

Seasonal variation in seed bank composition and its interaction with nutrient enrichment in the Everglades wetlands

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ABSTRACT

In the Florida Everglades, nutrient enrichment from agricultural outflow and the change in hydrology have collectively contributed to the expansion of cattails (*Typha* spp.). To assess the effectiveness of prescribed fire in controlling cattails and to predict vegetation dynamics after the fire, it is important to understand the seasonal variation of the soil seed bank and how the seed bank is affected by nutrient enrichment and fire. This paper investigates the effects of season, nutrient enrichment, and fire on soil seed bank species composition, richness, and density along a nutrient gradient in Water Conservation Area 2A (WCA 2A) of the Florida Everglades. Species richness was significantly affected by nutrient enrichment and season but not their interaction. Total seed density, however, was significantly affected by the interaction between nutrient enrichment and season. Yet, at species level, the relationship between seed density, nutrient enrichment and season varied. The highest seed density of cattail occurred in summer at highly enriched sites, but that of sawgrass occurred in fall regardless of enrichment; the seed density of water lily was very low regardless of season and nutrient enrichment, and the highest *Amarathus* seed density occurred at highly enriched sites year round. Moreover, germination timing differed greatly among species. While cattail seeds had a short incubation period and started to germinate 2–3 days after initiation of the germination assay, sawgrass seeds generally started to germinate 4 weeks later. Further, both the prescribed summer fire at the highly enriched site and the natural winter fire at the moderately enriched site reduced the seed density of cattail but not of sawgrass. Our results suggest that fire application for vegetation recovery in WCA 2A would benefit from explicitly considering seasonal dynamics of the seed bank.

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1. Introduction

In Water Conservation Area 2A (WCA-2A) of the Florida Everglades, changes in hydrology and nutrient enrichment from agricultural outflow have collectively contributed to the expansion of species like cattails (*Typha* spp.) into historically sawgrass (*Cladium jamaicense*)-dominated ridge and water lily (*Nymphaea odorata*)-dominated slough vegetation communities (Urban et al., 1993; David, 1996; Newman et al., 1996; Miao et al., 2000; Sklar et al., 2005). This vegetation change is one of the most visible signs of an Everglades in decline (Sklar et al., 2005). To curtail the rapid expansion of species like cattails, researchers and resource managers have considered prescribed fire treatments (Beckage et al., 2003; Lockwood et al., 2003). However, studies regarding the

effectiveness of fire in controlling cattails in other wetland ecosystems have been inconclusive (Ponzio et al., 2004).

A large-scale ecosystem study has been assessing whether repeated fires can accelerate recovery from cattail-dominated areas to native ridge/slough communities (Miao, in preparation). A few studies in the Everglades suggested that seeds of some important species from pristine communities could be absent and seeds of less desirable exotic species could be very abundant in the sediment seed bank at nutrient-enriched sites (van der Valk and Rosburg, 1997; Smith et al., 2002). As a result, a fire treatment may enhance the recruitment (germination) of undesirable, exotic species (Imbert and Delbe, 2006). Moreover, the effect of prescribed fire on post-fire species establishment and vegetation dynamics in the Everglades may be confounded by the interplay between the potential seasonal dynamics of the soil seed bank and the altered nutrient enrichment levels. Before fire is used as a tool, researchers must determine whether there is a significant seasonal variation of species richness and density in the sediment seed bank and how the plant

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community arising from the sediment seed bank is affected by nutrient enrichment and fire.

van der Valk and Rosburg (1997) used seedling germination assay to examine the seed bank in the Everglades wetlands and found that species richness and seed bank density differed significantly among sites with different nutrient-enrichment levels. They suggested that further studies were needed to provide finer-scale temporal information, particularly regarding the seasonal dynamics of important species in the seed bank. The objectives of the current study were to use the seedling germination assay to (1) assess seasonal variation in seed bank species richness and density along a nutrient-enrichment gradient; and (2) determine whether surface fire affects species composition and seed density of important species in the seed bank.

2. Methods

2.1. Study sites and data collection

Our study sites were located in WCA-2A (Fig. 1), encompassing an area of approximately 45,000 ha of wetlands that historically consisted primarily of shallow-water *C. jamaicense* and *N. odorata* marshes, and deeper-water *N. odorata* slough communities (South Florida Water Management District, 1992). Soils are Histosols,

including both Loxahatchee and Everglades peat formations (Gleason et al., 1974). Loading of nutrient-laden agricultural drainage over decades resulted in the now widespread phosphorus enrichment of surface soils in the area, with a gradient along the surface inflow structure from the northeastern boundary toward the southwest of the study area (Debusk et al., 2001). The Everglades is a fire-frequented and fire-dependent ecosystem, and the interannual variability of natural fire is predominantly driven by ENSO cycles (Beckage et al., 2005).

The sediment was sampled in three different seasons during 2005–2006: Fall (13 September 2005), winter (16 January 2006), and summer (15 July 2006) (Fig. 2). The experimental design included three sites with different levels of nutrient enrichment; the highly enriched site was located at the far north section, the moderately enriched site at the middle section of the transect, and the controls (references) near the reference zone (transect “U”). The control site was dominated by *C. jamaicense* and *N. odorata* and had small-scattered cattail patches, while the enriched sites were dominated by cattails. Each nutrient-enriched site contained two blocks, which were paired with the two permanent transects “E” and “F” established by the South Florida Water Management District. Each block contained a 90,000 m² plot with an access walkway running from the south to the north. Along each of the walkways there were three sampling stations; the first station was on the east side of the walkway, the second was on the west side,

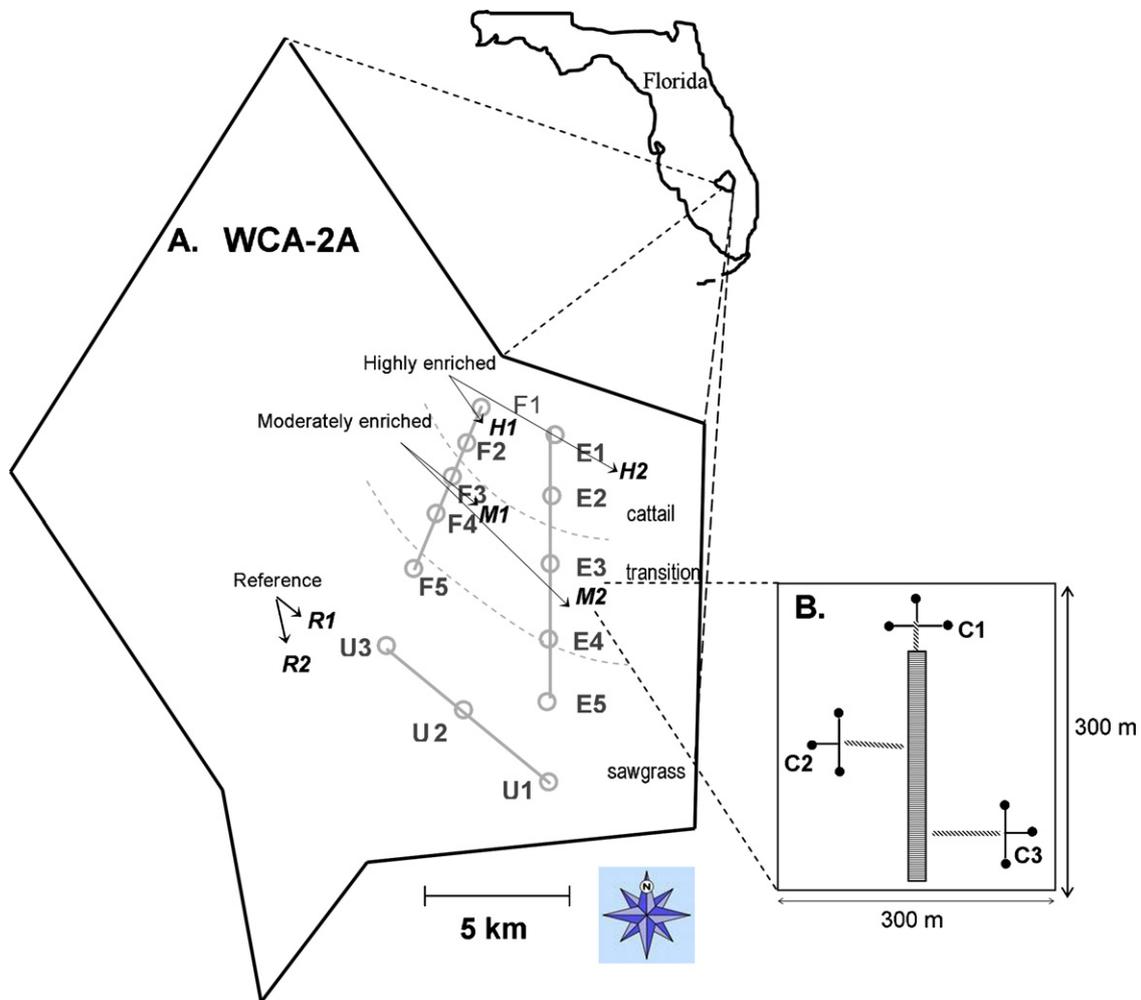


Fig. 1. A schematic diagram showing locations of sampling blocks and stations. (A) WCA-2A nutrient enrichment transects in Everglades (redrawn from Fig. 1 in van der Valk and Rosburg, 1997). (B) The layout of sampling points at each sampling station. “E”, “F”, “U” are three permanent transects established by the South Florida Water Management District in areas where canals carrying water from the Everglades agricultural area enter the northern Everglades.

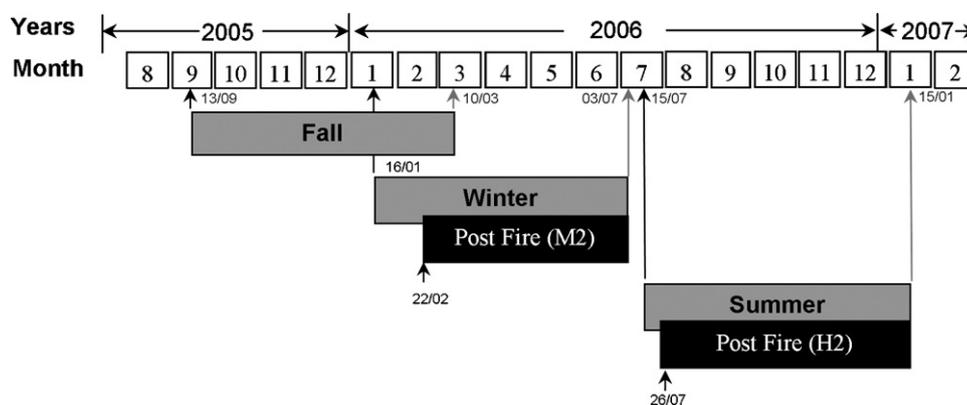


Fig. 2. A schematic diagram showing sediment sample collecting time, starting and conclusion dates of seed bank germination assays. The box width represents the germination duration with the black arrow on the left pointing to the sampling and also starting date and the lighter arrow on the right side of the box pointing to the date of conclusion. There were two germination assays associated with fire treatment (boxes in black). The summer fire was a planned, prescribed fire at highly enriched site and winter fire at the moderately enriched site was added to the experiment after a natural fire occurred 36 days after the winter seed bank germination was started. The soil samples for the seed bank assays were collected 1 day after the fire.

and the third was on the northern edge. At each sampling station, individual soil cores were collected 5 m from a known location 15 m off the walkway along three cardinal directions, resulting in nine samples per block and a total of 54 samples per season (three levels of nutrient enrichment \times two blocks \times nine samples) (Fig. 1B).

A prescribed burn was planned at both the highly and moderately enriched sites in summer to examine fire effects as well as the interaction between fire and nutrient enrichment. However, an unexpected wildfire occurred at the moderately enriched site in winter (February 2006), and it was impossible to implement a prescribed burn at the highly enriched site at that time; a prescribed fire was implemented at the highly enriched site in July 2006. Although the unplanned fire at the moderately enriched site meant that fire timing was confounded with enrichment, it provided an opportunity to perform a preliminary evaluation of fire timing. For both the winter and summer fire, post-fire soil samples (sediment) were collected 1 day after the fire using the same protocol described in the following paragraph. The schedule of sample collections and the seedling germination assays are presented in Fig. 2.

The soil samples were collected with a 9.9 cm internal diameter stainless steel corer to 10 cm depth; approximately 700 cm³ of soil was collected with each core. Soil samples were placed in coolers with ice and transported to a research greenhouse at Florida Atlantic University, Boca Raton, FL (26° 22' N, -80° 05' W; about 2 m above sea level). Rhizomes, roots, and other debris were manually separated from the soil samples, the remaining volume of soil was measured, and a maximum of 500 cm³ of soil was used for the seedling germination assay.

The seedling germination assays were carried out in the greenhouse, which had a glass roof that did not significantly attenuate or disrupt visible or near-infrared radiation (Summy et al., 2003). The greenhouse was well ventilated to maintain an inside temperature comparable to that of outside. The soil samples were spread as an even layer, 1 cm thick, in pots previously filled with washed sand to 25 cm depth, a procedure similar to that described by van der Valk and Rosburg (1997), Wetzel et al. (2001) and Miao et al. (2001). All pots were kept saturated with water for the duration of the assays. Newly emerged seedlings were identified, counted, and removed from the pots. If a seedling could not be identified, it was removed from the original pot and grown in a separate pot until it could be identified. The seedling germination assays continued until no additional seedlings emerged. Each seed germination assay lasted approximately 6 months.

2.2. Data analysis

Species richness was defined as the number of species detected per soil sample, and seed density was calculated as the number of viable seeds of a given species or a group of species on an equal volume of sediment (1 m \times 1 m or 0.1 m³) (van der Valk and Rosburg, 1997; Wetzel et al., 2001; Miao et al., 2001). Our analyses focused on five representative taxa: *Typha* spp., *C. jamaicense*, *N. odorata*, *Sagittaria lancifolia*, and *Amaranthus australis*. Their genus names will be used hereafter to increase readability. For each species, a two-way analysis of variance (ANOVA) model was conducted for species richness and the seed density; dependent variables included season, nutrient enrichment, and their interaction. Duncan's Multiple Range Test was used to separate means. The ANOVAs were performed with SAS (SAS 9.1.3; SAS Institute Inc., Cary, NC, USA).

3. Results

3.1. Effects of nutrient enrichment and seasonality

A total of 19 species were identified from the seedling germination assays, and the number of species detected was similar for the three sites: 17 species from the control or reference site, 17 species from the moderately enriched site, and 18 species from the highly enriched site (Fig. 3). Species richness was significantly affected by soil nutrient enrichment ($p = 0.01$) and season ($p = 0.05$) but not by their interaction ($p = 0.09$; Table 1). Overall, species richness was significantly higher at the nutrient-enriched sites (5.9 ± 0.2 and 5.4 ± 0.2 species sample⁻¹ for highly and moderately enriched site, respectively) than at the reference site (3.9 ± 0.2 species sample⁻¹). More species were found in summer than in fall and winter regardless of nutrient enrichment (Fig. 3).

For total seed density, the interaction between nutrient and seasonality was significant ($p = 0.018$; Table 1). Season significantly affected seed densities of all species except *Nymphaea* and *Amaranthus*, whereas nutrient enrichment affected seed bank densities of all species except *Sagittaria* (Table 1). At the reference site, seedling emergence of *Cladium* was significantly higher in fall than in winter or summer ($p < 0.05$) but there were no significant seasonal differences for *Typha*, *Nymphaea*, or *Amaranthus* (Table 2). At the moderately enriched site, seed density of *Typha* significantly increased in summer ($p = 0.01$) but *Cladium* seed density was significantly larger in fall ($p = 0.01$). At the highly enriched site, the

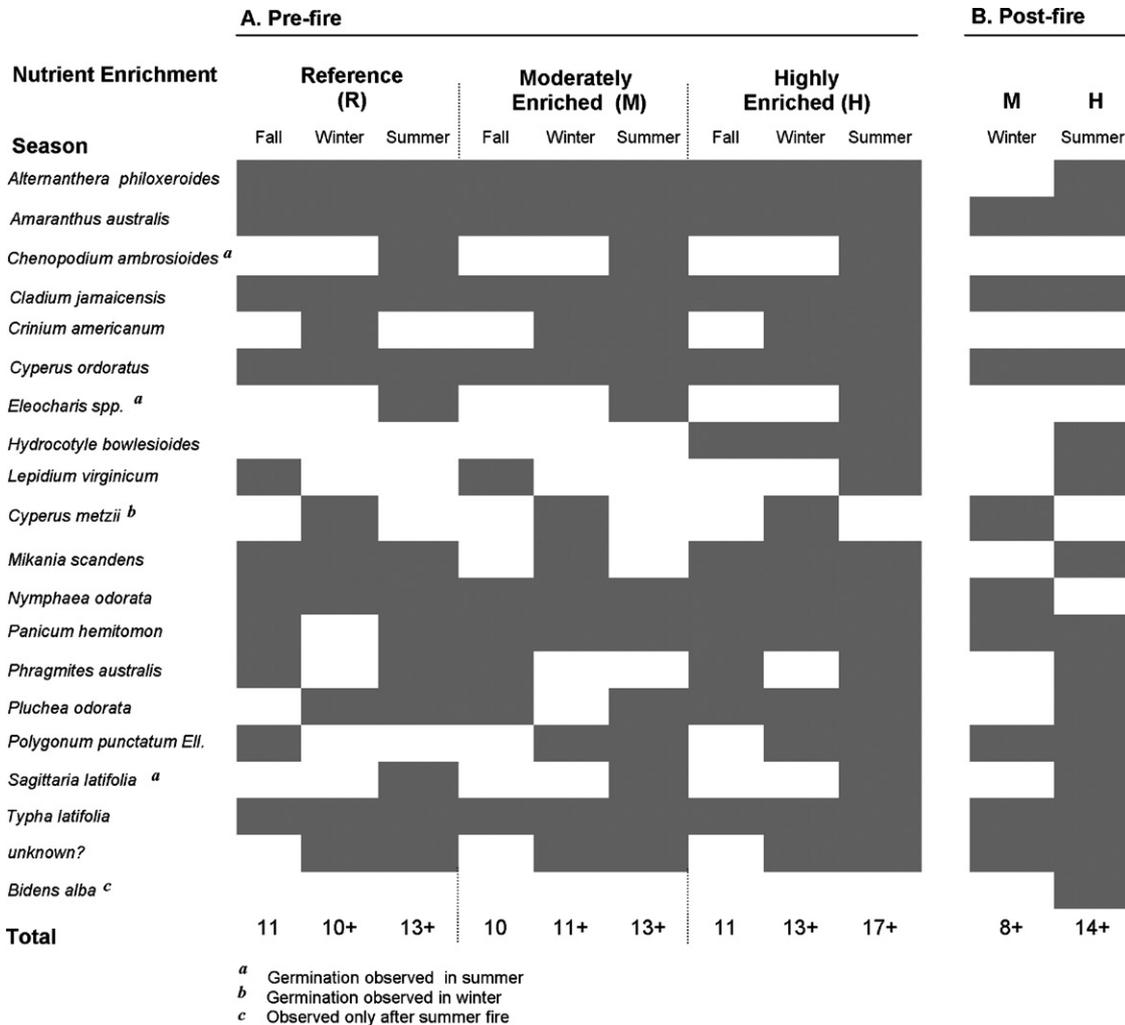


Fig. 3. A schematic diagram showing the species identified from the seedling assays during the three seasons, at three different nutrient enrichment levels (A), and after fire treatment (B). The shaded area following each species name represents the emergence of that species and the blank space indicates the absence of that species. A “+” with the number indicates that there were un-identified species in the germination assay for that column.

seed density of *Typha* significantly increased in summer while *Cladium* seed density declined in summer. *Sagittaria* seedlings emerged only in summer.

The total seed bank density at the reference site was relatively small, ranging from 296 ± 45 seedlings m^{-2} in the winter to 497 ± 70 seedlings m^{-2} in the fall (Table 2). At the moderately enriched site, however, the total seed bank density ranged from 818 ± 144 seedlings m^{-2} in the fall to 1471 ± 331 seedlings m^{-2} in the summer, more than twice the densities of the reference site

Table 1

Summary of statistics (%SS, sum of square) of analysis of variance (ANOVA) using two-way ANOVA model including season, nutrient enrichment, and their interaction for species richness (A) and seed bank density for overall and several dominant species (B) in the Florida Everglades wetlands

	Season	Nutrient	Season \times nutrient
A. Species richness	2.43*	24.70***	3.23
B. Total seed density	4.27*	8.38***	5.13*
<i>Typha</i>	22.72***	31.79***	17.67***
<i>Cladium</i>	8.96***	3.87**	1.58
<i>Nymphaea</i>	0.79	3.01*	0.026
<i>Sagittaria</i>	11.58**	1.04	3.16
<i>Amaranthus</i>	5.26**	23.12***	0.56

Different levels of significance: * $p < 0.05$; ** $p < 0.01$ and *** $p < 0.001$.

(Table 2). This increase was mainly due to the large increases of two species – *Typha* and *Amaranthus* – for all three seasons. The total seed bank densities at the highly enriched site ranged from 2295 ± 321 seedlings m^{-2} in the fall to 4643 ± 422 seedlings m^{-2} in the summer, which were two times higher than those measured at the moderately enriched site, again with the majority of the increase coming from *Typha* and *Amaranthus*. *Typha* had the largest seed density (3895 ± 373 seedlings m^{-2}) in the summer at the highly enriched site when the seed density of *Cladium* was the smallest (44 ± 7 seedlings m^{-2}) (Table 2).

3.2. Seed germination timing

The temporal variation in germination differed greatly among species (Fig. 4). *Typha* had a very short incubation period and germinated as quickly as 2–3 days after an assay was initiated. Its most intensive germination occurred within the first 45 days. *Typha* germinations appeared during the first, fourth, and sixth week in summer, fall and winter, respectively (Fig. 4A–C). *Cladium* usually began to germinate during the fourth week after assay initiation regardless of season (Fig. 4D–F). *Nymphaea* (Fig. 4G–I) and *Sagittaria* (Fig. 4J–L) had relatively low seed densities and germinated more sporadically than *Typha* and *Cladium*. *Amaranthus* (Fig. 4M, O and P) and the remaining species (Fig. 4Q–S)

Table 2Seasonal variation in seed bank densities of five representative taxa and all species (seedlings m⁻²) at different nutrient enrichment levels in the Florida Everglades wetlands

Species	Seasons	Reference site	Moderately enriched site	Highly enriched site
		Mean ± S.E.(n)	Mean (S.E.)	Mean (S.E.)
<i>Typha</i>	Fall	114 ± 42 (24) a	282 ± 71 (18) b	1224 ± 19 (18) b
	Winter	48 ± 8 (27) a	423 ± 69 (18) b	1126 ± 135 (18) b
	Summer	81 ± 15 (27) a	1060 ± 311 (18) b	3895 ± 373 (18) a
<i>Cladium</i>	Fall	283 ± 43 (24) a	260 ± 40 (18) b	166 ± 36 (18) a
	Winter	148 ± 32 (27) b	168 ± 33 (18) b	147 ± 26 (18) a
	Summer	115 ± 24 (27) b	152 ± 35 (18) b	44 ± 7 (18) b
<i>Nymphaea</i>	Fall	8 ± 4 (24) a	8 ± 5 (18) a	7 ± 3 (18) a
	Winter	11 ± 3 (27) a	15 ± 6 (18) a	2 ± 1 (18) a
	Summer	10 ± 4 (27) a	16 ± 7 (18) a	7 ± 4 (18) a
<i>Sagittaria</i>	Fall	0 ± 0 (24) b	0 ± 0 (18) a	0 ± 0 (18) b
	Winter	0 ± 0 (27) b	0 ± 0 (18) a	0 ± 0 (18) b
	Summer	2 ± 1 (24) a	5 ± 3 (18) a	8 ± 2 (18) a
<i>Amaranthus</i>	Fall	49 ± 17 (24) a	188 ± 53 (18) a	517 ± 105 (18) a
	Winter	15 ± 23 (27) a	185 ± 57 (18) a	491 ± 126 (18) a
	Summer	9 ± 16 (27) a	118 ± 39 (18) a	361 ± 64 (18) a
Total	Fall	496 ± 69 (24) a	818 ± 144 (18) a	2295 ± 320 (18) b
	Winter	295 ± 45 (27) b	1141 ± 195 (18) a	3304 ± 797 (18) ab
	Summer	304 ± 45 (27) b	1471 ± 330 (18) a	4643 ± 422 (18) a

At each nutrient level, Duncan Multiple Range Test separated seasons into groups based on mean test, with season(s) followed by letter "a" being significant larger in seed bank density than season(s) followed by letter "b" ($p < 0.05$) and seasons sharing the same letter being similar in seed bank density

germinated predominantly within the first 8 weeks after assay initiation.

3.3. Fire effect

The total species number in the seed bank was reduced following fire treatments (Fig. 3B). *Chenopodium ambrosioides*, *Crinum americanum*, *Cyperus*, and *Nymphaea* spp. were detected at the highly enriched site in the summer germination assay but not after the summer fire. *Alternanthera philoxeroides*, *Crinum* spp., and *Mikania scandens* were detected in the winter seed bank but not after the winter fire at the moderately enriched site. Fire also enhanced the emergence of *Bidens alba*, a species that was not observed in the nonburned sites. Fire treatment at the highly enriched site in the summer significantly increased species richness, from 6.6 (±2.1) to 8.4 (±2.1) species sample⁻¹. However, the natural fire at the moderately enriched site during the winter significantly decreased species richness from 5.9 (±1.6) to 3.7 (±0.8) species sample⁻¹.

The fire treatment at the highly enriched site significantly reduced the seed density of *Typha* (Fig. 5A; $p = 0.043$), but not of *Cladium*, *Amaranthus*, or the other species. The percentage of *Typha* seeds in the seed bank at the highly enriched site declined from 82% before the fire to 68% after the fire (Fig. 6A), whereas the percentage of *Cladium*, *Amaranthus* and the other species doubled (Fig. 6A).

At the moderately enriched site, however, the percentages of *Typha*, *Amaranthus*, and the other species were all significantly reduced after the winter fire ($p < 0.05$) (Fig. 5B). The density of *Typha* seed was reduced by more than 60%, from 423 seedlings m⁻² before the fire to 148 seedlings m⁻² after the fire ($p = 0.011$); similar or greater reductions occurred for *Amaranthus* and the other species ($p < 0.05$). In contrast, the seed bank densities for *Cladium*, *Nymphaea*, and *Sagittaria* changed only slightly. The percentages of seeds of *Typha*, *Amaranthus*, and the other species in the seed bank declined after the fire and, as a result, the percentage of *Cladium* seeds in the seed bank more than doubled, from 14.7% to 40.8% (Fig. 6B), and *Cladium* became the dominant species in the seed bank.

4. Discussion

4.1. Variation related to season and nutrient enrichment

Along a nutrient gradient in the Everglades wetlands, the variation in seed density and species richness in the seed bank was considerable. This variation was probably related to the phenology of seed production and dispersal and to seed longevity in the sediment seed bank. *Typha* seeds dispersed in May, and *Typha* seed viability decreased greatly within 3 months, whereas *Cladium* seeds dispersed in August and persisted much longer than *Typha* seeds (Miao et al., 1997). In this study, the maximum seed density of *Typha* was recorded in the summer, but this density dropped quickly to only one-third during the fall, again suggesting a short longevity for *Typha* seeds. Because of the extraordinarily large quantity of *Typha* seed produced per plant, *Typha* seeds dominated the seed banks at both moderately and highly enriched sites where *Typha* was the dominant species in the standing vegetation. However, the seed bank density of some species, like *Nymphaea* and *Amaranthus*, did not vary greatly with season.

Our data indicate that the increase in nutrient levels in the Everglades increased the overall seed bank size, which is consistent with results from other studies in the Everglades (Urban et al., 1993; Stewart et al., 1997; van der Valk and Rosburg, 1997; Miao et al., 2001). Our data also show, however, that the reference site had the smallest total seed density with a relative dominance of *Cladium*, whereas the highly enriched site had the largest seed bank with even higher percentages of *Typha* and *Amaranthus*.

The soil seed bank densities of small-seeded species like *Typha* and *Amaranthus* in our experiment could be over-estimated if the number of seeds that germinate is not proportional to the total number of seeds in the seed bank. For example, if germination under laboratory conditions is more favorable for small-seeded than large-seeded species, the assay would be biased toward detection of small-seeded species. Whether germination in the laboratory reflects germination in the field and the number of seeds in the seed bank should be tested and verified by directly extracting and counting seeds from the sediment and by comparing germination under laboratory and field conditions.

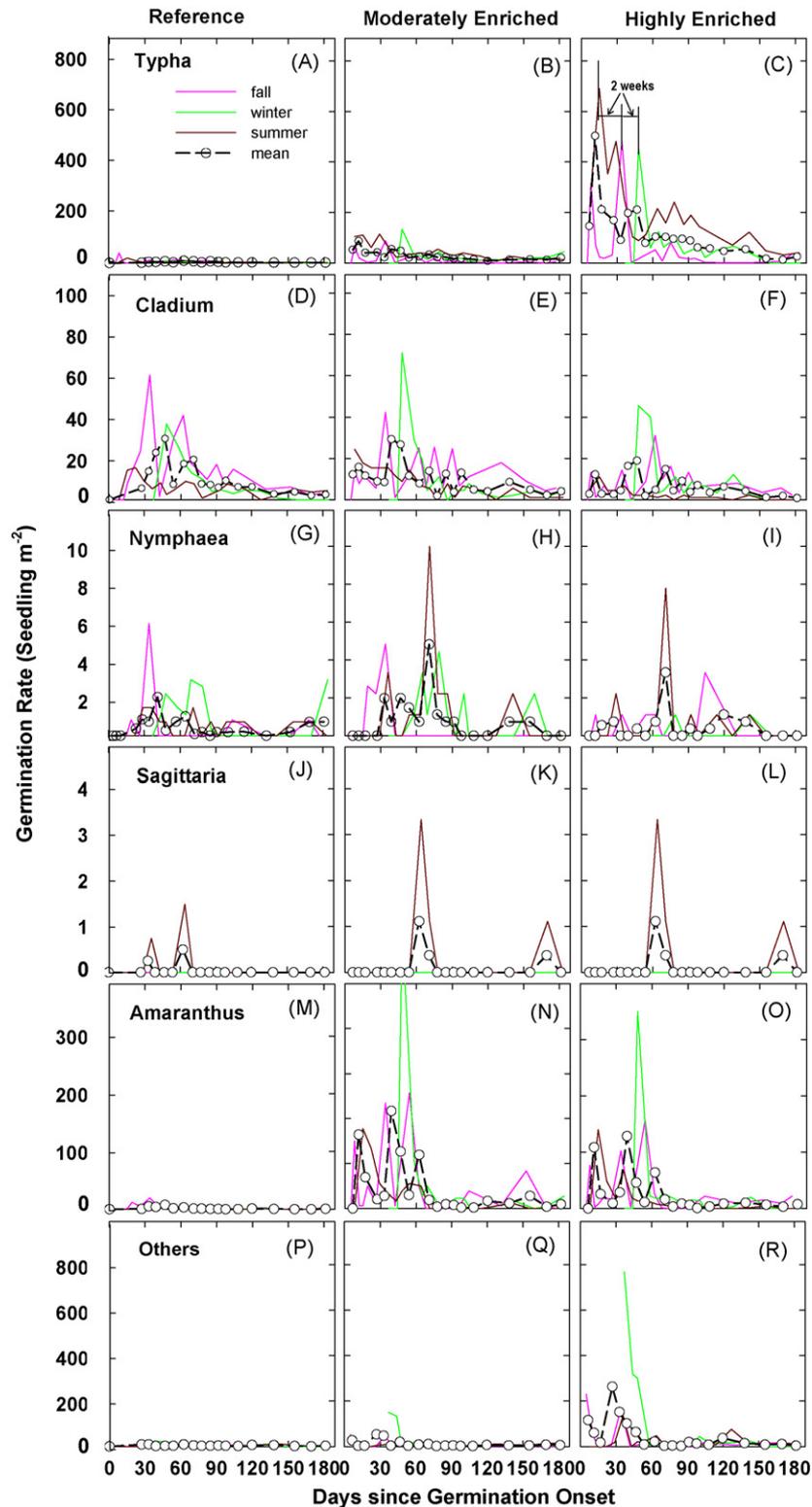


Fig. 4. The temporal variation of germination rates of major species and their interaction with season and nutrient enrichment levels.

While recognizing that the data from the germination assay may be biased in terms of absolute numbers of seeds in the seed bank, we believe that our germination data are useful because they show relative differences among sites differing in nutrient enrichment and exposure to fire. These relative differences provide insight into the ecological processes leading to the replacement of the large-

seeded, slow growing *Cladium* and *Nymphaea* communities by small-seeded weed species like *Typha* and *Amaranthus* at the WCA-A2 in the Everglades and also in the Atlantic coastal plain (Wisheu and Keddy, 1991).

The total number of species in the reference zone did not differ significantly from the number in the moderately and highly

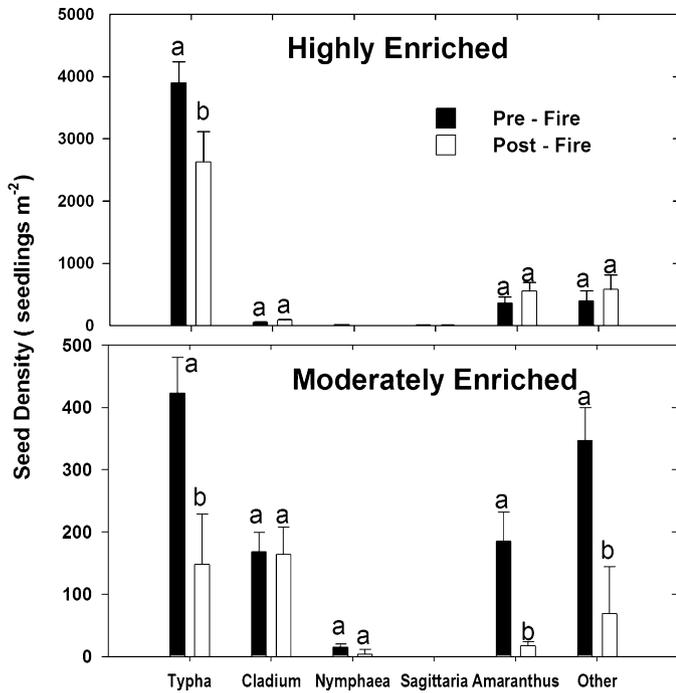


Fig. 5. The effect of fire on seed bank densities for major species at the highly enriched site (A) and at the moderately enriched plot (B).

enriched sites. The species richness (species sample⁻¹) however, was much higher at the nutrient-enriched sites than at the reference site. The reference zone (pristine Everglades) is a nutrient poor wetland, and we infer that this nutrient limitation restricts species richness (Grime, 1979; Wisheu and Keddy, 1989).

4.2. Seed bank strategies among dominant species

Thompson and Grime (1979) summarized seed bank strategies for temperate herbaceous communities, based on the intraannual variation and the percentage of the transient component to the total seed bank. Our results showed that the seed bank dynamics of the five species studied varied with season as well as habitat nutrient levels, but some different patterns were observed. In the reference site, seed banks of *Typha*, *Cladium*, *Nymphaea*, and *Amaranthus* were all relatively small but consistent in different seasons, which indicates a Type III persistent seed bank according to Thompson and Grime (1979). *Sagittaria* had a very small,

transient seed bank and germination only occurred in the summer, indicating a Type I transient seed bank. Seed bank strategies remain with increase in the soil nutrient for all species except for *Typha*. For both moderately and highly enriched sites, the *Typha* seed density increased greatly in summer and the *Typha* seed bank had a significant transient component in summer, indicating a Type IV seed bank of Thompson and Grime (1979).

4.3. Fire and seed bank dynamics

Fire has been widely used in wetland management, and a number of studies have documented the effect of fire treatment on controlling *Typha*. While some studies showed that burning followed by flooding reduced or eliminated *Typha* (Nelson and Dietz, 1966; Smith and Kadlec, 1985b; Mallik and Wein, 1986), many others found that *Typha* could reestablish and recover to pre-fire levels within a few years after burning (Krusi and Wein, 1988; Smith and Kadlec, 1985a; Gorbik, 1986; Mallik and Wein, 1986; Ponzio et al., 2004). Different outcomes of fire treatment might be a consequence of the timing of fire occurrence, climatic conditions at the time of burning, hydrological conditions after fire, and the soil properties, which are usually ecosystem specific (Smith et al., 2001).

In our study, a single fire treatment in summer was designed to test the effect of a prescribed surface fire on species richness and seed density at both highly and moderately enriched sites. However, an unexpected wildfire at the moderately enriched site prevented us from doing this test; yet it did provide a chance for us to examine effects of the timing of fire, although the design was imperfect (timing was confounded with enrichment level). Our results showed that fire, regardless of timing (winter or summer) and type (wild or prescribed fire), significantly reduced the size of the *Typha* seed bank. A natural winter fire at the moderately enriched site successfully transformed the seed bank from *Typha*- to *Cladium*-dominated. However, whether there will be an interaction between timing of fire and nutrient enrichment needs further study. Also requiring further study are whether fire changes species richness in the seed bank *in situ* and whether the change at the seed bank level benefits native vegetation recovery at the landscape scale.

In summary, significant seasonal variation in species composition and density existed in sediment seed bank in WCA-2A, and these temporal dynamics were affected by soil nutrient enrichment and also differed among species. Restoration approaches such as fire applications focusing on vegetation recovery should explicitly consider the temporal dynamics of the seed bank to

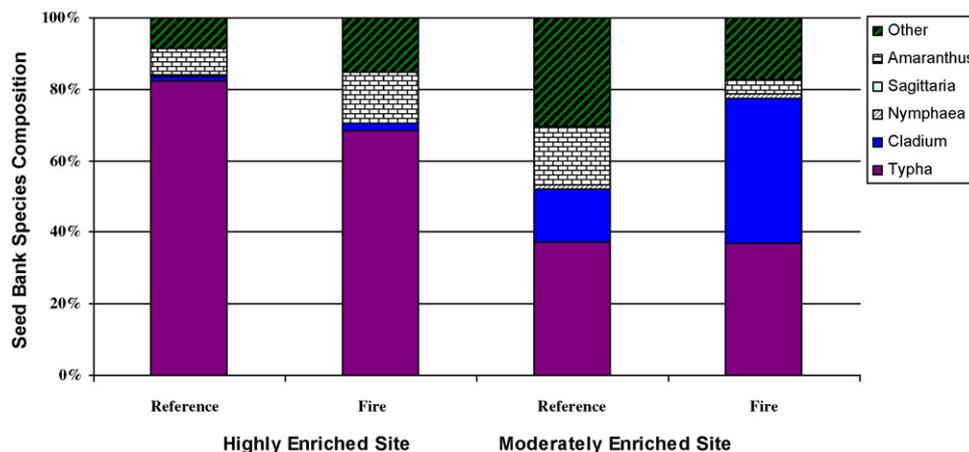


Fig. 6. The shift of seed bank composition and dominance after fire at the highly enriched site (A) and at the moderately enriched site (B).

determine the season of the application to enhance the treatment effect.

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