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RELATIONSHIPS OF SEED BANKS TO PLANT DISTRIBUTION PATTERNS IN A FRESHWATER TIDAL WETLAND[1]

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ABSTRACT

Study of seed banks, field seedling emergence, and survival of macrophytes in four zones (steep bank—SB; gentle bank—GB; midbank—MB; high marsh—HM) along transects perpendicular to a stream channel in a freshwater tidal wetland showed that many species are widely distributed. Of the 35 species in the seed bank, 50% were common to all zones; of the 20 species emerging in the field, 77% were observed in all zones. Density of seeds, seedlings, and mature plants of most species, however, varied significantly with habitat. The seed bank of each zone reflected the dominant vegetation of that zone. Most species, even those with high potential for water dispersal, were not evenly distributed. Reciprocal transplants and survival persistence data of dominants corresponded with their habitat preferences. Seed bank densities differed from zone to zone (SB 1,717 m^{-2}; GB 1,645; MB 2,730; HM 3,620). In all zones the maximum field seedling density was less than the comparable seed bank one (SB 38% less; GB 33%; MB 46%; and HM 10%). These data, coupled with the higher proportion of the total seed bank and total field seedlings occurring in the HM, suggest that the stream channel sites were more stressful early in the growing season than the HM. Because of differential establishment and survival, importance of a species relative to the rest of the vegetation may change with time and occurrence of a species in the vegetation may greatly outweigh its importance in the seed bank or even the seedling stage. Although seeds of annual species were numerous with seven species making up 85% of the seed bank, annual species comprised only about half of the species recorded in the seed bank of each zone. It is not possible at our present level of understanding of seed banks in the freshwater tidal marsh to predict vegetation change. Various combinations of species attributes contribute to the zonation patterns observed in the freshwater tidal wetland.

THE ESTABLISHMENT and distribution of a wetland species are functions of 1) its life history features, and 2) the environmental 'sieve' (e.g., no standing water or standing water) (van der Valk, 1981). The nature of seed dispersal and the persistent nature of the seed banks, interacting with the degree of flooding, determine the species which become established. The vegetation dynamics of prairie glacial marshes in long term drawdown cycles (van der Valk and Davis, 1976, 1978) and the yearly composition of vegetation along lake edges in Ontario (Keddy and Reznicek, 1982) show the influence of such interactions.

In tidal wetlands where the inundation pattern is daily rather than seasonal and the degree of inundation is spatial rather than temporal, different establishment requirements relative to standing water could contribute to the zonation observed. Much of the work involving tidal wetland species distribution has investigated salt water systems where distinct zonation patterns are determined by combinations of flooding (elevation) and salinity interacting with the differential competitive abilities of the dominants (Adams, 1963; Gray and Scott, 1967; Clarke and Hannon, 1969; Kerwin and Pedigo, 1971; Flowers, 1973; Mahall and Park, 1976a, b; Niering and Warren, 1980). Hopkins and Parker (1984) examined the seed bank of a California salt marsh in relation to zonation patterns and found its role in vegetation dynamics to differ from those freshwater wetlands where disturbance or extreme seasonal water level changes are characteristic. They found that the low density, low diversity seed bank reflected the composition of the dominants and was the source of the occasional establishment of new individuals in a long lived, perennial vegetation.

Freshwater tidal wetlands share with coastal salt marshes the overriding influence of tidal activity, but because salinity is not an aspect of that influence, freshwater tidal wetlands have high productivity, greater diversity, and, along

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the east coast of the United States, a large number of annuals which often are dominant over large areas (Simpson et al., 1983). Zonation patterns persist (Anderson, Brown and Rappleye, 1968; Whigham and Simpson, 1975; Odum, 1978; Odum, Dunn and Smith, 1979; Simpson et al., 1983); but are less conspicuous than in salt marshes because of the higher diversity, structural complexity, and the occurrence of certain dominants in several zones. Our field observations in a freshwater tidal marsh, which has been the focus of a number of studies (e.g., Whigham and Simpson, 1975, 1976, 1978; Leck and Graveline, 1979; Simpson et al., 1983), noted the dominance of certain species in specific zones along stream channels. In addition, an analysis of the seed bank of this marsh showed high seedling emergence of some species in soil from particular areas (Leck and Graveline, 1979). *Polygonum punctatum,* for example, was found in greatest abundance in soils from sites flooded most regularly and for the longest periods of time, while *Polygonum arifolium* was most abundant in soils from higher sites flooded for shorter periods of time. *Acnida cannabina* seeds did not occur in soil from the *Typha* site, yet were a sizable component (26.1%) of the total marsh seed bank. In contrast some studies report that almost all wetland seeds float (Sculthorpe, 1967) or are wind dispersed (e.g., *Typha* sp.) which in turn suggests widespread and uniform distribution (McAtee, 1925; Kelly and Bruns, 1975). In this study we examined the seed bank of a freshwater tidal wetland in relation to the vegetation zonation pattern along a stream channel. To this end we determined: 1) distribution of seeds in the seed bank (as measured by seedling emergence) and of seedlings and mature vegetation in the field; 2) survival of seedlings and transplants; and 3) flotation potential of seeds.

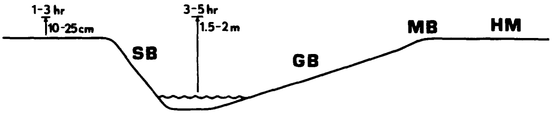

Fig. 1. A. Sectional diagram showing relationships of transect plots to slope, tidal depth, and tide duration (SB—steep bank, GB—gentle bank, MB—midbank, HM—high marsh).

MATERIALS AND METHODS—The Hamilton Marsh near Trenton, NJ covers an area of approximately 500 ha of which about 260 ha make up the northernmost tidal wetland on the Delaware River. Description of the vegetation (e.g., species composition, species distribution, phenology, and productivity), tidal influence, and other characteristics of the wetland can be found in Whigham and Simpson (1975) and Simpson et al. (1983). In fall 1978 the most apparent zones were the stream bottom with *Nuphar advena* and *Pontederia cordata,* the gentle bank (GB) (Fig. 1) with *Polygonum punctatum,* and the high marsh (HM) dominated by *Bidens laevis, Polygonum arifolium,* and *Impatiens capensis. Ambrosia trifida* and *Acnida cannabina* seemed most common along the top of the stream channel (MB).

Plots were established prior to germination in March 1979 to determine the species composition of the seed bank, field distribution, and survival of seedlings. Five primary transects were placed at approximately 20-m intervals perpendicular to the stream in a part of the marsh where streambanks were steep on one side (50–75° slope) and gentle on the other (10–25° slope) (Fig. 1). Each of the primary transects was dissected by four secondary transects 6 m long which were positioned as follows: a) 1 m above low slack water on the steep bank (SB); b) 1 m above low slack water on the gentle bank (GB); c) about 3 m beyond low slack water on the crest of the bank (midbank MB); and d) 10 m beyond the midbank in the high marsh (HM). Along these secondary transects at meter intervals four 20 × 20 cm plots were randomly selected, two for the seed bank study and two for field germination and survival studies. These provided ten replicates, two at each transect, for SB, GB, MB, and HM zones.

In mid-March 1979, before field germination began, two intact soil blocks 20 × 20 × 5 cm were collected along each secondary transect for the seed bank study. Each soil block was transferred to aluminum trays (20 × 20 × 5 cm) and placed in a greenhouse. The blocks were maintained in a saturated condition and seedling emergence was monitored every 2–3 days for 6 wk and weekly thereafter until 20 June 1979. The greenhouse was maintained at 18 C minimum temp., with ambient photoperiod and light intensity ~50% full sunlight. Seedlings were removed as soon as they could be identified to species. Those not identifiable as seedlings were transplanted into pots. Two trays with sterile soil were placed among the samples to determine greenhouse contaminants which were not included in the data. The seed bank data presented are based on seedling emergence in the greenhouse. We are aware of the problems inherent in this method (Major and Pyott, 1966; Thompson and Grime, 1979).

Field germination and subsequent survival were recorded every two weeks throughout the growing season, 14 March to 16 October, in the remaining two 20 × 20-cm plots along each secondary transect. Because of the nature of the habitat and the interval between observation dates, it was impossible to follow individual seedlings. The data represent the total for a given species on a given date and do not include seedlings which germinated and died during the interval.

Four replicate transplant gardens were established to study survival of five annual species in GB, MB, and HM zones along four of the five transects. Seedlings were obtained in a location where a given species was abundant. Except for *Acnida cannabina* which were very small, most seedlings had true leaves. Ten seedlings each of *Acnida cannabina, Ambrosia trifida, Bidens laevis, Impatiens capensis,* and *Polygonum punctatum* were planted about 7 cm apart in rows about 7 cm apart. Placement of species was consistent from garden to garden. The garden areas were cleared of other seedlings. Survival was recorded every 2 wk until mid-September.

In late July and mid-October field species composition was evaluated using two 0.5-m × 0.5-m quadrats placed on undisturbed portions of each secondary transect giving ten replicates for SB, GB, MB, and HM zones. Within each quadrat, density (July) or cover (October) and frequency of each species were determined.

The potential for seeds of six annual species to be dispersed by water was examined by determining flotation time. Twenty-five seeds (4–5 replicates) were placed into a glass dish (5 cm high × 10 cm diam) containing 100 cc of deionized water within 24 hr of field collection. The contents of each dish were stirred slowly for a brief period (20 sec) and the number of floating seeds counted at hr intervals for 6 hr and daily thereafter. Viability was not determined, but only seeds which appeared sound were used.

Nomenclature follows Fernald (1970). The exception is *Zizania aquatica* var. *aquatica* L. which follows Dore (1969).

RESULTS—*Seed bank study*—Ten species, seven annuals and three perennials, accounted for 92.8% of the total number of seedlings germinating in soils from the four freshwater tidal marsh zones under greenhouse conditions (Table 1). These were *Bidens laevis* (28.9% of total), *Callitriche heterophylla* (28.3%), *Acnida cannabina* (13.2%), *Pilea pumila* (5.4%), *Typha latifolia* (4.6%), *Polygonum punctatum* (3.4%), *Polygonum arifolium* (3.2%), *Impatiens capensis* (2.3%), *Sagittaria latifolia* (2.0%), and *Juncus* sp. (1.5%). Only four species were evenly distributed (χ^2; $P < 0.01$; Table 1). Two uniformly distributed species, *Callitriche heterophylla* and *Pilea pumila,* were not dominant components of the vegetation (Whigham and Simpson, 1975; Parker and Leck, pers. observ.). *Bidens laevis* and *Typha latifolia* were the only dominant species whose seeds were uniformly distributed across all zones (Table 1). Generally, however, the importance of species, as determined by numbers and/or frequency, varied from zone to zone but only seven species (*Acnida cannabina, Bidens laevis, Callitriche heterophylla, Impatiens capensis, Pilea pumila, Polygonum arifolium, Polygonum punctatum,* and *Typha latifolia*) were ranked among the five most numerous in all zones (Table 1).

Duncan's Multiple Range Test (Kramer, 1956) showed the following significant ($P \leq 0.05$) site-seed bank differences: *Acnida cannabina*—MB from HM and GB; *Bidens laevis*—HM from SB, GB, and MB; *Callitriche heterophylla*—MB from SB; *Impatiens capensis*—HM from SB, GB, and MB; *Peltandra virginica*—HM from SB; *Polygonum arifolium*—HM from SB; and *Sagittaria latifolia*—MB from GB. *Ambrosia trifida, Gratiola neglecta, Pilea pumila,* and *Zizania aquatica* var. *aquatica* showed no significant site differences, often due to large sample variability or very small sample size.

Seedlings of most species, however, were most common in a given zone or zones. For example, only 5% of *Acnida cannabina* seeds occurred in the HM while 75% occurred in MB and SB zones. *Polygonum punctatum* seeds were completely restricted to the stream bank zones with 54% of its seed resources in the GB samples. For *Bidens laevis* (68%), *Impatiens capensis* (54%), *Polygonum arifolium* (54%), and *Typha latifolia* (45%), most seeds were in soils from HM sites.

In addition to these patterns, the total density of seeds differed by zone. The SB and GB sites had the fewest seeds, 1,715 ± 195 SE m^{-2} and 1,645 ± 373 SE m^{-2}, respectively. MB had 2,730 ± 630 SE m^{-2} and the HM averaged 3,620 ± 514 SE m^{-2}. ANOVA showed that the HM seed bank had significantly more seeds than the other sites ($P < 0.01$), but the variance was too great for the MB seed bank to be statistically different from SB or GB. These trends remained whether annuals and perennials were considered separately or together.

Thirty-five species, 18 annuals, 15 perennials, and 2 woody species, germinated (Table 1). The number of species varied from 20 in GB samples to 26 in MB samples. Thirteen species were present in all four zones, three

TABLE 1. *Number of seedlings* m^{-2} ± *SE of species that emerged in the greenhouse from soils collected from steep bank (SB), gentle bank (GB), midbank (MB), and high marsh (HM) sites (N = 10). Rank of a species at each site and % of site total are given in parentheses. (P = perennial: W = woody; all others are annual except possibly those identified only to family)*

Species	Site: SB	Site: GB	Site: MB	Site: HM	Relative abundance[a] (%)	Freq. (%)[b]
Acnida cannabina L.	318 ± 92 (2, 19%)	218 ± 73 (3, 13%)	663 ± 264 (2, 24%)	83 ± 50 (7, 2%)	13.2+	88
Agrostis alba L. (P)	3 ± 3 (15, <1)	3 ± 3 (16, <1)			<0.1	5
Ambrosia trifida L.			3 ± 3 (20, <1)	3 ± 3 (18, <1)	<0.1	5
Bidens laevis (L.) BSP.	220 ± 78 (3, 13)	293 ± 165 (2, 18)	378 ± 252 (3, 14)	1,928 ± 384 (1, 53)	28.9+	93*
Bidens sp.			3 ± 3 (20, <1)		<0.1	3
Boehmeria cylindrica (L.) Sw. (P)	3 ± 3 (15, <1)		3 ± 3 (20, <1)		<0.1	5
Callitriche heterophylla Pursh.	650 ± 94 (1, 38)	563 ± 174 (1, 34)	915 ± 401 (1, 34)	625 ± 256 (2, 17)	28.3	95*
Cuscuta sp.			8 ± 8 (13, <1)	25 ± 17 (11, <1)	0.3	10
Cyperus erythrorhizos Muhl.			3 ± 3 (20, <1)		<0.1	3
Cyperus flavescens L.	5 ± 3 (14, <1)			5 ± 3 (16, <1)	0.1	10
Cyperus sp. (P)	3 ± 3 (15, <1)	3 ± 3 (16, <1)		3 ± 3 (18, <1)	0.1	8
Fraxinus americana L. (W)				5 ± 3 (15, <1)	0.1	5
Gratiola neglecta Torr.	18 ± 7 (10, <1)	8 ± 5 (14, <1)	10 ± 6 (12, <1)	8 ± 4 (15, <1)	0.4	33
Hibiscus palustris L. (P)			3 ± 3 (20, <1)		<0.1	3
Impatiens capensis Meerb.	10 ± 6 (12, <1)	10 ± 6 (11, <1)	18 ± 13 (10, <1)	185 ± 74 (4, 5)	2.3+	40
Juncus tenuis Willd. (P)				3 ± 3 (18, <1)	<0.1	3
Juncus sp. (P)	55 ± 19 (6, 3)	28 ± 11 (8, 2)	50 ± 12 (9, 2)	10 ± 6 (12, <1)	1.5	53
Ludwigia palustris (L.) Ell. (P)	3 ± 3 (15, <1)			3 ± 3 (18, <1)	0.1	5
Lythrum Salicaria L. (P)	3 ± 3 (15, <1)				<0.1	3
Mikania scandens (L.) Willd.				3 ± 3 (18, <1)	<0.1	3
Nasturtium officinale R.Br. (P)			5 ± 5 (17, <1)		0.1	3
Nuphar advena (Ait.) Ait.f. (P)			5 ± 5 (17, <1)		0.1	3
Panicum dichotomiflorum Michx.		5 ± 5 (15, <1)			0.1	5

TABLE 1. *Continued*

Species	Site								Relative abundance[a] (%)	Freq. (%)[b]
	SB		GB		MB		HM			
Paulownia tomentosa (Thunb.) Steud. (W)							3 ± 3	(18, <1)	<0.1	3
Peltandra virginica (L.) Schott & Endl. (P)	3 ± 3	(15, <1)	23 ± 19	(9, <1)	15 ± 10	(11, <1)	53 ± 22	(9, 1)	1.0	28
Pilea pumila (L.) Gray	118 ± 57	(4, 9)	145 ± 97	(5, 9)	136 ± 49	(4, 5)	123 ± 41	(6, 3)	5.4	80
Polygonum arifolium L.	13 ± 6	(11, <1)	35 ± 22	(7, 2)	93 ± 76	(6, 3)	175 ± 66	(5, 5)	3.2	50
Polygonum punctatum Ell.	68 ± 19	(5, 4)	170 ± 134	(4, 10)	88 ± 60	(7, 3)			3.4	55
Polygonum sagittatum L.	3 ± 3	(15, <1)	10 ± 6	(11, <1)	8 ± 4	(13, <1)			0.2	18
Sagittaria latifolia Willd. (P)	50 ± 21	(8, 3)	10 ± 10	(11, <1)	73 ± 27	(8, 3)	60 ± 16	(8, 2)	2.0	48
Typha latifolia L. (P)	53 ± 17	(7, 3)	58 ± 41	(6, 4)	135 ± 70	(5, 5)	205 ± 96	(3, 7)	4.6	65*
Zizania aquatica var. *aquatica* L.	10 ± 7	(12, <1)	15 ± 8	(10, <1)	8 ± 5	(13, <1)	30 ± 17	(10, <1)	0.7	30
Compositae (P)					3 ± 3	(20, <1)			<0.1	3
Cruciferae (P)							3 ± 3	(18, <1)	<0.1	3
Gramineae (P)	3 ± 3	(15, <1)	3 ± 3	(16, <1)	8 ± 4	(13, <1)	10 ± 6	(12, <1)	0.3	20
Umbelliferae (P)	20 ± 8	(9, 1)	8 ± 5	(14, <1)	5 ± 3	(17, <1)	10 ± 6	(12, <1)	0.4	33
Other	73 ± 18		40 ± 24		90 ± 31		60 ± 23		2.7	
Total species	23		20		26		25			
Total seedlings m^{-2}	1,715 ± 195		1,645 ± 373		2,730 ± 630		3,620 ± 514		9,728	

[a] Percent relative to the total number of seedlings (9,728).
[b] Frequency based on all plots at all sites ($N = 40$).
* Uniformly distributed in all zones (χ^2; $P < 0.01$).
[+] Density varied significantly with site (ANOVA $P \leq 0.05$).

occurred in three zones, four in two zones, and 11 species occurred in only one zone.

Field establishment and success—Maximum numbers of seedlings found in field plots (Table 2) were less than totals recorded from the seed bank study (Table 1); 10% less for HM, 23% for GB, 38% for SB, and 46% for MB. Twenty species, 12 annuals and 8 perennials with a range of 16 to 18 species per zone, were recorded. Fourteen species occurred in all zones, one in three zones, two in two zones, and two in one zone. The ten most numerous species, nine annuals and one perennial, accounted for 93.6% of the total maximum seedling counts (values do not account for seedling death). These were *Bidens laevis* (50.1% of total), *Callitriche heterophylla* (11.4%), *Acnida cannabina* (11.1%), *Gratiola neglecta* (5.8%), *Impatiens capensis* (5.3%), *Polygonum arifolium* (3.7%), *Polygonum punctatum* (2.6%), *Pilea pumila* (2.5%), *Sagittaria latifolia* (1.5%) and *Zizania aquatica* var. *aquatica* (1.3%).

Only four species were evenly distributed (Table 2). Of the ten most numerous species, *Callitriche heterophylla, Pilea pumila, Polygonum arifolium,* and *Sagittaria latifolia* had similar numbers of seedlings in all zones, but even these tended to be more common in certain (higher, wetter, lower) sites. *Gratiola neglecta, Pilea pumila,* and *Polygonum sagittatum* had similar frequencies in all zones. Generally, as in the seed bank studies, the importance of a species, as determined by numbers and/or frequency, varied from zone to zone. Two-way ANOVA showed significant ($P \leq 0.05$) variation in density by site, by species, and by both site and species.

Duncan's Multiple Range Test (Kramer, 1956) showed the following significant ($P \leq 0.05$) site-seedling differences: *Acnida cannabina*—HM from SB, GB, and MB; *Bidens laevis*—HM from SB, GB, and MB; *Gratiola neglecta*—MB from HM; *Impatiens capensis*—HM from SB, GB, and MB; *Peltandra virginica*—HM from GB; and *Polygonum punctatum*—GB from HM; *Ambrosia trifida, Callitriche heterophylla, Pilea pumila, Polygonum arifolium, Sagittaria latifolia,* and *Zizania aquatica* var. *aquatica* showed no significant site differences, often due to large sample variability or small sample size.

Total seedling density increased from March until late April to early May. The number of seedlings declined thereafter, especially in the HM habitat where densities dropped from ~3,000 seedlings m^{-2} in late April to 300 m^{-2} by mid-June (Fig. 2A). Seedlings of perennials were not present in high numbers (max. 48 ± 13 m^{-2}) and did not survive to August (Fig. 2A). As in the seed bank, the HM had significantly greater numbers of seedlings (3×, $P < 0.001$) than any of the other three zones, and, although the MB had slightly higher numbers than SB and GB, the three were not statistically different. Maximum seedling densities for SB (678 ± 139 m^{-2}) occurred on 10 May, for GB (873 ± 192 m^{-2}) on 16 May, for MB (1070 ± 236 m^{-2}) on 10 May, and for HM (2,843 ± 365 m^{-2}) on 26 April. All zones had approximately similar densities from mid-June until the end of August (Fig. 2A). Compared with other dominant species ten times more *Bidens laevis* seedlings were found in the HM where peak seedling density reached 2,503 ± 354 SE individuals m^{-2} and remained at significantly higher density ($P < 0.001$) until early July (Fig. 2C).

Comparison of survival data for five selected annuals (Fig. 2B–F) shows that, although seeds of each species germinated in all four zones, by July some were more successful in establishing populations in certain zones than others. For example, *Acnida cannabina* and *Polygonum punctatum* were more successful in SB, GB, and MB sites with *Polygonum punctatum* surviving until the end of the growing season only in the GB habitat. *Bidens laevis,* however, while a substantial component of the vegetation in all zones for most of the summer, persisted to the end of the growing season only in the HM and was severely limited in its growth and reproduction outside the HM (personal observation). *Impatiens capensis* survived through the growing season only in HM sites although present in limited numbers in the MB in October (Table 3). Early in the season, *Polygonum arifolium* had similar population density in all zones, but persisted in three zones until late August and to mid-September only in the MB. Late season vegetation analysis, however, confirms its continuing importance in all zones (Table 3).

For *Acnida cannabina, Bidens laevis, Impatiens capensis,* and *Polygonum punctatum,* maximum seedling densities (Table 2) and survival (Fig. 2) appear related. The bulk of *Acnida cannabina* germination (97%) occurred along the stream bank (SB, GB, MB) and little on the HM, and survival was best in SB and MB zones. The highest density of *Polygonum punctatum* seedlings was observed in the GB zone, and subsequent survival was also best there (Fig. 2F). Over 75% of *Bidens laevis* and *Impatiens capensis* germination occurred in the HM, the zone where survival was best. In contrast, *Polygonum arifolium* appeared to germinate equally in all sites and survived well in all sites (Fig. 2E, Table 3).

Examination of persistence of each species

TABLE 2. *Maximum number of seedlings ($m^{-2} \pm SE$) observed in field plots located in steep bank (SB), gentle bank (GB), midbank (MB), and high marsh (HM) sites (N = 10). Rank of a species at each site and % of site total are given in parentheses. (P = perennial except possibly those identified only to family, others are annuals)*

Species	Site: SB	Site: GB	Site: MB	Site: HM	Relative abundance[a] (%)	Freq. (%)[b]
Acnida cannabina	325 ± 82 (11, 30%)	228 ± 53 (3, 18%)	205 ± 113 (3, 14%)	25 ± 15 (9, <1%)	11.1	83
Ambrosia trifida	25 ± 13 (9, 2)	15 ± 13 (11, 1)	3 ± 3 (15, <1)		0.6	18
Bidens laevis	170 ± 47 (3, 16)	328 ± 114 (1, 26)	523 ± 231 (1, 36)	2,520 ± 381 (1, 77)	50.1	100*
Callitriche heterophylla	178 ± 49 (2, 17)	258 ± 92 (2, 20)	235 ± 49 (2, 16)	138 ± 69 (3, 4)	11.4	83
Cuscuta sp.	3 ± 3 (16, <1)	5 ± 5 (13, <1)	5 ± 5 (13, <1)	13 ± 10 (13, <1)	0.4	13
Gratiola neglecta	83 ± 27 (4, 8)	118 ± 35 (4, 9)	173 ± 53 (4, 12)	33 ± 19 (8, 1)	5.8	75*
Impatiens capensis	40 ± 22 (7, 4)	38 ± 21 (8, 3)	30 ± 18 (9, 2)	268 ± 96 (2, 8)	5.3	50
Nuphar advena (P)			3 ± 3 (15, <1)		<0.1	2.5
Peltandra virginica (P)	30 ± 3 (8, 3)	5 ± 5 (13, <1)	12 ± 6 (11, <1)	45 ± 16 (5, 1)	1.3	38
Pilea pumila	50 ± 16 (6, 5)	80 ± 35 (6, 7)	97 ± 49 (5, 7)	35 ± 13 (6, 1)	2.5	75*
Polygonum arifolium	58 ± 30 (5, 5)	43 ± 29 (7, 3)	75 ± 46 (6, 5)	83 ± 16 (4, 3)	3.7	65
Polygonum punctatum	25 ± 14 (9, 2)	88 ± 23 (5, 7)	45 ± 13 (7, 3)	25 ± 12 (9, <1)	2.6	78
Polygonum sagittatum	5 ± 3 (15, <1)	3 ± 3 (16, <1)	5 ± 3 (13, <1)	5 ± 5 (14, <1)	0.3	15*
Saggitaria latifolia (P)	23 ± 13 (11, 2)	25 ± 11 (10, 2)	38 ± 14 (8, 3)	18 ± 12 (11, <1)	1.5	45
Typha latifolia (P)	8 ± 4 (14, <1)			3 ± 3 (16, <1)	0.2	10
Zizania aquatica var. *aquatica*	10 ± 8 (12, <1)	30 ± 27 (9, 2)	15 ± 10 (10, 1)	35 ± 23 (6, 1)	1.3	35
Cruciferae (P)	3 ± 3 (16, <1)			3 ± 3 (16, <1)	0.1	5
Gramineae (P)				3 ± 3 (16, <1)		2.5
Umbelliferae (P)	10 ± 8 (12, <1)	8 ± 4 (12, <1)	10 ± 8 (12, <1)	15 ± 6 (12, <1)	0.6	30
Other	3 ± 3 (16, <1)	5 ± 5 (13, <1)		5 ± 5 (14, <1)	0.2	10
Total species	18	16	16	17		
Total seedlings m^{-2}	1,068 ± 184	1,270 ± 221	1,470 ± 291	3,263 ± 405		

[a] Percent relative to the total number of seedlings (7,071).
[b] Frequency based on all plots at all sites ($N = 40$).
* Species uniformly distributed in all zones (χ^2; $P \leq 0.01$).

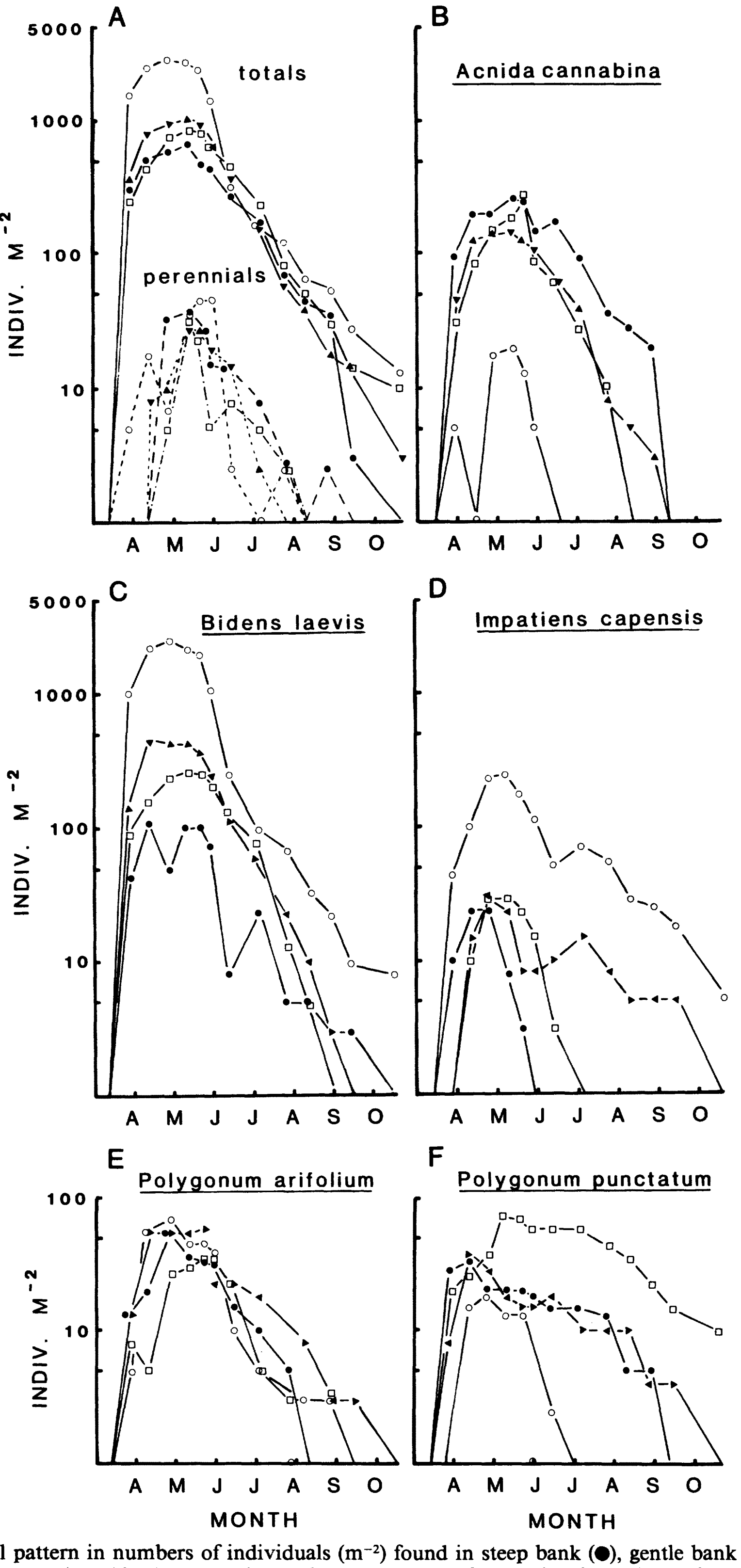

Fig. 2. Seasonal pattern in numbers of individuals (m^{-2}) found in steep bank (●), gentle bank (□), midbank (▲), and high marsh (○) zones (n = 10). **A.** shows site totals and numbers of perennials found in the field. Individual species are also illustrated: **B.** *Acnida cannabina*; **C.** *Bidens laevis*, **D.** *Impatiens capensis*; **E.** *Polygonum arifolium*; and **F.** *Polygonum punctatum*.

TABLE 3. *Field vegetation analyses for 24–25 July and 12 October 1979 in four marsh sites (SB—steep bank, GB—gentle bank, MB—midbank, and HM—high marsh). + indicates that the species was present, but did not contribute to density or cover estimates. (P indicates perennial species)*

	Site								
	SB		GB		MB		HM		
Species	Relative density	Freq.	Relative density	Freq.	Relative density	Freq.	Relative density	Freq.	Total freq.[a]
% RELATIVE DENSITY AND FREQUENCY (24–25 JULY 1979)									
Acnida cannabina	33.6	80	26.9	70	11.7	70	0.7	10	58
Ambrosia trifida	0.4	10	1.4	20	10.4	40	2.1	20	23
Bidens laevis	23.7	90	19.8	70	28.1	80	47.8	50	73
Gratiola virginica	1.9	10	1.4	10	0	0	0	0	5
Impatiens capensis	0.4	10	0.7	10	9.8	50	32.1	80	38
Peltandra virginica (P)	+	10	0	0	0	0	0	0	3
Pilea pumila	3.9	50	0.7	10	3.2	10	1.4	10	20
Polygonum arifolium	2.4	40	2.1	20	14.3	50	14.2	50	40
Polygonum punctatum	28.2	100	39.7	90	13.0	50	0	0	60
Polygonum sagittatum	0	0	0	0	0.6	10	0	0	5
Zizania aquatica var. *aquatica*	2.4	30	6.3	60	8.4	50	1.4	10	38
Other	+		0.7	10	+				5
% RELATIVE COVER AND FREQUENCY (10 OCTOBER 1979)									
Acorus calamus (P)	0	0	1.3	10	0	0	0	0	3
Acnida cannabina	1.9	10	1.9	10	1.4	10	0	0	8*
Ambrosia trifida	0.6	10	0	0	4.9	20	7.1	20	13
Bidens laevis	8.2	30	5.1	30	18.3	60	18.8	40	40
Impatiens capensis	0	0	0	0	4.9	10	18.3	50	15
Nuphar advena (P)	8.8	50	5.7	30	4.9	40	+	10	33
Peltandra virginica (P)	0.6	10	0	0	0	0	1.2	20	8
Polygonum arifolium	36.6	80	37.6	90	41.5	100	48.4	90	90*
Polygonum punctatum	31.9	50	43.1	60	9.8	50	0	0	40
Polygonum sagittatum	0	0	0	0	7.2	20	1.2	10	10
Sagittaria latifolia (P)	8.2	30	2.5	20	4.2	20	2.7	20	23*
Typha latifolia (P)	0	0	2.4	10	1.4	10	0.6	10	8*
Zizania aquatica var. *aquatica*	0	0	0.1	10	0	0	0	0	3
Other	0	0	0	0	1.4	10	1.7	20	8

[a] Total frequency based on all quadrats for all sites ($N = 40$) for each date. Frequency for each site based on $N = 10$.
* Species uniformly distributed in all zones (χ^2, $P < 0.01$).

in field plots also reflects differences in the ability of species to survive (Table 4). Two-way ANOVA showed persistence to vary significantly ($P < 0.05$) by species and by both site and species but not by site alone.

Duncan's Multiple Range Test (Kramer, 1956) showed the following significant ($P \leq 0.05$) site-persistence differences: *Acnida cannabina*—HM from SB, GB, and MB; *Ambrosia trifida*—HM from SB; *Bidens laevis*—HM from SB and GB, and SB from MB; *Callitriche heterophylla*—HM from MB; *Gratiola virginica*—HM from GB and MB; *Impatiens capensis*—HM from SB, GB, and MB; *Polygonum punctatum*—GB from SB, MB and HM, HM from MB, and HM from SB. *Peltandra virginica, Pilea pumila, Polygonum arifolium, Sagittaria latifolia,* and *Zizania aquatica* var. *aquatica* showed no significant site-persistence differences due to small sample size. As might be expected, the dominants of a given zone often survived best there, e.g., *Impatiens capensis* in the HM, *Acnida cannabina* in the SB, and *Polygonum punctatum* in the GB. Others, such as *Callitriche heterophylla* and *Pilea pumila,* made up a substantial portion of the seed bank (Table 1), but did not persist as well as the dominants, perhaps indicative of an earlier flowering pattern or a suboptimal habitat. *Zizania aquatica* var. *aquatica,* often a codominant (Whigham and Simpson, 1975), and *Gratiola neglecta* flowered early and did not have long persistence. Except for *Peltandra virginica* in GB sites, seedlings of perennials also did not persist for long periods. *Polygonum arifolium* seemed to persist relatively well in all zones and its importance, relative to other species, increased at the end of the season (Table 3).

Independent measurements of field dominance based on density or cover and frequency (Table 3) related well with the seedling and

TABLE 4. *Species persistence (% of sampling periods present) in field plots in steep bank (SB), gentle bank (GB), midbank (MB) and high marsh (HM) sites. Sampling occurred on 13 dates, usually at 2-wk intervals*

Species	Site			
	SB	GB	MB	HM
Acnida cannabina	54%	44%	48%	23%
Ambrosia trifida	48	23	31	
Bidens laevis	42	53	61	78
Callitriche heterophylla	38	32	45	35
Cuscuta sp.	8	8	8	8
Gratiola neglecta	23	25	30	15
Impatiens capensis	15	27	62	68
Nuphar advena (P)				8
Peltandra virginica (P)	19	46	15	20
Pilea pumila	25	19	25	20
Polygonum arifolium	42	38	48	42
Polygonum punctatum	47	74	36	23
Polygonum sagittatum	12	31	12	15
Sagittaria latifolia (P)	18	12	17	21
Typha latifolia (P)	8			8
Zizania aquatica var. *aquatica*	27	26	44	20
Cruciferae (P)	8			15
Gramineae (P)				15
Umbelliferae (P)	31	23		20
Other	23	8	8	8
No. species	18	16	17	18

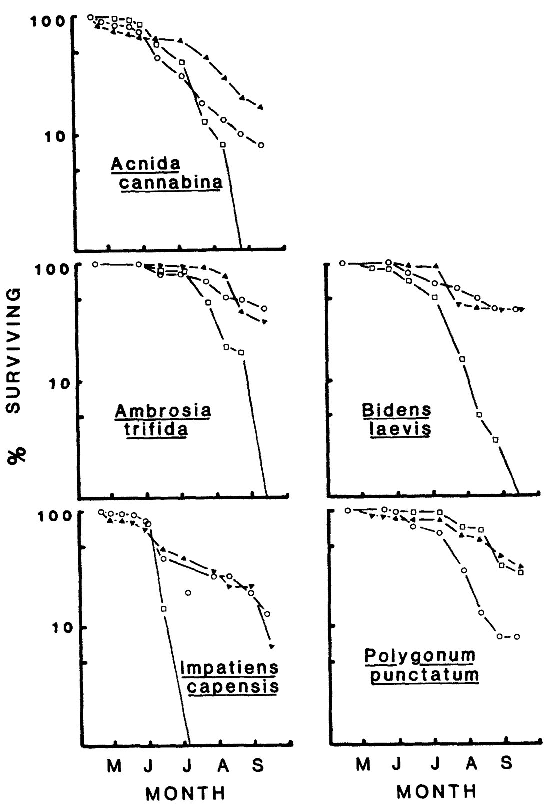

Fig. 3. Survival of transplants into gentle bank (□), midbank (▲), and high marsh (O) zones.

survival data, but, in addition, comparison of July and October values showed the change in importance (based on relative density or cover) in species during the season. In July, for example, the important species in the SB sites were *Acnida cannabina, Polygonum punctatum, Bidens laevis, Pilea pumila* and *Polygonum arifolium,* while in October they were *Polygonum arifolium, Polygonum punctatum, Nuphar advena, Bidens laevis,* and *Sagittaria latifolia. Acnida cannabina,* and *Zizania aquatica* var. *aquatica,* were both important in several zones during July, but had declined considerably by October. In contrast, *Polygonum arifolium* and several perennials increased in importance from July to October. Most species, however, remained relatively the same.

Analysis of vegetation data (Table 3) for random distribution (χ^2; $P < 0.01$) showed no species to be randomly distributed in the four zones in July. In October, however, *Acnida cannabina, Polygonum arifolium, Sagittaria latifolia,* and *Typha latifolia* were distributed randomly. Of these only *Polygonum arifolium* was a large component of the vegetation.

Transplant gardens—Data for all transplanted seedlings (Fig. 3), except *Impatiens capensis* which appeared not to transplant well, corresponds with habitat preference and survival noted in the field (Fig. 2; Table 3). *Acnida cannabina* survived best in MB sites; *Ambrosia trifida* and *Bidens laevis* in HM and MB sites, and *Polygonum punctatum* in GB and MB sites.

Flotation studies—The potential effectiveness of water dispersal varied with species (Fig. 4). For some, such as *Impatiens capensis* and *Bidens laevis,* a portion of the seed populations can apparently float indefinitely. Others, such as *Ambrosia trifida* and *Zizania aquatica* var. *aquatica,* did not float well, so that within 5 hr more than 70% of the seeds sank and all sank in 3 days. Over 80% of *Pilea pumila* seeds floated for 2 wk and then the numbers declined rapidly. Seeds of *Polygonum arifolium* did not float unless covered with the perianth, but when the perianth was present, a common occurrence in the field, seeds floated for up to 17 days. The perianth covering of *Polygonum punctatum* seeds also extended the duration of floating, but these smaller seeds were buoyant for some time even without the perianth.

DISCUSSION—Many species were widely distributed. In the seed bank study, 50% of the species were common to the four zones studied. In the field emergence study 77% were recorded

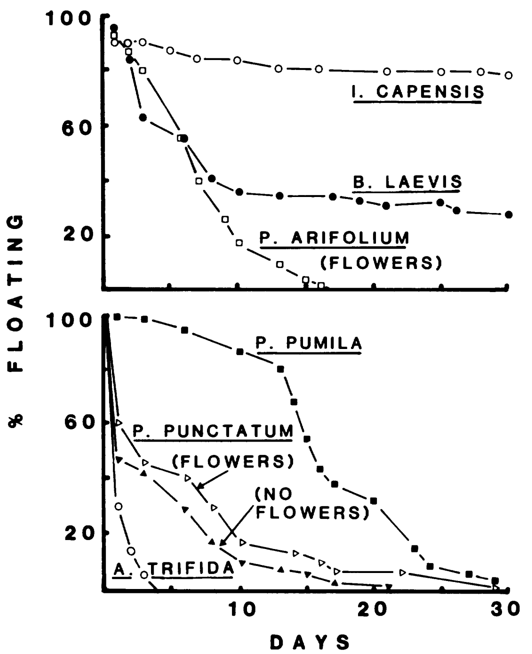

Fig. 4. Comparison of the flotation potential (percentage of seeds remaining afloat) for several dominant annual species. *Polygonum arifolium* seeds without perianth did not float.

in all zones. Vegetational analysis showed 58% of the species recorded to be present in all zones in July and 24% in October. Frequency of distribution and densities, however, varied from zone to zone. Density of seeds, seedlings, and mature plants varied with habitat, and survival of a species also varied from zone to zone (Fig. 2, 3; Table 4). The relationship of seed bank and field densities (Tables 1, 2) to flotability is not clear. Species, such as *Impatiens capensis, Bidens laevis,* and *Polygonum arifolium* with good flotation potential (Fig. 4) were found predominately (>55%) in the HM. *Polygonum punctatum* seeds, however, also had good dispersal potential (Fig. 4), but were found primarily in stream bank areas (SB, GB, MB) and not the HM. In contrast, *Pilea pumila* had good dispersal potential (Fig. 4), but seed densities were relatively evenly distributed (Table 1) and field germination frequencies were similar (Table 2). For those species with poor dispersal potential, such as *Zizania aquatica* var. *aquatica* (Rogosin, 1951) and *Ambrosia trifida* (Fig. 4), short distance dispersal could occur by toppling over of 3–4-m tall plants with attached seeds or by tidal movement of seeds or litter.

In all zones maximum field seedling numbers (Table 2) were less than comparable seed bank values (Table 1): 38% less in SB; 33% in GB; 46% in MB; and 10% in HM. The relatively high divergence in seed bank and field seedling densities for the stream bank zones suggests these sites were more stressful and that a given seedling had a greater probability of dying more quickly there than on the HM. Furthermore, a higher proportion of the total seed bank and field seedlings were found in the HM than in the stream bank sites, 37% and 46%, respectively. This contrasts with a salt marsh study which found greater seed bank and field seedling densities associated with areas of greater tidal activities, whether tidal front or along channels (Hopkins and Parker, 1984).

We feel that a combination of physical and biotic stress gradients, spatially inverse in intensity, has caused the vegetation patterns noted here. The daily tidal influx and efflux of water, especially marked along the stream channels, may be important in explaining the establishment and distribution in SB and GB zones. The physical action of tides can dislodge seedlings and prevent their establishment (Chapman, 1964; Wiehe, 1935). The duration, velocity, and depth of tidal water are much greater along the stream banks than on the high marsh, and are certainly the most significant influences on zonation pattern (Gosselink and Turner, 1978). Inundation has physiological impact and has been shown to be a key factor in the survival of plants in tidal salt marshes (Gray and Scott, 1967; Rozema and Blom, 1977; Mahall and Park, 1976b; Hopkins and Parker, 1984). In our study such influences were illustrated by transplanted seedlings and in field plots where individuals of different species varied in height, survival, and reproduction between zones (Fig. 2; Table 4; and pers. observ.). *Bidens laevis* individuals, for example, in stream bank habitats (field plots and transplants) remained small (<0.5 m) and had few flowers, a considerable contrast to vigorous plants (>1 m) with greater survival (Fig. 2, 3) and with many flowers on the HM (pers. observ.). This has also been found for *Ambrosia trifida* which flowered and set seed in only 3 of 8 transplant sites (Sickels and Simpson, 1983).

The HM is one of the most productive of all habitats with up to 2,300 g m^{-2} yr^{-1} (Whigham et al., 1978), mainly in aboveground biomass (Whigham and Simpson, 1978). Furthermore, as noted earlier, maximum seedling densities were much greater in the HM. This combination of high aboveground productivity and high seedling densities suggests intense biotic competition, and, in fact, plant density in the HM drops to values similar to the other zones by late summer (Fig. 2). The types of interactions on the HM are, no doubt, varied, but competition for space and light would quickly become limiting with the more vigorous seedlings or species having advantage. The dominant species (Fig. 2, Table 4) all may reach heights >2 m (McCormick, 1977) and limit light available to shorter species. The shading caused by high numbers of early germinating species (e.g., *Polygonum arifolium, Bidens laevis,* and *Impatiens capensis*) or those with large cotyledons (*Impatiens capensis* or *Ambrosia trifida*) could alter the light regime and prevent germination of other species (Smith, 1982). *Typha latifolia* germination, for example, is reduced at low light intensities (Sifton, 1959; Grace, 1983). Buttery and Lambert (1965) described a case of marsh zonation where the sharp transition seemed to result, in part, from light competition. Another type of interaction is possible, as potential for allelopathic interactions has been demonstrated for marsh species (McNaughton, 1968; Szczepańska, 1971; Bonasera, Lynch and Leck, 1979).

Because of differential establishment and survival, occurrence in the vegetation may greatly outweigh a species importance in the seed bank or even in the seedling stage. For example, *Ambrosia trifida* was not a sizable component of the seed bank (Table 1) or field seedling community (Table 2), but it was an important component of the vegetation in HM and MB sites (Table 3) and persistence values (Table 4) suggest that seedlings had great survival ability during intense density-dependent thinning. *Polygonum punctatum,* in contrast, was an important seed bank and field seedling component (Tables 1, 2), but its importance in the vegetation especially late in the season (Table 3) was suggestive of greater ability to survive physically stressful stream channel areas relative to other species. Not only could a given species survive best in a given zone or zones, but its importance relative to the rest of the vegetation could change with time (Tables 1–3). For example, *Zizania aquatica* var. *aquatica* was important mid-season (July), and *Bidens laevis, Polygonum arifolium, Polygonum punctatum, Ambrosia trifida,* and *Impatiens capensis* were dominant later (Table 3). While seasonal change in biomass and dominance has been documented (Whigham and Simpson, 1976), this study suggests that a complete understanding of vegetational dynamics of this annual dominated wetland must include consideration of the seed rain which determines the seed bank composition, proceed through the seed bank stage, a seedling community stage, and then through various stages of the established vegetation.

Although their seeds were numerous, annual species comprised only about half of the species recorded in the seed bank of each zone. The significance of the perennial component in the seed bank (Tables 1, 2), however, is not known; it is difficult at our present level of understanding to predict the course of vegetation change even of annuals. Some perennials, e.g., *Peltandra virginica, Sagittaria latifolia,* and *Nuphar advena,* are important components of the extant vegetation. Others, such as *Hibiscus palustris* and *Lythrum salicaria,* are not well represented in the portion of the Hamilton Marsh under study, but are important in other areas (Whigham and Simpson, 1975). Survival of the perennial seedlings also varies with zone. *Peltandra virginica* has widely distributed seeds, yet established plants are absent from stream banks and seedling mortality is high (Whigham, Simpson and Leck, 1979). Unfortunately, our data for perennials are limited. Numbers of germinating seeds (Table 1) were low, and field germination (Table 2) and survival (Fig. 2A) were poor. In contrast to most upland habitats where there is general lack of correspondence between the seed bank and the established vegetation (e.g., Major and Pyott, 1966; Livingston and Allessio, 1968; Kellman, 1970; Whipple, 1978; Thompson and Grime, 1979), most wetlands surveyed seem to possess seed banks which are reflective of the dominant surface vegetation (van der Valk and Davis, 1978; Leck and Graveline, 1979; Thompson and Grime, 1979; van der Valk, 1981; Hopkins and Parker, 1984) although certain common species may be missing. This study, which sampled seed banks in relation to observed well-defined zonation patterns along a stream channel, corroborates an earlier study by Leck and Graveline (1979) that the seed banks of specific zones reflect the dominant vegetation of those zones despite the high flotation and dispersal potential of many species (Fig. 4). Keddy and Reznicek (1982) found that with a few exceptions the relationship of the seed bank along a lake edge to the previous vegetation at a given site indicated considerable seed deposition in situ although there was evidence of limited input from other communities. In this freshwater tidal wetland, the seed bank and the previous year's vegetation were also similar, and limited input from other communities also occurred (e.g., *Paulownia tomentosa* from a nearby hillside).

A number of studies (van der Valk and Davis, 1976, 1978, 1979; van der Valk, 1981; Keddy and Reznicek, 1982) have shown that in wetlands which experience occasional drawdown and fluctuating water levels, the seed banks contain propagules of species which can colonize following change in water level. The preservation of seeds in seed banks allows the regeneration of various stages and is the key to the dynamics of cyclic vegetational change (van der Valk and Davis, 1978, 1979) and the preservation of a specific floral component (Keddy and Reznicek, 1982). However, in our study and that of Leck and Graveline (1979), the large annual component of the seed bank is the key to yearly regeneration of the annual-dominated vegetation.

As noted earlier, this freshwater tidal wetland is characterized by strong physical and biotic stress gradients that clearly influence the vegetation. Dispersal potential, seed bank availability, establishment, and persistence appear to dictate the spatial and temporal distribution patterns observed here. However, the details of this interaction must await detailed studies of species life histories.

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