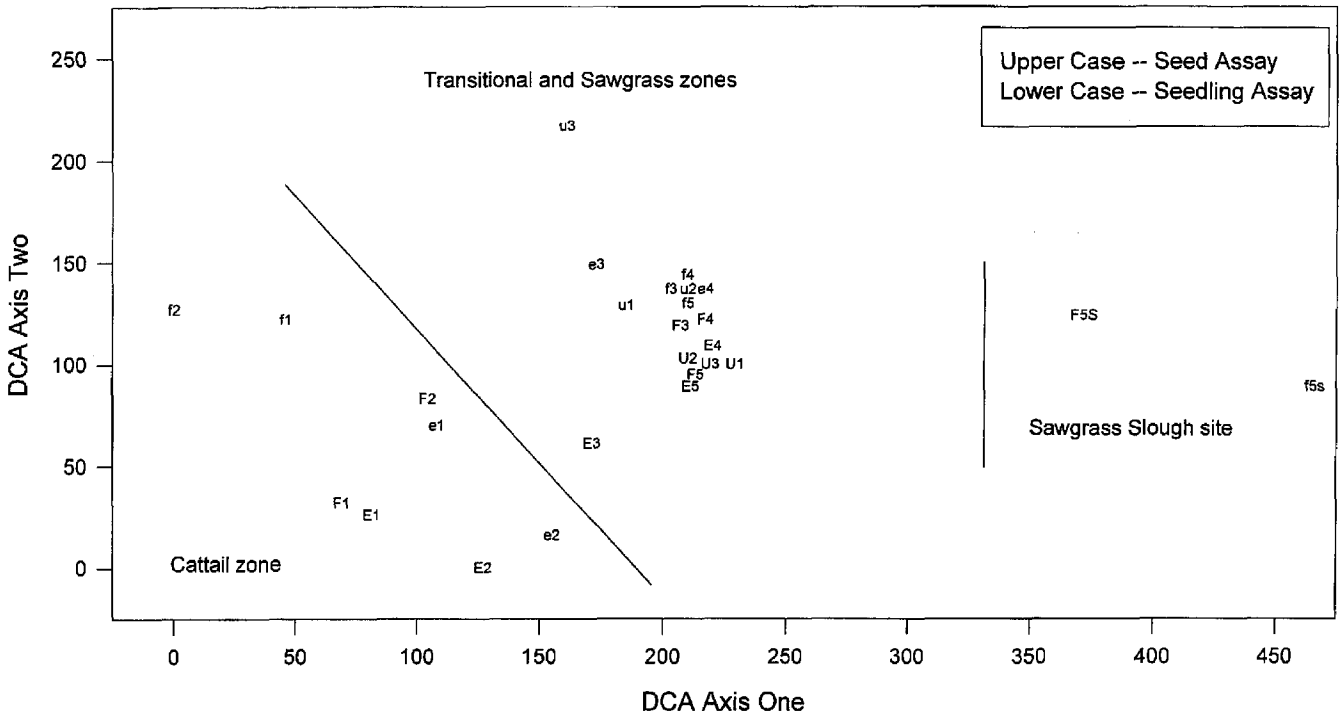

Figure 3. DECORANA ordination of seed and seedling data from the 13 emergent sites collected along three transects (E, F and U) and one slough site (F5S) collected in the sawgrass dominated area near site F5. The Eigenvalues for the DCA axes are: DCA 1 = 0.753 and DCA 2 = 0.327.

holes, dominated by cattails (van der Valk and Davis 1978). In prairie wetlands, these areas quickly become dominated by *Typha* again after the previous *Typha* stands have been removed.

From this study, it is impossible to establish whether the seed banks of species in the Everglades are persistent or transient. Species with a transient seed bank have seed that remain viable for less than one year (Thompson and Grime 1979). No data are available on *Typha* flowering and fruiting patterns in WCA-2A. Consequently, it is impossible to establish a minimum age for the *Typha* seeds in our seed-bank samples. We were unable, however, to find a single *Typha* flowering or fruiting shoot while we were collecting seed-bank samples. Previous studies have indicated that *Typha* spp. have persistent seed banks, e. g, van der Valk and Davis (1979). The hydrology of the Everglades (Duever et al. 1994) and WCA-2A (Urban et al. 1993) is driven by interannual wet-dry cycles. This suggests that the seed banks of many, if not all, species in this ecosystem are persistent because they could be flooded for several years. For example, our data suggest that *Cladium* has a persistent seed bank since its viable seed was found in areas where the species has not grown for many years. Nevertheless, it is possible that *Typha* and other species in the Everglades have shorter-lived seed than has been reported for seeds of species from temperate wetlands. In general, seed longevity is expected to be shorter in subtropical and tropical environments than in temperate ones because of the year-round activity of seed predators. Whether *Typha* has a transient or persistent seed bank in the Everglades needs to be established conclusively because it has significant management and restoration implications.

Intact *Typha* seed was found at only one site (U1) and seedlings at two sites (U1 and E3) outside of areas dominated by cattail. This suggests that significant dispersal of *Typha* seed into areas far ahead of the front of expanding cattail stands in WCA-2A has not occurred. Consequently, disturbances in these cattail-free areas, such as fires, should not result in the immediate replacement of sawgrass by cattail. In this respect, the seed banks of WCA-2A are different from those found in other freshwater wetlands in which *Typha* seed can be as abundant in areas not dominated by cattail as in those that it dominates (van der Valk and Davis 1976, 1978). Most previous studies, however, have been conducted in wetlands much smaller than WCA-2A. Thus, seed-bank samples were collected much closer together in previous studies than in the present study. It is possible that *Typha* seed is present some distance ahead of the front of advancing cattail, but our study was done at too coarse a scale to detect this.

Although the number of intact seeds has been estimated on the basis of the appearance of the seed, no

attempt was made to determine if these seeds were viable and would germinate. Previous studies of seeds that appear to be intact recovered from seed banks have had viabilities of as low as 3% (Gross 1990) and as high as 90% (Roberts 1981). Data on the composition of the seed banks of two North Dakota wetlands obtained from both seed and seedling assays found in Poiani and Johnson (1988) have been used to estimate the percentage of seed in the seed banks of these North Dakota wetlands that actually germinated. Mean germinability for the entire seed bank was about 33%. Because seedling assays underestimate the amount of germinable seed present (Gross 1990), this is a minimum estimate of the mean seed germinability. The mean germinability of intact seed in WCA-2A is estimated to be only 1.3%, and the highest germinability recorded was only 10% for *Typha* seed. Whether this low germinability in the seed banks from the Everglades is due to most of the intact seed being nonviable or due to conditions in the seedling assay not being optimal for seed germination cannot be determined from this study.

Three of the species with the most germinable seeds in the seed banks were those that were almost entirely restricted to the cattail zone: *Cyperus odoratus, Mikania scandens,* and *Typha* sp. The only other species whose seeds showed comparable germinabilty is *Nymphaea odorata,* which was found in the cattail and sawgrass zones. These data suggest that species whose seeds have higher germinabilties can become established more readily after a disturbance has killed the existing vegetation in an area. The relatively high germinability of its seed when compared to that of *Cladium,* at least in part, may explain why *Typha* has replaced *Cladium* in areas in WCA-2A disturbed by changes in hydrology and increased nutrient loadings caused by canals from the Everglades Agricultural Area.

Additional studies are needed to obtain a complete picture of the seed banks of the Everglades, including (1) an expanded seed bank study of vegetation types and areas not included in this study, (2) a study of the composition of the seed banks at selected times throughout the years to determine which species have transient and which have persistent seed banks, (3) a study of the vertical distribution of seeds in the cattail zone to determine if seeds of *Cladium* in this zone can be used to re-establish *Cladium,* (4) a study of the seed germination characteristics of common Everglades species to determine the environmental conditions (e.g., water depths and/or soil moistures, temperatures, light, etc.) under which these species are most likely to be recruited from the seed bank, (5) a seed longevity study of selected species in both the cattail and *Cladium* dominated areas, and (6) a year-round study of autochthonous and allochthonous seed inputs into WCA-2A. Although it is known that changes in environmental conditions in the Everglades can result in changes in species distributions and abundances, e.g., Urban et al. (1993) and David (1996), field studies also are needed to determine to what extent these changes are the result of recruitment from seed banks.

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