Germination Responses of 64 Wetland Species in Relation to Seed Size, Minimum Time to Reproduction and Seedling Relative Growth Rate

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Abstract. Three germination attributes (lag time, maximum germination rate, and final germination proportion) were measured for 64 species of herbaceous wetland plants. The environmental conditions approximated the drawdown environment known to stimulate germination in wetland plants: a period of cold stratification followed by position of the seed on the surface of wet, but not inundated, substrate in the presence of light and with a 20/30 °C daily temperature cycle. Correlations were sought between the three germination attributes and average individual seed weight, seedling relative growth rate and a categorical variable indicating miminum time to reproduction (annuals, facultative annuals and obligate perennials). Average seed weight was not correlated with any of the three germination attributes. Seedling relative growth rate was negatively correlated with time to initiation of germination. Species capable of setting seed their first year (annuals and facultative annuals) initiated germination sooner, a larger proportion germinated per day once germination began, and a larger proportion of seeds had germinated by the end of the experiment in comparison with species which require more than 1 year to set seed (obligate perennials). A discriminant analysis showed that the time to initiation of germination could accurately classify 89% of the perennial species as being either facultative annuals or obligate perennials.

Key-words: Annuals, drawdown, facultative annuals, germination, perennials, plant strategies, regeneration, seed size, wetlands

Introduction

An important goal of community ecology is to obtain relationships linking organisms to their environments. Theoretically, one could use species-specific relationships and add these together to obtain information concerning entire communities. In practice, there are far more species than there are ecologists and so community ecology must rely on correlations among the traits possessed by organisms in order to obtain more general, but less precise, linkages between species and the environments that they inhabit. In other words, community ecology requires a set of predictive relationships that transcends taxonomic boundaries and allows one to extrapolate from the particular to the general. It is therefore important to know how general the relationships are that we now possess, and how accurately these relationships can predict.

The suite of traits of interest in this study are related to the regeneration capacities of wetland plants; by 'wetland plants' we refer to plants that occur regularly in at least some wetland habitats even though some also occur commonly in other habitats as well. The large comparative study of Grime *et al.* (1981) found:

1 That annuals tended to have shorter t_{50} values (time to 50% germination) than perennials.

2 That t_{50} values increased with average seed weight in interspecific comparisons.

3 That species with high seedling relative growth rates tended to have shorter t_{50} values.

Shipley *et al.* (1989) carried out a comparative study of 25 wetland species, including measurement of germination attributes, and found that the time taken for an average seed to germinate increased with seed weight, decreased with seedling relative growth rate and decreased if the species was a facultative annual (there were no obligate annuals).

The qualitative patterns reported in Grime *et al.* (1981) were therefore corroborated by the results of the small number of wetland species included in Shipley *et al.* (1989). If the reported correlations exist more widely in wetland plants then one can obtain information concerning regeneration events in an entire assemblage of wetland plant species from a small set of easily measured attributes. This ability to extrapolate from the specific

to the general would have important practical applications because the success of the most common technique for managing wetland vegetation, the drawdown (Kadlec, 1962; Harris & Marshall, 1963), is dependent on regeneration of species from the seed bank. The drawdown technique consists of maintaining flooded conditions until the established emergent vegetation is killed, and then lowering the watering level, exposing the substrate and stimulating regeneration.

The purpose of this study was therefore to provide an independent test of the relationships reported in Grime *et al.* (1981) and Shipley *et al.* (1989) and to measure the strength of the relationships if they exist.

Most germination studies vary the environmental conditions while restricting the number of species. The approach taken in this study is orthogonal, but complementary, to traditional approaches: we examine the germination responses of a large number (64) of herbaceous wetland species to a single set of environmental conditions. This 'community-based' approach is particularly relevant to temperate wetland species because most wetland plants achieve maximum germination proportions under broadly similar environmental conditions (Keddy & Ellis, 1985; Galinato & van der Valk, 1986; Keddy & Constabel, 1986; Moore & Keddy, 1988) provided that open-water species are not included (Poiani & Johnson, 1988). These conditions include a period of cold stratification followed by position of the seed at the surface of wet, but not inundated substrate in the light and exposed to fluctuating temperatures. These conditions are also those under which most wetland seeds germinate in the field (Kadlec, 1962; Harris & Marshall, 1963; Meeks, 1969; Salisbury, 1970; van der Valk & Davis, 1978).

Materials and methods

Seed collection and storage

Seeds were collected from populations in south-eastern Ontario, south-western Quebec or southern Nova Scotia, Canada during September and October 1988, but seeds of a few species were collected at other times. The Appendix summarizes this information. We will refer to all propagules containing a single embryo as a 'seed' for simplicity. Seeds of each species were collected from a single location because of time constraints.

After collection, seeds were cleaned of support tissues, placed in porous nylon bags and buried in wet sand (75% saturated, by weight). Containers were then stored at 4°C until July 12 1989, representing 9 months of cold stratification. These storage conditions are similar to those of Galinato & van der Valk (1986), Moore & Keddy (1988) and Shipley *et al.* (1989).

Experimental design

Each of 64 species, except for *Eleocharis erythropoda* Steud., was represented by 100 seeds. For each species the 100 seeds were placed into freely draining pots (3·5 cm diameter) with 10 seeds per pot, for a total of 10 pots per species and 637 pots in the experiment; *E. erythropoda* was represented by only 70 seeds and therefore seven pots. In order to prevent systematic differences in germination due to environmental variations within the glasshouse the 637 pots were divided into 10 blocks with one pot per block for each species. Position of species within each block was randomized.

Seeds were removed from cold storage and 100 seeds of each species were counted into 10 groups of 10 seeds each (except for *E. erythropoda*) and placed in petri dishes. After counting, the seeds were returned to cold storage until the commencement of the experiment, a period of 1–3 days. Seeds of all species were sown on the same day. Each pot was filled to within 1 cm of the top with acid-washed sand and the remaining 1 cm was filled with a commercial potting soil. Seeds were placed on the top of the potting soil, the pots were placed in plastic trays and the trays were arranged on benches in the McGill University Phytotron using the block structure described above. The plastic trays were then filled with water and the experiment began on July 12 1989. Holes in the walls of the plastic trays regulated the water level to 1 cm below the surface of the potting soil. This water level insured that the soil was continually wet but not inundated. The water level was checked daily during the experiment.

Germination was monitored daily from July 13 until August 11 1989 (30 days) and seedlings were removed daily as they were counted. A seed was considered to have germinated if any part of the embryo had emerged from the seed coat.

The computer regulating the Phytotron was programmed to provide a smoothly changing 20/30°C daily temperature cycle with the minimum temperature (20°C) occurring at midnight and the maximum temperature (30°C) occurring at noon. This temperature cycle was found by Galinato & van der Valk (1986) to produce maximal germination in wetland species. There were small

deviations ($\pm 3\,°C$) from this cycle from day to day but all seeds experienced the same conditions. Natural lighting was used, corresponding to approximately 15 h of daylight daily.

The environmental conditions used correspond to those that previous authors have found to approximate optimal germination conditions for a wide range of wetland species. Nonetheless, we have no evidence that these conditions actually are optimal for all of the test species. This experiment, like all screening experiments, therefore only approximates such conditions.

Species attributes

We observed three properties for each species' germination sequence: the lag time (L, the time in days between the beginning of the experiment and the commencement of germination), the final germination proportion at the end of the experiment (G), and the maximum germination rate (G_{max}, maximum proportion of germinated seeds that germinate in a single day). Thus, a species whose seeds first began to germinate 5 days after the experiment began had a lag time of 5 days. If 60 of the 100 seeds of the species had germinated by the end of the experiment then G was 0·6. If 50 of the 60 germinated seeds did so in a single day then G_{max} was 50/60.

We use the maximum germination rate because the daily germination rate did not remain constant during the experiment and its distribution was usually quite skewed with maximum values occurring soon after the end of the lag period. We use the proportion of germinated seeds in determining this maximum rate, rather than the total number of seeds sown, in order to differentiate between the rate of germination and the proportion of seeds capable of germinating. The three germination parameters for each species are given in the Appendix.

The use of lag time, maximum germination rate and final germination proportion proved to be satisfactory definitions for most species. For the few species that had less than 10% final germination, these definitions introduced structural (rather than biological) correlations. For instance, there may be a structural correlation between lag time and final germination proportion if germination does not begin until late in the experiment. Similarly, there may be a structural correlation between maximum germination rate and final germination proportion if very few seeds germinate; in the extreme case of only one germinated seed, the maximum germination rate is necessarily

1 day^{-1}. For this reason, we have excluded all species having less than 10% final germination proportion from the statistical analyses. Unfortunately, such structural correlations exist in any set of indices unless one can confidently know that all seeds capable of germinating have done so by the end of the experiment.

Apart from the germination attributes, we obtained three other plant traits from previously published work. Average seed weights were obtained from Shipley *et al.* (1989) or Shipley & Peters (1990a). We determined average seed weights for species lacking previously published estimates using the method in Shipley & Peters (1990a). Seedling relative growth rates for 44 species were obtained from Shipley & Peters (1990a). Finally, classification of perennials based on the ability to flower in the first growing season (facultative annuals) is based on our observations, or those of Boutin & P.A. Keddy (unpublished observations) of plants grown in the glasshouse or in a common garden experiment. Our term 'facultative annual' denotes only the ability to produce seeds in the first growing season, and therefore the potential to function ecologically as an annual. It does not imply monocarpic reproduction; in fact, all of the facultative annuals in this study, except *Artemisia campestris* L., are polycarpic perennials. All perennials that had not been screened for the ability to flower in the first growing season were assumed to be obligate perennials; the implications of this assumption will be discussed later.

Statistical analysis

The transformation of lag time and average seed weight to their natural logarithms and the transformation of maximum germination rate and final germination proportion to the natural logarithm of their odds ratio (Draper & Smith, 1981) stabilized the variance and improved the distribution of the residuals. Minimum time to reproduction was constructed as a categorical variable in two ways: first, as a three level variable (annual, facultative annual and obligate perennial) and second, as a two level variable (annual/facultative annual and obligate perennial).

Correlations between the quantitative variables were calculated using the usual Pearson correlation coefficient. Systematic differences in the mean values of the continuous variables when contrasted between the categorical variables were tested using an analysis of variance. Homogeneity of variance between groups was tested using Bartlett's test (described in Sokal & Rohlf, 1981).
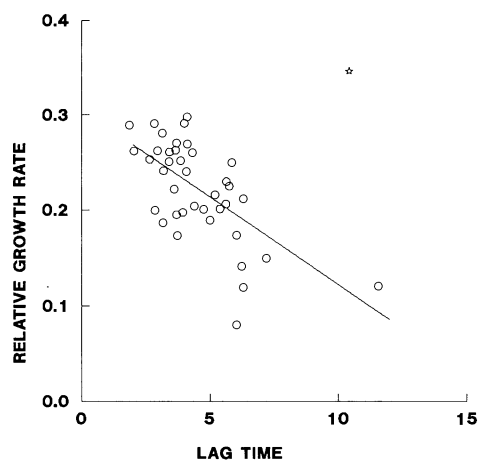
Fig. 1. The relationship between the time (days) from the beginning of the experiment until the first seed germinates (lag time) and seedling relative growth rate $(R, g\,g^{-1}\,day^{-1})$ in 40 species of herbaceous wetland species $(r = -0.36)$. The relationship between the two variables (excluding the outlier shown by the open star, *H. ellipticum*) is $R = 0.30 - 0.018L$, $r = -0.63$.

Post hoc tests between group means were done using the Tukey–Kramer multiple comparisons test adjusted for unequal counts per group (described in Sokal & Rohlf, 1981). Statistical significance was evaluated at the 95% probability level using two-tailed tests.

Results

Twelve out of the original 66 species had less than 10% germination during the experiment. Seven species (*Alisma plantago-aquatica* L., *Eleocharis smalli* Britton, *Eriocaulon septangulare* With., *Sagittaria latifolia* Willd., *Scirpus cyperinus* (L.) Kunth., *Scirpus torreyi* Olney and *Sparganium eurycarpum* Engelm.) are known to have very low germination proportions (Shipley *et al.*, 1989; Shipley & Peters, 1990a) although the two species with thick seed coats (*S. torreyi* and *S. eurycarpum*) can be stimulated to germinate if the seed coat is broken. One species (*Gnaphalium uliginosum* L.) is known to have high germination proportions under similar conditions; presumably this species was represented by defective seeds. We have no previous experience with the last four species (*Carex lupulina* Muhl., *Euthamia galetorum, Molugo verticillata* L. and *Polygonum hydropiperoides* Michx.), although many seeds of the last species had germinated during cold storage and so the seeds used in the experiment may have been defective.

Of the three germination attributes, there were significant correlations between lag time *vs* maximum germination rate $(r = -0.34, n = 54$ species) and final germination proportion $(r = -0.48, n = 54$ species). There was no correlation between seed weight and either lag time, germination rate or final germination proportion.

Species whose seedlings had high relative growth rates tended to have shorter lag times $(r = -0.36, n = 40$ species). Fig. 1 shows this relationship. There is one obvious outlier (*Hypericum ellipticum* Hook). This species had a very poor estimate of seedling relative growth rate (Shipley & Peters, 1990a) due to low levels of replication. If this one species is excluded, the correlation coefficient is increased to -0.63. Seedling relative growth rate was not correlated with either final germination proportion $(r = 0.31)$ or with maximum germination rate $(r = 0.05)$.

There were significant differences among the three types of species with respect to lag time $(P < 0.0005)$ and maximum germination rate $(P = 0.03)$, but not with respect to final germination proportion $(P = 0.14)$ (Fig. 2). However, further analysis showed that there were significant differences in find germination proportion between obligate perennials and a composite group involving both true annuals and facultative annuals $(P = 0.02)$. As well, the significant differences in lag time were due to the contrast of obligate perennials with either true or facultative annuals (Fig. 2) since there were no significant differences between the true and facultative annual species $(P = 0.99)$. Thus, in contrast to obligate perennials, the 'annual' species tended to begin germination sooner (shorter lag time), tended to germinate at a faster rate resulting in most seeds germinating within a few days of initiation of germination (maximum germination rate), and tended to have a higher proportion of seeds germinate by the end of the 30-day experiment.

Since seedling relative growth rate was correlated with lag time, we tested whether the three types of species (annuals, facultative annuals and obligate perennials) exhibited similar trends with respect to seedling relative growth rate. There were highly significant differences in seedling relative growth rate between the three groups $(P < 0.003)$ but no significant differences when comparing only annuals and facultative annuals $(P < 0.80)$. Thus, the relevant contrast is again between those species capable of setting seed their first year and those that require more than 1 year $(P < 0.001)$.
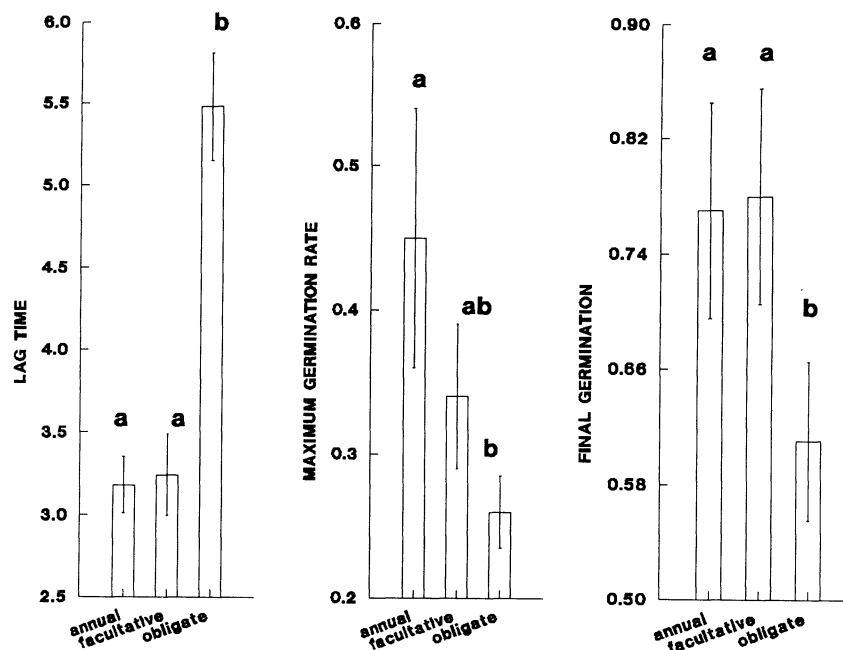
Fig. 2. Means (±SE) of transformed values of lag time (days), maximum germination rate (maximum proportion of germinable seeds that germinate in a single day) and final germination proportion for 54 species of herbaceous wetland species, classified as either annuals, facultative annuals or obligate perennials. Groups with common letters are not significantly different at $P = 0.05$.

Some species had been in cold storage for longer than 9 months and so we performed a Kruskal–Wallis one-way ANOVA to determine whether this difference could explain some of the significant contrasts. However, no differences were found for any of the three germination properties nor for seedling relative growth rate.

Because the categorization of perennials as either facultative annuals or obligate perennials is time and labour intensive, we next performed a discriminant analysis in order to determine how well germination properties could discriminate between the two types of perennials. This analysis used only those perennial species for which we had data on minimum time to reproduction and which had at least 10% final germination. Differences in lag time alone could correctly classify 89% (26 out of 28) of these species; inclusion of the other two germination attributes did not increase accuracy. Table 1 gives the coefficients of the group classification functions; each species is assigned to the group whose group classification function is larger. Application of the resulting classification function to those species excluded from the analysis, due to having less than 10% final germination, allowed all but one (*A. plan-tago-aquatica*) to be accurately classified. Of the 17 perennial species not included in the analysis

due to a lack of observational evidence for time to reproduction, only three species were predicted to be facultative annuals (*Dulichium aurundinaceum* (L.) Britton, *Eupatorium maculatum* L., and *Scirpus atrovirens* Willd.). These three species all typically occur in the same type of habitat that the known facultative annuals inhabit: fertile sites with gap-producing disturbances. Similarly, all 12 obligate annual species, although not included in the discriminant analysis (since there was no *a priori* ambiguity about their classification), were accurately identified as 'annuals'.

Table 1. Shown are the coefficients of the discriminant classification functions for the two groups of perennial species with differing minimum times to reproduction. 'Facultative annuals' refers to perennial species capable of setting seed during the same growing season that they germinate. 'Obligate perennials' refers to perennial species that require at least two growing seasons before they can set seed. A species is predicted to belong to the group whose classification function value is larger. 'Lag' refers to the time between planting a seed lot and the first seed to germinate.

Variable	Facultative annuals	Obligate perennials
Lag	1·003	1·560
Constant	−2·627	−1·560

Discussion

A number of authors (Grime, 1979; Shipley *et al.*, 1989) have suggested that there exists a suite of correlated attributes of plants, related to the ability of a plant to regenerate from seed, and associated with the frequency and intensity of density-independent mortality that the plants experience. Thus, Grime *et al.* (1981) found the time to 50% germination (a combination of lag time and germination rate) tended to be shorter in annuals than in perennials, shorter in small-seeded species and shorter in species with higher seedling relative growth rates. Much the same pattern was detected in the wetland species studied by Shipley *et al.* (1989): there was a negative correlation between the time taken for an average seed to germinate (also a combination of lag time and germination) and seed size, and a positive correlation with seedling relative growth rate. There were no annuals in the data of Shipley *et al.* (1989) but species known to be facultative annuals tended to germinate more quickly, more abundantly and to have seedlings with higher relative growth rates.

The present study revealed some of the same results. Species with high seedling relative growth rates had seeds capable of germinating more quickly once placed in a favourable environment. Species capable of setting seed in one growing season had shorter lag times, more rapid rates of germination, a larger proportion of seeds germinating by the end of the experiment and higher seedling relative growth rates.

On the other hand, seed size was not associated with any of the germination attributes. The most likely explanation is that seed size is often (Salisbury, 1942), but not always, smaller in annual species than in perennial species. Seed size is found to vary predictably with the other regeneration attributes discussed above in data sets in which this correlation holds. Seed size does not relate to the other generation attributes in data sets, such as this one, in which there are broadly overlapping ranges of seed weight between annuals and perennials. In fact, in our study, there was no significant difference in mean seed weight between either of the two classifications of minimum time to reproduction. Thus, annuals with large seeds (*Bidens cernua* L., *Bidens frondosa* L.) exhibited germination attributes typical of other annuals and obligate perennials with small seeds (*Eriocaulon septangulare, Rhyncospora capillacea* Torr., *Sabatia kennedyana* Fern., or *Xyris difformis* Chapman) exhibited germination attributes typical of other obligate perennials. Shipley & Peters (1990b) did a literature survey of the

relationship between seed size and seedling relative growth rate, involving seven studies and 204 species, and found that although a negative correlation did exist, the relationship was weak and quite variable between studies.

The importance of minimum time to reproduction, suggested by Shipley *et al.* (1989), was shown in the present study. The usual classification of plants as annuals, biennials or perennials is based on maximum life-span. The classification based on minimum time to reproduction (annuals and facultative annuals *vs* obligate perennials) revealed clearer differences than the usual classification. In fact, lag time was able to discriminate between the two classes of perennials with high accuracy. To test the ability of our discriminant functions in identifying facultative annuals, we used the data of Shipley (1987, Appendix 3.4), which gives the time course of germination in 22 species of wetland plants. Only four out of 22 species were misclassified. Such an independent test is particularly significant because the environmental conditions were quite different in Shipley (1987): temperatures were not controlled and the seeds were placed on moist filter paper.

The purpose of this study was to determine the generality and strength of reported correlations between juvenile attributes of plants. The correlations found in Grime *et al.* (1981) and in Shipley *et al.* (1989) were also found in this study, with the exception of those relationships involving seed size. On the other hand, most correlations were rather weak and therefore have little predictive ability. The one exception was in relation to minimum time to reproduction, which showed strong relationships to most of the juvenile traits. This attribute (minimum time to reproduction) therefore deserves more detailed attention by community ecologists.

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Appendix 1

Lag time (L, days) is the number of days from the beginning of the experiment until the first seed germinates. Maximum germination rate (G_{max}, % day^{-1}) is the maximum proportion of germinable seeds that germinate in 1 day. Bracketed values indicate rates calculated from less than 10 seeds. Final germination proportion (G, $\times 100$) is the per cent of the seeds (out of 100, except for *Eleocharis erythropoda*) that had germinated by the end of the 30-day experiment. Seed weight (S, 10^{-5}g) is an average over at least 25 seeds. R (g g^{-1} day^{-1}) is the seedling relative growth rate, from Shipley & Peters (1990a). Type is the classification of species based on the mimimum time from seed germination until seed production (years). OP indicates obligate perennials (perennials requiring at least two growing seasons to reproduce), FA indicates facultative annuals (perennials which can set seed in one growing season) and OA indicates true (obligate) annuals. Predict is the predicted classification of perennials based on the discriminant analysis. Taxonomy follows Gleason & Cronquist (1963).

Species	L	G_{max}	G	S	R	Type	Predict
Acorus calamus	6	0·13	91	91	0·17	OP	OP
Agrostis stolonifera	4	0·10	52	5	0·28	FA	FA
Alisma plantago-aquatica	7	(0·10)	2	33	—	FA	OP
Artemisia campestris	3	0·33	23	30	0·21	FA	FA
Asclepias incarnata	4	0·05	27	295	0·20	FA	FA
Bidens cernua	3	0·12	86	1047	0·26	OA	
Bidens frondosa	2	0·21	98	174	—	OA	
Carex crinita	5	0·09	73	63	0·19	OP	OP
Carex folliculata	6	0·14	61	692	0·13	—	OP
Carex lupulina	12	(1·00)	1	479	—	—	OP
Carex projecta	5	0·47	76	19	—	—	OP
Carex retrorsa	12	0·10	54	166	—	—	OP
Carex tuckermani	6	0·09	77	550	—	—	OP
Chenopodium polyspermum	3	0·18	47	39	—	OA	
Coreopsis rosea	6	0·21	50	11	0·26	OP	OP
Cyperus aristatus	4	0·61	91	4	0·21	OA	
Cyperus diandrus	3	0·62	87	7	—	OA	
Cyperus esculentus	6	0·14	27	13	—	OP	OP
Cyperus rivularis	3	0·58	81	15	0·25	OA	

Appendix 1. (*continued*).

Species	L	G_{max}	G	S	R	Type	Predict
Digitaria ischaemum	3	0·46	7	51	—	OA	
Dulichium aurundinaceum	4	0·14	85	53	0·19	—	FA
Echinocloa crus-galli	3	0·14	66	74	0·29	OA	
Eleocharis erythropoda	5	0·17	49	31	0·21	OP	OP
Eleocharis obtusa	4	0·10	87	16	0·24	OA	
Eleocharis smallii	8	(0·12)	7	145	0·10	OP	OP
Epilobium ciliatum	3	0·12	29	7	0·29	FA	FA
Eragrostis hypnoides	3	0·30	86	8	—	OA	
Eriocaulon septangulare	11	(0·29)	2	10	0·01	—	OP
Eupatorium maculatum	3	0·22	40	16	0·24	—	FA
Eupatorium perfoliatum	4	0·29	70	10	0·25	FA	FA
Euthemia galetorum	4	(1·00)	2	5	—	FA	FA
Gratiola aurea	5	0·12	68	0·1	—	—	OP
Hypericum ellipticum	10	0·11	38	3	0·35	OP	OP
Iris versicolor	6	0·11	61	1413	0·13	OP	OP
Juncus bufonius	3	0·49	20	1	0·19	OA	
Juncus canadensis	5	0·14	79	10	0·22	OP	OP
Juncus effusus	4	0·27	61	1	0·27	OP	FA
Juncus filiformis	4	0·24	80	2	0·18	FA	FA
Leersia oryzoides	4	0·09	71	91	0·28	FA	FA
Lycopus americanus	3	0·56	90	15	0·26	FA	FA
Lythrum salicaria	3	0·27	92	5	0·26	FA	FA
Mimulus ringans	4	0·26	81	10	0·26	FA	FA
Panicum capillare	4	0·19	87	29	—	OA	
Panicum longifolium	5	0·15	65	21	0·19	OP	OP
Penthorum sedoides	4	0·32	82	1	0·30	FA	FA
Phalaris aurundinacea	3	0·10	93	31	—	OP	FA
Plantago major	2	0·17	99	16	0·28	FA	FA
Polygonum hydropiperoides	7	(1·00)	1	74	—	OP	OP
Polygonum lapathifolium	4	0·09	11	124	0·28	OA	
Rhyncospora capillacea	6	0·20	60	110	0·09	—	OP
Rumex verticillatus	4	0·41	77	110	0·20	OP	FA
Sabatia kennedyana	7	0·10	20	1	0·16	—	OP
Scirpus americanus	12	0·17	10	263	0·13	OP	OP
Scirpus atrovirens	4	0·45	95	4	—	—	FA
Scirpus cyperinus	6	(0·31)	4	1	0·19	OP	OP
Scirpus torreyi	5	(0·30)	3	355	0·13	OP	OP
Scirpus validus	6	0·09	47	98	0·20	—	OP
Sium suave	6	0·15	18	100	0·22	—	OP
Sparganium eurycarpum	—	—	0	30919	—	OP	—
Spartina pectinata	6	0·17	41	71	0·22	OP	OP
Triadenum fraseri	6	0·16	92	10	—	—	OP
Verbana hastata	2	0·32	84	24	0·26	FA	FA
Xyris difformis	5	0·11	66	2	—	—	OP