WETLANDS, Vol. 16, No. 2, June 1996, pp. 208–218

ESTABLISHMENT, PERSISTENCE, AND MANAGEMENT IMPLICATIONS OF EXPERIMENTAL WETLAND PLANT COMMUNITIES

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Abstract: We inoculated 120 wetland microcosms representing 24 different environmental treatments with seeds from a carefully chosen pool of 20 wetland plant species. The treatments were chosen to represent a variety of riverine and lacustrine wetlands, including those with slow-growing, rare species. In the first season, an annual (*Bidens cernua*) was most abundant in all the microcosms. Both flooding and high fertility negatively effected the other species establishment. Short-term information about establishment was not predictive of longer-term trends. After 5 years, most of the microcosms became dominated by *Lythrum salicaria* and, when this occurred, other dicot species were extirpated. After 5 years, flooding and fertility remained the main factors affecting species composition in the microcosms. *Lythrum* establishment (and dominance) was minimal when fertility was low and when the microcosms were seasonally flooded. Establishment and growth of *Typha angustifolia* was poor, and this was attributed to coarse substrate. These results suggest possible measures to minimize the growth of unwanted plant species in created or restored wetlands. Our results also suggest that high diversity, low biomass wetlands will be difficult to create; therefore, protection of such wetlands may deserve a higher priority.

Key Words: cattails, establishment, fertility, *Lythrum*, microcosms, water level fluctuation, wetlands

INTRODUCTION

The general importance of seed banks in wetland regeneration is now well established (van der Valk 1981, Keddy and Reznicek 1986, Leck 1989, Wilson et al. 1993). However, the manner in which different sets of environmental factors can constrain vegetation development from seed banks is poorly understood. We know that a wide range of environmental factors can conceivably affect germination. These include soil texture (Keddy and Constabel 1986), litter (van der Valk 1986), moisture (van der Valk 1981, Keddy and Ellis 1985), and burial by sediment (van der Valk et al. 1983). In this experiment, we explore the impacts of combinations of these and other factors in establishment of species from a known seed bank.

We have assembled a known seed bank and allowed it to establish in 24 different controlled and replicated treatments. The experiment was conducted in order to observe how the assembly of wetland plant communities was affected by environmental conditions. The treatments were chosen to represent a variety of riverine and lacustrine wetlands, including those with slow-growing, rare species. In this paper, we focus on three key issues: (1) What were the general effects of the treatments on seedling establishment in the first year? (2) Are the effects on establishment useful predictors of trends over a longer time period (5 years)? (3) What are the management implications of these observations?

METHODS

The experimental conditions were chosen in order to approximate the variation in northeastern temperate riverine and lacustrine wetlands. The wetlands found along the Ottawa River (in eastern Ontario, Canada) and described by Day et al. (1988) were used as a model for choosing species and treatment levels. Day et al. (1988) found that the main factors affecting community structure were water depth, litter, and fertility. Ottawa River wetlands vary from highly productive cattail marshes to wave- and ice-disturbed sand beaches. The sand beaches are highly diverse and support a rich array of life-forms (e.g., evergreen isoetids, tussock-forming sedges, interstitial dicots, grasses, and annuals). Oligotrophic river and lakeshores with pronounced water-level fluctuations can also support coastal plain plants, many of which are rare (Keddy 1981, Hill and Keddy 1992). Intermediate to these ex-

Table 1. Species list, functional types, numbers of seeds per microcosm, germination rate in the laboratory, and mean cover in year 5. Species names as in Gleason and Cronquist (1963) except *E. smallii* Britton and *X. difformis* Chapm.

Species	Functional Type[1]	Number of Seeds in Seed Mixture[2]	Germ. Rate in Growth Chamber (%)	Mean % Cover in Year 5
Acorus calamus L.	tussock	100	87	<0.02
Aster nemoralis Ait.	stress tolerator	50	50	0
Bidens cernua L.	obligate annual	100	95	6.96
Carex crinita Lam.	tussock	50	80	35.36
Eleocharis smallii Britton	reed	50	5	37.4
Epilobium ciliatum Raf.	facultative annual	100	100	0.28
Eupatorium perfoliatum L.	facultative annual	100	80	0.38
Glyceria canadensis (Michx.) Trin.	clonal dominant/tussock	100	85	13.3
Gnaphalium uliginosum L.	obligate annual	100	50	0
Hypericum ellipticum Hook.	interstitial clonal	100	100	0
Juncus filiformis L.	reed	100	100	3.02
Lythrum salicaria L.[3]	facultative annual	100	100	190.16
Myrica gale L.	shrub	50	80	0
Panicum longifolium Torr.	reed	50	35	0
Penthorum sedoides L.	interstitial clonal	100	70	0.12
Rumex verticillatus L.	tussock	50	67	<0.02
Scirpus acutus Muhl.	clonal dominant	100	83	24.38
Typha angustifolia L.	clonal dominant	100	75	2.84
Verbena hastata L.	facultative annual	100	90	<0.02
Xyris difformis Chapm.	stress tolerator	100	85	0

[1] Functional types from Boutin and Keddy 1993.
[2] Amount of seed per species was determined by availability.
[3] Non-native species.

tremes are wet meadows, which may be dominated by monocots (e.g., *Eleocharis smallii, Carex crinita*) or by *Lythrum salicaria.*

Seed Mixture

Seeds from 91 candidate species were screened for viability. From this group, 20 species were carefully chosen to represent the range of morphologies and life history types found in eastern temperate riverine and lacustrine wetlands (see Table 1 for a species list). The seeds were collected over a 3-year period from eight wetlands in Ontario and one in Nova Scotia. Seeds were stored in the dark at 4°C in wet sand. Because the seeds had been stored, they were screened for viability. The purpose of testing for viability was to ensure that the seeds were not all dead; it was not done to estimate seed germination in the experiment. Viability screening occurred in a growth chamber with 12 hr/12 hr photoperiod, at 25°C day and 15°C night temperatures ($n=100$). Species with less than 20% germination were excluded from further consideration, except *Eleocharis smallii.* Although its germination rate was low, this species was included because it is very common. Seeds were counted into uniform lots of seed mixture (Table 1).

General Growth Conditions

The seed mixture was sown onto 120 microcosm containers in June, 1987 and was grown in an outdoor garden for five years. There were 12 general treatments repeated at two fertility levels. A randomized block design was used with 5 replicates. Each container was 63 by 42 cm (internal dimensions) in area, 26 cm high, with 13 cm washed (non-sterile) concrete sand (nominal particle size 0.6 mm, range 0.075–6 mm, approximately 60% quartz, 20% feldspar, 20% others including carbonates). The size of the container corresponds to the standard quadrat size used in taking field observations (Day et al. 1988). Wetland soils along the Ottawa River average about 80% sand and less than 6% organic matter (Day et al. 1988), making sand a reasonable and pragmatic choice for a substrate. The containers were placed on plastic sheeting to minimize unwanted weed growth in the outdoor compound at Carleton University (Ottawa, Canada 45° 25′ N, 75° 45′ W). Within each block, the containers were placed in a double row 40 cm apart, and blocks were separated by 150 cm. The containers were watered with municipal tap water. Drain holes were used to adjust water level. For overwintering, the containers were flooded to 10 cm above the soil surface.

Experimental Treatments

The microcosms were fertilized at two levels that we refer to as "fertile" and "infertile." Two liquid (hydroponic) fertilizers were used for both treatments (B and B Hydroponics). Part 1 (15-0-0) contained, by weight, Ca (19%), N (as nitrate 15%), and Mg (3.98%). Part 2 (7-11-27) contained, by weight, N (7%), Mg (3.75%), P (11%), K (27%), S (4.8%), Fe (0.1%), Mn (0.085%), Zn (0.03%), B (0.027%), Cu (0.0041%), and Mb (0.009%). The two fertilizers were mixed in equal proportions. The fertile treatments received an initial soil P concentration of about 19 μg P g^{-1} soil. This value is about twice the mean soil P in the fertile wetlands described by Day et al. (1988), but it is less than the maximum found. Fertilization occurred every three weeks during the growing season to give an annual P loading rate of 8.21 g P yr^{-1} $container^{-1}$. The infertile treatments received the same fertilizer at 1/16 the concentration of the fertile treatments; therefore, soil P was initially about 1 μg P g^{-1} soil, and annual P loading was 0.51 g P yr^{-1}.

Six habitat variables were manipulated; each is known to affect the distribution of wetland plant species. The treatment levels were carefully chosen based partly on the observed variation described by Day et al. (1988) and on the constraints imposed by working with containers in a garden setting. Decisions regarding treatments and their levels were made based on three simple conceptual goals: (1) to recreate a diversity of wetland conditions that correspond to real gradients found in nature, (2) to set the levels of each treatment toward the ends of the observed gradients, and (3) to recognize the logistical limitations of a semi-controlled experiment (e.g., sand rather than deseeded wetland soil, discreet treatment levels, balancing replication with diversity of treatments).

The experiment was designed to model the development (assembly) of wetland plant communities in different kinds of wetland habitat. Strictly speaking, rather than modeling several environmentally distinct wetlands, the experiment was more similar to a single created wetland or wetland complex with many environmentally distinct microhabitats. The distinction is largely due to the constraint of having a single garden for experimentation and the possibility of cross-inoculation of the microcosms after year one. This aspect of the design adds reality to the experiment, as real wetlands are not absolutely insular.

Six main factors were included in the experiment. Water depth was included because it is a fundamental determinant of wetland community structure (see also Hutchinson 1975, Spence 1982, Day et al. 1988). Seasonal fluctuation in water depth was included because it can also strongly affect wetland community structure (van der Valk 1981, Keddy and Reznicek 1986, Keddy 1991, Hill and Keddy 1992). Leaf litter is known to affect seed germination and establishment in wetlands (van der Valk 1981) and can affect community structure (Day et al. 1988). Similarly, soil surface texture can also affect seed germination and establishment (Keddy and Constabel 1986), and some rare species are associated with gravel or cobble shorelines (Moore et al. 1989). The timing of the start of the experiment was altered because little is known about how small changes in the timing of disturbances or flooding events might alter communities. Lastly, invasion of communities by a large clonal species (cattail) was also included.

Five water level regimes were employed as treatments: (1) water level was maintained at 5 cm below the soil surface (Low); (2) water level was maintained at the soil surface (control); (3) water level was maintained at 5 cm above the soil surface (High); (4) water level was held 5 cm above the soil surface until mid-July when it was lowered to the soil surface (High/0); and (5) water level was held 5 cm above the soil surface until mid-July when it was lowered to 10 cm below the soil surface (High/Low). For all other treatment factors, the water level was held constant at the soil surface.

Leaf litter was added at a high level (LITTER, 150 g $container^{-1}$ or 1.5 cm) and at a low level (Litter, 50 g $container^{-1}$ or 0.5 cm). Along the Ottawa River, mean leaf litter is about 40 g per 0.25 m^2 and ranges from 0 to 320 g. Leaf litter was collected just before the experiment commenced (mainly *Scirpus fluviatilis*, with some *S. americanus*, *Eleocharis smallii*, and *Typha angustifolia*). To alter soil surface texture, small pebbles (0.5 to 1.25 cm in diameter) were added to a uniform depth of 1.25 cm (Pebbles), or a single layer of larger rocks (2.5 to 7.5 cm in diameter) was added (Cobbles). We altered the length of the initial growing season by delaying seed inoculation, where the seeds were added two weeks after the other treatments (+14 days) or four weeks later (+28 days). In order to simulate the successful invasion of a large clonal species, *Typha* ramets were added in the spring of the second year. Four ramets, each with one shoot and approximately 10 cm of rhizome were placed in the corners of the containers. Note that in the first year this treatment was identical to the control (*Typha*).

Each of these 12 treatments were grown at the two fertility levels and replicated five times. The treatments

Table 2. The dominant and co-dominant species in each treatment in year 1 (mean percent cover values are shown in parentheses, the range of values is shown in subscript). Co-dominants are shown if cover was at least one in one of the containers. The treatments were ordered according to the classification shown in Figure 1. Note: F = Fertile, I = Infertile, p = present but not touched by a sampling rod.

Treatment	Dominant	Co-dominant	Co-dominant
Flooded			
High Water–F	*Bidens* (185.2_{44-312})	—	—
High Water–I	*Bidens* (12.8_{10-20})	—	—
High/0–F	*Bidens* ($181.6_{118-318}$)	—	—
High/Low–F	*Bidens* (160.4_{18-264})	*Rumex* (0.4_{p-2})	—
High/0–I	*Bidens* (6.8_{4-10})	—	—
High/Low–I	*Bidens* (8.8_{6-14})	*Glyceria* (0.4_{p-2})	—
Not Flooded			
Fertile			
LITTER–F	*Bidens* (92.4_{0-254})	*Epilobium* (44.8_{16-66})	*Rumex* (26.0_{6-86})
Cobbles–F	*Bidens* ($200.0_{118-276}$)	*Verbena* (96.4_{62-142})	*Lythrum* (28.8_{14-52})
Pebbles–F	*Bidens* (164.8_{46-282})	*Rumex* (32.4_{2-86})	*Lythrum* (25.6_{4-50})
Litter–F	*Bidens* (219.2_{6-392})	*Epilobium* (56.4_{4-212})	*Rumex* (39.6_{6-104})
(Typha)–F	*Bidens* (192.0_{94-398})	*Lythrum* (41.6_{6-116})	*Epilobium* (24.4_{8-36})
LITTER–I	*Bidens* (1.6_{0-6})	*Rumex* (1.2_{0-4})	*Carex* (1.2_{0-4})
+14 days–F	*Bidens* (157.6_{14-224})	*Lythrum* (15.2_{p-52})	*Rumex* (12.0_{p-56})
Low–F	*Bidens* (69.2_{32-104})	*Lythrum* (42.0_{12-76})	*Verbena* (31.6_{2-74})
Control–F	*Bidens* ($306.8_{232-390}$)	*Lythrum* (24.4_{12-32})	*Verbena* (21.6_{2-50})
Infertile			
+14 days–I	*Bidens* (3.6_{2-6})	*Epilobium* (0.8_{p-2})	3 spp. (0.4)
Pebbles–I	*Bidens* (3.6_{2-4})	*Verbena* (3.2_{p-6})	*Carex* (0.8_{p-2})
+28 days–I	*Bidens* (4.0_{2-8})	*Rumex* (1.2_{p-4})	3 spp. (0.4_{p-2})
Low–I	*Bidens* (2.8_{p-6})	3 spp. (0.8_{0-4})	—
Control–I	*Bidens* (3.6_{p-6})	*Rumex* (1.2_{p-4})	*Verbena* (1.2_{p-2})
(Typha)–I	*Bidens* (3.2_{2-6})	*Verbena* (1.2_{p-4})	*Carex* (0.8_{p-2})
Cobbles–I	*Bidens* (3.2_{2-6})	*Rumex* (2.0_{p-4})	*Verbena* (1.6_{p-4})
Litter–I	*Bidens* (3.2_{p-6})	*Carex* (2.0_{p-6})	2 spp. (1.6_{0-4})
+28 days–F	*Bidens* (29.6_{12-60})	*Verbena* (10.0_{4-16})	*Lythrum* (6.8_{2-14})

with water level at the soil surface (with no other modification) can be considered as shared controls because they represent a common reference point to which all the other treatments can be compared. The design can therefore be considered as series of six factorial designs (with factors: water level, water-level fluctuation, litter, surface texture, starting date, and *Typha* addition each crossed with fertility) (Manly 1992a).

A non-destructive point sampling technique was used to survey the plant assemblage in the late summer of each year. A gridded quadrat was placed over the whole microcosm and was used to drop 50 small rods into the container in a uniform pattern. The total number of contacts for each species was used to measure percent cover (percent cover for species $i = 2 \sum_{n=1}^{50}$ (no. of times species i touched rod n)) (Kershaw 1973, Mueller-Dombois and Ellenberg 1974). Because each species can touch a rod more than once, the procedure is synonymous with "cover repetition" (Goodall 1952). Although cover repetition also tends to be correlated with yield and biomass, such relationships vary with taxa and environment (Mueller-Dombois and Ellenberg 1974).

We have presented our data as two dependent variables: percent cover and incidence (from presence/absence data). Both variables are important. Cover information provides a picture of the plant assemblage based on the dominant species. Incidence is the number of microcosms in which each species was able to become established; therefore, low incidence scores mean low establishment and low diversity.

SYSTAT was used to classify the treatments using unweighted pair-group mean averaging of Euclidean distances from incidence data that will be presented in Table 3. Manly's program RT (Randomization Testing, Manly 1992b) was used to test for differences in mean species richness in the flooded vs. non-flooded treatments. The test is equivalent to a t test. The program uses Monte Carlo methods to compute exact probabilities; we used 20,000 randomizations for each test. Manly's RT was also used to test for differences between the mean number of species in the non-flooded

Table 3. Species incidence in year 1. Incidence is the number of microcosms in which each species was able to establish (5 replicate microcosms per treatment). Treatments were ordered according to the classification in Figure 1.

	Acorus	*Aster*	*Bidens*	*Carex*	*Eleocharis*	*Epilobium*	*Eupatorium*	*Glyceria*	*Gnaphalium*	*Hypericum*	*Juncus*	*Lythrum*	*Myrica*	*Panicum*	*Penthorum*	*Rumex*	*Scirpus*	*Typha*	*Verbena*	*Xyris*
Flooded																				
High–F	0	0	5	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
High–I	0	0	5	1	4	0	0	2	0	0	0	0	0	0	0	1	0	2	0	0
High/0–F	0	1	5	0	4	0	0	2	0	0	1	0	0	0	1	5	1	1	0	0
High/Low–F	0	1	5	0	3	0	0	2	0	0	3	0	0	0	0	5	3	0	0	0
High/0–I	3	0	5	1	4	0	0	4	0	0	2	0	0	0	0	3	0	2	0	0
High/Low–I	5	0	5	0	3	0	0	5	0	0	0	0	0	1	0	4	1	2	0	0
Not Flooded																				
Fertile																				
LITTER–F	2	0	3	4	1	5	3	5	1	0	0	1	0	0	0	5	5	1	5	0
Cobbles–F	3	0	5	4	2	5	5	5	3	0	0	5	0	0	3	5	5	0	5	0
Pebbles–F	3	0	5	4	2	5	3	5	1	2	1	5	0	0	3	5	5	0	5	0
Litter–F	1	0	5	3	0	5	3	5	2	2	0	5	0	0	3	5	5	1	5	0
(Typha)–F	1	1	5	2	2	5	4	4	3	2	0	5	0	1	1	4	5	1	5	0
LITTER-I	2	1	4	4	4	5	3	5	1	2	0	4	3	0	2	4	5	2	5	0
+14 days–F	4	1	5	3	4	5	4	5	4	3	2	5	1	1	3	5	5	3	5	0
Low–F	4	1	5	4	1	5	4	5	5	4	3	5	0	1	3	5	5	2	5	2
Control–F	2	0	5	3	1	5	5	5	4	5	1	5	0	1	3	4	5	1	5	0
Infertile																				
+14 days–I	5	1	5	5	4	5	2	5	3	0	1	5	0	2	5	2	5	2	5	1
Pebbles–I	5	2	4	5	5	3	3	5	3	1	1	5	2	5	2	5	5	0	5	0
+28 days–I	5	0	5	4	4	4	4	5	5	1	1	4	2	2	1	5	5	5	5	0
Low–I	5	1	5	5	4	5	5	4	5	0	0	5	4	4	3	5	5	5	5	0
Control–I	4	3	5	5	5	5	4	5	4	0	2	5	3	3	3	5	5	5	5	0
(Typha)–I	4	2	5	5	4	5	5	5	4	2	1	5	3	1	4	4	4	5	5	2
Cobbles–I	4	2	5	5	4	5	4	4	5	1	0	5	3	2	4	5	4	3	5	3
Litter–I	4	1	5	5	5	4	5	5	4	2	1	5	5	5	4	3	5	4	5	1
+28 days–F	5	2	5	3	5	5	3	5	5	4	3	5	2	3	4	3	5	5	5	3

fertile treatments as compared to the non-flooded infertile treatments. Sigmastat (Jandel Corp.) was used to perform a Chi-squared test to check if the number of times species were able to establish was dependent on fertility level. Similarly, species were grouped as monocots and dicots, and the Chi-squared test was repeated. In order to test if fertility affected individual species incidences of establishment, Manly's RT was used to perform a Monte Carlo t test. A Pearson product-moment correlation was computed between species total incidence (number of occurrences) in year 1 and year 5 using Sigmastat.

RESULTS

Species Establishment

After one season, *Bidens cernua* was the dominant species in every treatment (Table 2). At high fertility, several other dicots also often had relatively high cover (*Epilobium ciliatum, Rumex verticillatus, Lythrum salicaria, Verbena hastata*), while monocots tended to have low cover values. Many species had negligible cover but were present. As might be expected, low fertility brought about a nearly uniform reduction in mean cover of *Bidens.*

Species incidence is shown in Table 3 in order to show the number of times each species became established in each treatment. Table 3 was used to compute a classification to show the relative similarities in how the treatments affected species establishment (Figure 1). The strongest effects on establishment occurred in the flooded treatments, where many species were unable to become established (Table 3). Establishment was lower in the flooded treatments (testing mean species richness in the flooded vs. non-flooded treatments, difference between the means = 9.06, $p < 0.0001$). After flooding, fertility showed the strongest effects. This was due to lower establishment (species richness) at high fertility, as the mean number of species in the non-flooded, fertile treatments was less than the mean number of species in the non-flooded, infertile treatments (difference between the means = 2.37, $p = 0.0114$). At high fertility, several soil texture treatments (Cobbles, Pebbles, Litter) also formed a small group (Figure 1).

Within the different flooding treatments, constant high water of only 5 cm effectively inhibited the establishment of most species; only *Bidens* prospered. When flooding was restricted to the early summer (High/0, High/Low), an additional group of species became established (*Rumex, Glyceria canadensis,* and to some extent *Juncus filiformis* and *Acorus calamus*), but none of these species were abundant. Even within the fluctuating water-level treatments, the effects of fertility were evident, as the infertile treatments formed a group that was different from the other high water treatments (Figure 1). Here, *Acorus* and *Typha angustifolia* had higher establishment at low fertility, while *Scirpus acutus* preferred high fertility (Table 3).

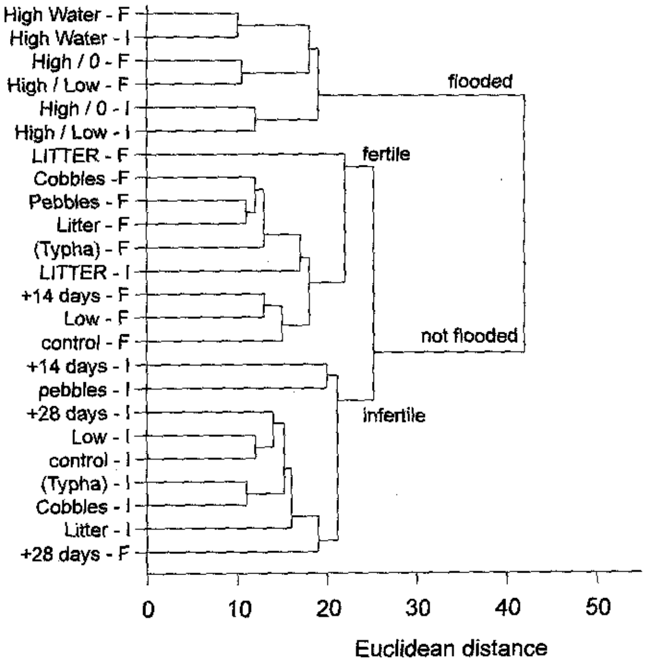

Figure 1. Classification of the treatments by UPGMA of Euclidean distances, the data is shown in Table 3. Treatments within branches tend to effect species establishment similarly.

Within the unflooded groups in the classification, only two fertility treatments were misaligned (Figure 1). High litter (but low fertility) apparently caused similar effects on species establishment (in terms of presence and absence) as did high fertility. Its average species richness was 10.8, which was lower than any other low fertility, unflooded treatments. The fertile +28 day treatment had total species incidence and average diversity that was more similar to the infertile treatments, and in fact, it had the highest average diversity (16.0) of any treatment. The shorter growing season apparently allowed more species to coexist in the first year.

In general, most species had higher establishment (incidence) at low fertility, but there were notable exceptions. The species varied in their relative abilities to establish at the two fertility levels ($X^2 = 52.052$, $p < 0.001$, d.f. = 19, when testing if species incidence was independent of fertility level). Three species that showed nearly uniform establishment were also nearly ubiquitous among the microcosms (*Bidens, Lythrum, Verbena*). One species (*Hypericum ellipticum*) tended to have higher establishment in the fertile treatments, but the pattern was not significant (Monte Carlo com-

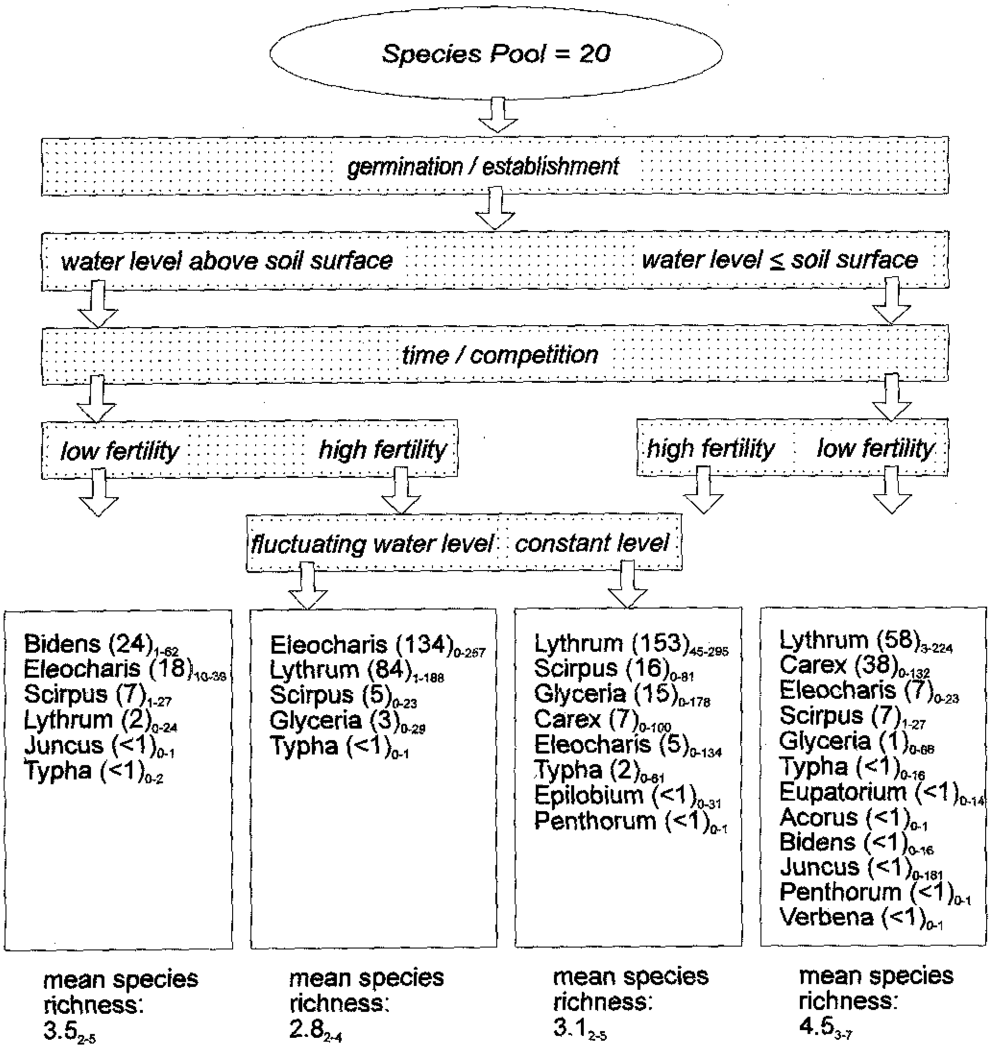

Figure 2. The major community types after five years (mean percent cover values are shown in parentheses, with the range of values shown as subscript) and the major factors associated with their development (adapted from Weiher and Keddy 1995). Each of the five factors can be thought of as a filter that removes species or alters abundances. Note the common control treatments (constant water at the soil surface, sand) are included in the two communities on the right.

parison of means, $p = 0.152$, Manly 1992b). Two others showed widely varying responses to fertility and had no clear pattern (*Eupatorium perfoliatum, Juncus filiformis*). Monocots did not differ from dicots in terms of apparent fertility preference ($X^2 = 3.453$, $p = 0.178$, d.f. = 2, testing if total incidence of monocots and dicots was independent of fertility level).

Establishment Versus Persistence

One critical point for long-term prediction and management is the degree to which year one establishment controls later vegetation composition. The microcosms were therefore allowed to grow for five years. In year five, the species assemblages had converged on four main community types that corresponded to combinations of flooding and fertility. Figure 2 graphically shows species mean cover and the major factors that gave rise to the different community types, while Table 4 shows the mean percent cover values for the most abundant species in each treatment in year 5. The factors in Figure 2 are arranged in order of importance in determining community assembly and are not arranged to simply maximize parsimony. Water levels have a strong effect on establishment and on initial community trajectory. However, early differences can be overcome through fertilization. Treatments with constant high water and high fertility eventually converged with microcosms with low water levels and high fertility (Figure 2, center). More specifically, most of the microcosms became dominated by *Lythrum* (Table 4). Early dominance by *Bidens* was generally not sus-

Table 4. The dominant and co-dominant species in each treatment in year 5 (mean percent cover values are shown in parentheses, the range of values is shown in subscript). Co-dominants are shown if cover was at least one in three of the containers. The treatments were ordered according to the classification shown in Figure 1. Note: F = Fertile, I = Infertile, p = present but not touched by a sampling rod.

Treatment	Dominant	Co-dominant	Co-dominant
Flooded			
High Water–F	*Lythrum* ($371.6_{302-590}$)	*Scirpus* (66.0_{0-162})	*Bidens* (12.0_{0-32})
High Water–I	*Bidens* (24.0_{p-52})	*Eleocharis* (18.8_{0-48})	*Scirpus* (16.4_{0-36})
High/0–F	*Eleocharis* (272.8_{0-514})	*Lythrum* (155.6_{p-376})	—
High/Low–F	*Eleocharis* (266.4_{66-558})	*Lythrum* (182.0_{10-342})	*Scirpus* (11.2_{0-19})
High/0–I	*Bidens* (62_{22-122})	*Eleocharis* (41.2_{20-78})	*Scirpus* (19.2_{p-54})
High/Low–I	*Bidens* (57.2_{p-128})	*Eleocharis* (50.4_{36-68})	*Lythrum* (13.2_{0-48})
Not Flooded			
Fertile			
LITTER–F	*Lythrum* ($256.4_{178-370}$)	*Carex* (70.6_{0-182})	*Scirpus* (24.8_{10-32})
Cobbles–F	*Lythrum* ($277.2_{160-366}$)	*Carex* (39.2_{0-152})	*Scirpus* (37.6_{12-66})
Pebbles–F	*Lythrum* ($328.8_{190-456}$)	*Glyceria* (110.8_{0-356})	*Scirpus* (20.4_{4-50})
Litter–F	*Lythrum* ($310.0_{204-510}$)	*Scirpus* (71.2_{16-126})	—
(Typha)–F	*Lythrum* (228.0_{90-314})	*Typha* (43.6_{16-122})	*Scirpus* (20.8_{0-80})
LITTER–I	*Lythrum* (140.0_{40-218})	*Carex* (70.6_{0-182})	*Scirpus* (24.8_{10-32})
+14 days–F	*Lythrum* ($355.6_{134-538}$)	*Scirpus* (31.2_{0-74})	—
Low–F	*Lythrum* ($340.8_{232-436}$)	*Scirpus* (31.2_{6-50})	*Carex* (17.2_{0-64})
Control–F	*Lythrum* ($326.4_{198-490}$)	*Scirpus* (50.4_{30-86})	—
Infertile			
+14 days–I	*Lythrum* (107.6_{8-196})	*Carex* (94.8_{26-222})	*Scirpus* (23.6_{0-54})
Pebbles–I	*Lythrum* ($152.0_{132-164}$)	*Carex* (63.0_{48-72})	*Scirpus* (18.5_{12-26})
+28 days–I	*Lythrum* (62.4_{36-86})	*Eleocharis* (24.8_{14-46})	*Scirpus* (18.4_{8-34})
Low–I	*Lythrum* (199.6_{62-448})	*Carex* (112.8_{0-216})	*Eleocharis* (7.6_{p-22})
Control–I	*Lythrum* (62.0_{6-124})	*Carex* (56.4_{2-134})	*Scirpus* (23.2_{4-32})
(Typha)–I	*Lythrum* (99.2_{62-136})	*Carex* (22.8_{2-38})	*Typha* (15.2_{4-32})
Cobbles–I	*Lythrum* (128.4_{82-198})	*Carex* (123.2_{0-264})	*Eleocharis* (24.8_{10-36})
Litter–I	*Lythrum* (116.8_{20-242})	*Carex* (110.0_{26-218})	*Eleocharis* (12.4_{6-28})
+28 days–F	*Lythrum* ($349.2_{270-398}$)	*Eleocharis* (24.4_{0-98})	*Scirpus* (20.4_{6-48})

tained over the course of five years growth, except in the infertile and flooded treatments. The changes in dominance that occurred over time imply that information about establishment was generally unreliable for longer-term predictions.

In year 5, 13 species were present in at least one microcosm; however, only 7 were present with cover values large enough to be classified as dominant or co-dominant (Table 4). Of these, *Typha* was a co-dominant only where it was planted as ramets. While *Typha* was often present in other microcosms, its cover was low. Even though *Lythrum* was, on average, the dominant species for many treatments, at low fertility there were several instances where *Carex* was most abundant (e.g., within the Litter-I and +14 day-I groups).

When the species are grouped by simple functional groups (monocots, dicots, and *Lythrum*) and plotted over five years, the decline of dicots appears to be linked with the spread of *Lythrum* and monocots (Figure 3). Where water levels were kept at the soil surface, early dominance by mixed dicots (mostly *Bidens*) gave way to monocots and *Lythrum*. *Lythrum* dominance occurred quickly in the fertile treatments, while at low fertility, *Lythrum* or *Carex* became most abundant. In both cases, the dicots other than *Lythrum* were all extirpated by year 5. In the fluctuating water-depth treatment (High/0) with low fertility, *Lythrum* establishment was poor and remained so throughout the experiment. In the near absence of *Lythrum* and without extremely large numbers of monocots (mostly *Eleocharis*), *Bidens* remained as a codominant species. At higher fertility, *Bidens* (and *Rumex*) sharply declined in year 4, and they were extirpated by year 5. This coincided with the spread of *Eleocharis* and *Lythrum*. *Lythrum* was likely released from suppression by soil accretion. By the end of the experiment we could see that litter accumulation had made the 5-cm flooding negligible, so that water levels remained at or below the soil surface.

The weak correlation between species incidence in year 1 and incidence after five years was not signifi-

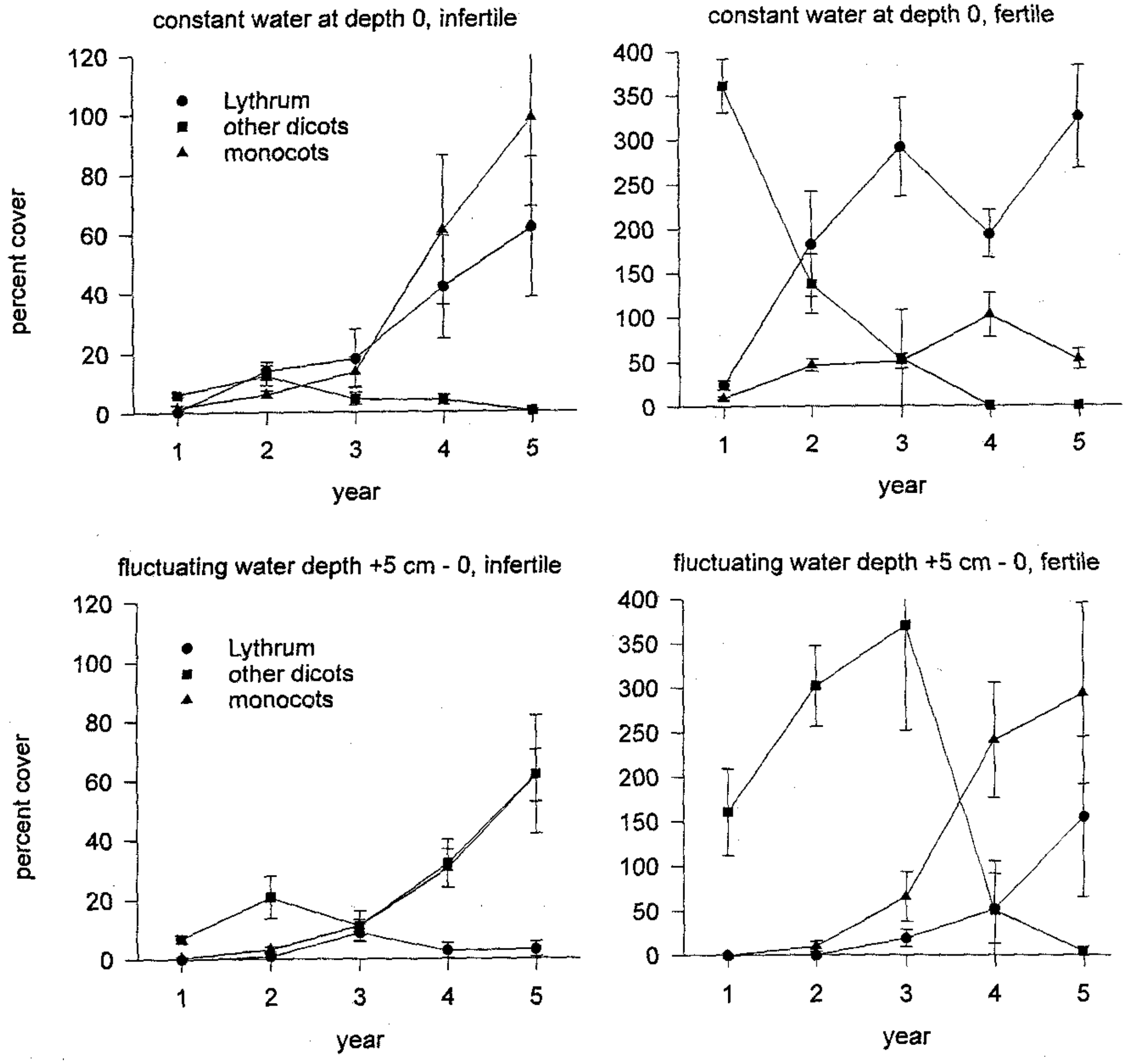

Figure 3. Percent cover (± standard error) of functional groups of species versus time. Note that cover scales for the fertile and infertile treatments are not equal.

cant (Figure 4). The majority of species declined precipitously, and many were extirpated from the experiment. Only three species increased in incidence after year 1, and we cannot know if this was due to longevity in the seed bank or due to cross-inoculation of the microcosm containers. The experimental containers were open systems, and it would have been unrealistic to cover them and stop birds and frogs from visiting.

In all treatments other than flooded with low fertility, *Lythrum* was present. Conversely, *Scirpus* expanded to more flooded microcosms. None of the species that had low incidence in the first year increased with time. There were, however, some apparent early successional species that did well in the first year but did not persist. Among these, *Rumex, Verbena,* and *Epilobium* showed the most striking declines. Similarly, *Acorus, Eupatorium, Gnaphalium,* and *Penthorum* may also be considered as early successionals. Nearly all of these species are dicots. While the dicots declined, *Lythrum* and several monocots persisted.

DISCUSSION

Short-term information about establishment was not predictive of longer-term trends in these wetland mi-

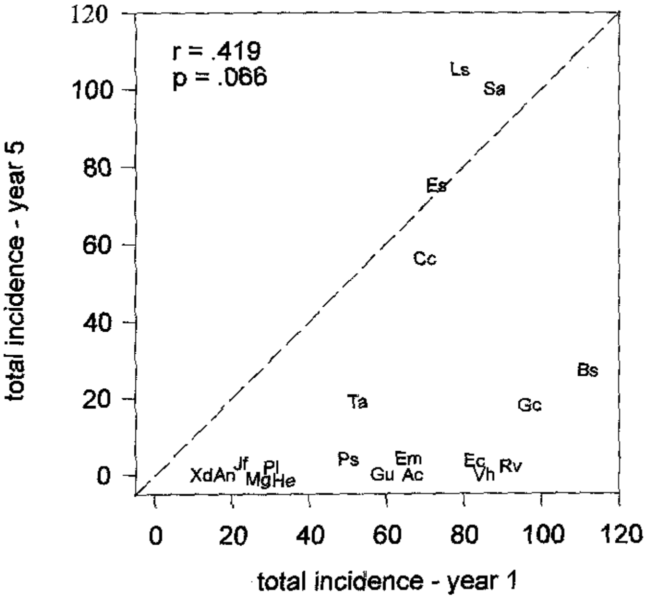

Figure 4. The total incidence for each species (number of microcosms where present) in year 5 plotted as a function of total incidence in year 1. The dashed line represents no net change over the course of the experiment. Codes for species are abbreviations based on genus and species names, see Table 1 for complete species names. Pearson product-moment correlation (r) and significance level are shown.

crocosms. Over the course of the experiment, early successional species either declined in numbers or were extirpated, leaving only a few species to dominate in most of the microcosms. The final assemblages were relatively similar, with *Lythrum* often dominating. This suggests that for the species pool and range of conditions used, there is one strong "attractor" to which the assemblages are drawn. Therefore, it may be unlikely that stochastic founder effects are of overriding importance in temperate riverine wetland plant assemblages. Furthermore, if the strong attractor for *Lythrum* dominance is more generally applicable, then it may be exceedingly difficult to create wetlands that are free of *Lythrum* dominance, given its capacity for producing large numbers of small seeds (Thompson et al. 1987).

This experiment also points out several potential lessons about creating, managing, and restoring wetlands.

1. *Lythrum* (purple loosestrife) establishment may be greatly reduced with flooding to a depth of only 5 cm, although this may also restrict establishment of other taxa. No other factors successfully controlled *Lythrum* establishment. Annual flooding of only 5 cm inhibited *Lythrum* establishment for 5 years when fertility was low. In the high fertility treatments, *Lythrum* establishment was also low for the first several years, but the inhibition was broken, apparently due to soil accretion. Therefore consistent spring and early summer flooding can inhibit *Lythrum* establishment even where soil fertility is high. Increasing water levels and holding them at 60 cm has been shown to reduce adult *Lythrum* cover (Thompson et al. 1987). Our results strongly confirm that *Lythrum* infestations are best dealt with early and that avoiding *Lythrum* establishment is easier than its eradication (Thompson et al. 1987). Although *Lythrum* establishment can be reduced with herbicide (Welling and Becker 1993) or by heavily seeding (non-native) competitors such as *Echinochloa crus-galli* var *frumentacea* (Roxb.) Wight (Japanese millet, Malechi and Rawinski 1985), our results suggest that spring and early summer flooding is another possible option.

2. *Typha* (cattail) establishment might be kept low where sand or other coarse material can be used as a substrate. Unwanted *Typha* dominance is a problem for wetland restoration (Odum 1988), partly because natural recolonization can often lead to monospecific *Typha* stands (Levine and Willard 1990, Reinartz and Warne 1993). In the microcosm experiment, *Typha* did not dominate in any of the treatments; one common factor was the use of coarse substrate. *Typha angustifolia* was shown to have decreased recruitment when grown on substrate with particle sizes of >4 mm (Keddy and Constabel 1986, recruitment was defined as having occurred upon the appearance of the first leaf). We have repeatedly grown wetland plants, including *Typha* spp., in garden plots (e.g., Boutin and Keddy 1993, Gaudet and Keddy 1994, Keddy et al. 1994, and others cited above), and *Typha* spp. do not establish well on sand. We have observed in 1993 and 1994 pot experiments that the addition of commercial potting soil to sand (1:3) can dramatically increase the size of *Typha* plants even when supplied with high levels of fertilizer. Our experiments were not designed to find conditions under which *Typha* spp. are intolerant, but our experience is that they are difficult to grow from seed in sand-filled pots. The use of sand and other coarse-textured substrates in wetland restoration projects may supress unwanted *Typha* growth.

3. High species richness is difficult to maintain. Although all the species germinated and reached the seedling stage, only six species were found in large numbers after 5 years (*Bidens, Carex, Eleocharis, Glyceria, Lythrum, Scirpus*). This was the case even though many of the species in the experiment that failed to persist (*Aster, Epilobium, Eupatorium, Gnaphalium, Hypericum, Myrica, Panicum, Penthorum, Verbena, Xyris*) are found on the infertile, sandy shores that we were attempting to model. Furthermore, *Lythrum* dominance coincided with the loss of other dicots. The rapid loss of species suggests that in the absence of disturbance, competitive exclusion by *Lyth-*

rum can be swift—as little as five years or less. Consistent with our experimental results, wetland restoration projects have also seen rapid dominance and loss of biological diversity (e.g., Levine and Willard 1988, Erwin 1990).

4. Although low biomass wetlands having high diversity are desirable because of the many rare and endangered species they support (Keddy 1985, Moore et al. 1989), it is apparently very hard to artificially create them. The experiment was designed to model river or lake shorelines with slow growing, rare species (such as *Xyris* and *Panicum,* Keddy 1985, Wisheu and Keddy 1989) by including such variables as cobbles and water-level fluctuations. The convergence of communities in this experiment attests to the difficulty managers and restorers will likely have when dealing with such habitats. Our results again support the idea that infertile wetlands may deserve a higher conservation priority because of the difficulty of reconstructing them.

ACKNOWLEDGMENTS

The authors would like to thank Qiang Wu, Harold Lee, and Kristin Nielsen for their work in the field. Thanks also to Beth Middleton, Maureen Toner, Rochelle Lawson, James Reinartz, and one anonymous reviewer. Funding was provided by Natural Sciences and Engineering Research Council of Canada.

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Manuscript received 22 May, 1995; revisions received 23 October 1995 and 15 February 1996; accepted 6 March 1996.