The Effect of Hydroperiod on Seed Banks

in Semi-permanent Prairie Wetlands.

by

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(ABSTRACT)

In 1985, 24 bottom samples were collected in each of two slightly brackish, semi-permanent prairie wetlands (P1 and P4) with different hydroperiods. The main objective was to determine if hydroperiod affected seed pool characteristics. Additionally, 48 samples were collected in 1986 from wetland P1 to determine if seed bank composition changed annually without a change in mature vegetation.

Seed bank composition was determined by placing soil samples in a greenhouse, then counting and identifying emerged seedlings. As a check against the seedling emergence method, seeds were separated and identified microscopically in one-third of the 1985 samples. Results indicated that the emergence method was an accurate technique for assessing seed pool composition.

The wetlands did not differ in floristic composition (i.e., presence/absence) but did in species densities. The mean relative density of mudflat annuals in all seed pool samples was significantly greater in wetland P4 (82%) than in P1 (52%). A shorter hydroperiod in this wetland produces more frequent drawdowns and a greater input of mudflat annual seeds. Conversely, seeds of emergent species were more abundant in the seed bank of wetland P1 (48%) compared to P4 (17%). The former wetland has a longer hydroperiod and less frequent drawdowns, and thus, the primary seed input is from emergent plants.

Hydroperiod may have also influenced within wetland seed densities. In the wetland with a longer hydroperiod (P1), seed density in open water areas was significantly lower than in areas of emergent vegetation. Seed densities were not significantly different between these areas for the wetland with a shorter hydroperiod (P4).

Floristic composition did not differ between years when mature vegetation remained constant. Variability in species densities, however, was high, probably due to the extremely heterogeneous distribution of seeds in prairie wetlands.

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Introduction

Northern prairie wetlands undergo cyclic changes in the ratio of emergent cover to open water in response to fluctuations in water level (Weller & Spatcher 1965). The wetland cover cycle normally has four phases: the dry marsh, the regenerating marsh, the degenerating marsh, and the lake marsh (van der Valk & Davis 1978). The dry marsh phase is initiated by exposure of the marsh bottom. Subsequently, emergent and ephemeral species, whose seeds and propagules are mostly present in the exposed soil or shallow water, germinate and colonize the substrate. Emergent genera include *Typha*, *Scirpus*, *Juncus*, *Carex*, and *Eleocharis*, while ephemerals include *Chenopodium*, *Rumex*, and *Polygonum*. This phase, caused by drought and drawdown and characterized by a high proportion of the marsh bottom comprised of young plants is called the dry marsh.

A return to more normal rainfall initiates the regenerating marsh phase. Emergent species are partially inundated and their zones expand by vegetative reproduction. Ephemeral species are inundated and die. In areas where standing water becomes deeper and more permanent, submerged and floating aquatic seeds and propagules germinate, including *Potamogeton*, *Zannichellia*, and *Utricularia*.

The degenerating marsh phase begins as water level continues to rise and emergent vegetation becomes stressed. Secondary factors such as herbivory and disease may cause a further decline in cover.

If the water level continues to rise or if deep water stabilizes, emergent cover will decline further and the lake marsh phase will be attained. This stage consists of a high proportion of open water to emergent cover, the latter usually restricted to the shoreline. The open marsh is dominated by submerged and floating aquatic plants. The lake phase remains until drought and drawdown reinitiate the cycle. A complete wetland cover cycle usually requires from 5 to 20 years. At any point in the cycle, natural events such as severe flood and/or drought can interrupt the generalized pattern.

Most plants that regenerate during the dry marsh phase originate from the seed bank, and therefore the existence of buried seeds in the soil plays a prominant role in the cyclic vegetation patterns described above. (The term "seed bank" refers to the viable seeds, fruits, propagules, and other reproductive plant structures existing in the soil.) Likewise, seeds and propagules of submerged and floating species present in the soil determine the vegetation composition during the lake marsh phase.

A variety of other factors also control the composition and distribution of vegetation. Important physical/chemical parameters include salinity, substrate composition, and water quality, while biotic factors include competition, allelopathy, pathogens, and use of vegetation by herbivorous and nesting animals (van der Valk 1981).

Van der Valk (1981) hypothesized that vegetation composition at any stage in the wetland cover cycle can be predicted with three crucial pieces of information: 1) the potential flora of the wetland, including the actual flora plus all additional species represented only by propagules in the seed bank, 2) the life history type of each species, including life-span, propagule longevity, and establishment requirements (Galinato &

van der Valk 1986), and 3) the water level. His qualitative model was applied to two wetland ecosystems, the development of papyrus swamps on Lake Naivasha, Kenya (Gaudet 1977) and the cyclic changes in prairie marsh vegetation (van der Valk 1981). In both examples, the model accurately predicted qualitative changes in vegetation (van der Valk 1981).

Quantification of the conceptual model would improve its use as a management tool. For example, the value of prairie marsh habitat for waterfowl depends on the plant composition. The ratio of emergent cover to open water also influences the quality of wetland habitat for breeding birds (Weller & Spatcher 1965, Weller & Frederickson 1974, Kaminski & Prince 1984). A necessary step in the development of a quantitative model of cyclic vegetation change for a prairie wetland is the detailed study of its seed bank.

As a prelude to the construction of a quantitative model, I investigated the seed banks of two North Dakota prairie marshes. Specific objectives were: 1) to determine the similarity in overall composition and relative proportions of life history types in two seed banks for wetlands with similar water permanence and water quality (Stewart & Kantrud 1971) but with a different hydroperiod (i.e., the period of time that standing water is present), 2) to determine the annual variation in seed pool composition without a change in mature vegetation, and 3) to determine the reliability and accuracy of the seedling emergence technique, the primary method employed in assessing seed bank composition in wetlands (van der Valk & Davis 1978, Leck & Graveline 1979, Keddy & Reznicek 1982, Hopkins & Parker 1984, Smith & Kadlec 1983). This method may fail to germinate some species and therefore may bias composition (Thompson & Grime 1979, Roberts 1981, Galinato & van der Valk 1986, R. Pederson pers. comm.) compared to actual recovery and identification of seeds, i.e., the seed separation technique (Kropac 1966, Roberts & Ricketts 1979, Standifer 1980, Roberts 1981).

Study site

The Cottonwood Lake Waterfowl Production Area includes a complex of various sized wetlands owned by the U.S. Fish & Wildlife Service and located approximately 28 miles northwest of Jamestown, Stutsman County, North Dakota (Fig. 1). It is near the eastern edge of a large glacial drift complex, the Missouri Coteau (Winter & Carr 1980), which consists of end moraine, stagnation moraine, ice-contact, and outwash deposits with a thickness of greater than 130 m. The drift is comprised of clayey and silty till and includes a large number of silt, sand, and gravel lenses. Average relief of the Missouri Coteau is 30 m (Winter & Carr 1980). Wetland density over the study site and surrounding area is approximately five potholes/km^2.

The climate of North Dakota is continental, characterized by warm summers and cold winters with wide variations in extreme temperatures and precipitation (Winter & Carr 1980). The mean annual temperature for the study site is approximately 4^0 C. The extreme mean monthly temperatures for January and July are -14^0 C and 21^0 C, respectively. The mean length of the freeze-free period is 120 days (Winter & Carr 1980).

Precipitation for the study area averages 45 cm, with most (35 cm) occurring between April and September. Snowfall averages 87 cm per year. The mean date of the

first significant snowfall is December 5 and the last significant snowfall is March 23 (Winter & Carr 1980).

Soils in the study area are classified as Barnes-Buse, rolling (Winter & Carr 1980). These soils have a thick black surface layer (Chernozem) or a thin surface layer (Regosol) and either a very limey subsoil (Calcium Carbonate Solonchak) or a claypan subsoil (Solonetz). Parnell and Tetonka soils occupy the lowlands, are rich in organic matter and are poorly drained (Winter & Carr 1980).

The two wetlands studied (P1 and P4) were situated approximately 200 m apart at an elevation of 560 m (Fig. 1). Both wetlands are classified as slightly brackish (subclass B) and semi-permanent (class IV), dominated by tall rank emergent plants (e.g., *Typha* spp.) in the deep part of the basin (Stewart & Kantrud 1971). The wetlands differ, however, in their hydroperiod, the length of time the bottom of the wetland is covered by water (George Swanson pers. comm.). Wetland P1 has both a deeper basin and a larger catchment than that of P4. Consequently, standing water in P4 covers less surface area and is significantly shallower (in July 1985 standing water in P1 had a maximum depth of 46.5 cm while in P4 it only reached 27.5 cm). Wetland P4 with shallow water dries up more often and therefore has a shorter hydroperiod than P1.

Due to the differences in hydroperiod, these wetlands also differ in their cover type. Cover type is simply the ratio of emergent cover to open water or exposed soil (Stewart & Kantrud 1971). P4 is classified as cover type 1 because open water or bare soil covers less than 5% of the wetland area. P1 is cover type 3, with central expanses of open water or bare soil (comprising more than 5% of the wetland area) surrounded by peripheral bands of emergent cover averaging 2 m or more in width (Stewart & Kantrud 1971). In addition, transpiration from the more extensive emergent cover in P4 increases water loss compared to P1 (Bernatowicz et. al., Eisenlohr 1966, 1972). This increase in water loss exacerbates the already shorter hydroperiod in wetland P4.

Each wetland is several hectares in size with vegetation arranged as bands or zones (Fig. 2). The open water zone (OWZ) is located in the deepest part of the basin and is dominated by submerged and free-floating aquatic vegetation. Species diversity is greater in the OWZ of wetland P1 than in the smaller and shallower OWZ of P4 (Fig. 2). The next three adjacent zones, the deep marsh emergent zone (DMEZ), the shallow marsh emergent zone (SMEZ), and the wet-meadow zone (WMZ), are dominated by emergent grasses and sedges (Fig. 2). Species are progressively smaller and finer in texture landward. All three emergent zones are similar in composition between P1 and P4 (Fig. 2).

Methods

Field Sampling

In mid-July 1985, 24 bottom samples were collected each from wetlands P1 and P4. Samples were taken along four transects in each wetland. The four transects were a subset of six U.S. Fish & Wildlife Service permanent transects, each 60^0 apart, beginning at a random compass point.

Six samples were collected along each transect. Samples were finally collected by hand (using a pre-measured surface area for consistency) after numerous mechanical devices were tried (i.e., soil coring devices, Eckman dredge, shovel, etc.). Each device was ineffective in either the open water area because of extremely loose organic sediments or in the emergent zones because of deep detritus and thick rhizomes.

Each sample had an approximate surface area of 676 cm^2 and depth of 5 cm. The number of samples collected in each vegetation zone was proportional to zone width. In P1, 12 samples were collected in the OWZ, 8 samples in the DMEZ, and 4 samples in the SMEZ. In P4, sample sizes were 2, 18, and 4, for the OWZ, DMEZ, and SMEZ,

respectively. Within each zone, sample locations along transects were chosen randomly. The dominant vegetation and water depth was recorded at each sample site. Extra soil, about 20% of the emergence sample, was also collected at each sample point for use in the seed separation method.

In mid-July 1986, 48 additional samples were collected from wetland P1 to determine annual variation in seed bank composition and to use a new coring device to obtain a more accurate estimate of sample surface area. Samples were taken along all six permanent transects and two additional transects located halfway between two pairs of the permanent transects (188° and 308°).

Six samples with a surface area of 452 cm^2 and an approximate depth of 5 cm were collected along each transect with a 24-cm diameter, heavy, toothed aluminum corer. Sample intensity within zones was determined as in 1985 (OWZ = 24 samples, DMEZ = 16 samples, SMEZ = 8 samples).

Seedling Emergence

The seedling emergence method (van der Valk & Davis 1978) was used to estimate the seed pool composition. Each sample was thoroughly mixed by hand. The soil was then divided into two equal parts and spread over 2 cm of sterilized potting soil in plastic flats. One subsample was placed in the greenhouse in a drawdown environment where the soil was exposed but kept moist. The other subsample was kept nearby in the greenhouse in a submerged environment where water levels were kept 2-3 cm above the soil surface. Control flats consisting of sterilized potting soil were also placed in each treatment. Experiments were initiated in late July 1985.

All identifiable plants were counted and removed from flats. All flats were completely harvested the following January and unknown species were transplanted to encourage flowering. Several seedlings died before they could be identified and were necessarily omitted from statistical summaries. Nomenclature follows Great Plains Flora Association (1986). The number of plants per greenhouse flat was converted to the number of plants per square meter of soil in the field.

Seed Separation

The reliability of the emergence method in estimating seed bank composition was determined by the seed separation technique. Two 50-g subsamples each of sixteen 1985 field soil samples were analyzed by the separation procedures. This constituted one-third of the total number of 1985 emergence samples. Samples were randomly chosen from each zone in each wetland.

To isolate seeds from soil particles, two separation methods were tried. First, I attempted to float seeds in a high density solution (Malone 1967, Roberts 1981, Roberts & Ricketts 1979). Magnesium sulphate was used as the flotation medium, and a mixture of sodium hexametaphosphate and sodium bicarbonate was used as a soil particle dispersant (Malone 1967). This method is most often used in agricultural soils which have very small weed seeds (< 1 mm). In my samples, large seeds such as *Scirpus* spp. (> 1.5 mm) did not always float, even after increasing the amount of solute from 25-50 g. Therefore, I abandoned this approach and adopted a method of sieving seeds.

In the second method, each subsample was mixed thoroughly with water and poured through a series of soil sieves with decreasing pore size, separating the seeds,

organic debris and mineral soil into smaller sized groups while washing away the silt and clay. The smallest sieve opening (0.140 mm) captured the smallest seeds (Malone 1967). The debris on each sieve was washed into aluminum pans and allowed to air dry. The seeds in each size group were hand sorted, counted and identified using a binocular stereomicroscope. Seeds were identified using seed keys (Martin & Barkley 1961, Montgomery 1977), the reference seed collection of George Swanson (U.S. Fish & Wildlife Service) from the Cottonwood Lake Area, and seeds in VPI&SU Herbarium. Only sound seeds (full when dissected) were counted.

Life history groups

All species identified from either method were classified according to their life history characteristics (van der Valk 1981). Classification by life history types yields important information about how plants in the seed bank might respond collectively to changes in water level. Life history types were assigned based on seed bank data, field observations, and the literature (van der Valk 1981, Smith & Kadlec 1985, Larson 1979, Stevens 1963). First, species were classified according to their life-span: annual (A), perennial (P) with a limited life-span, or vegetatively reproducing (V) perennial without a limited life-span. Next, all taxa that were present as long-lived seed pool species were identified (S). Finally, plant species were classified as either requiring (II) or not requiring (I) standing water for germination and establishment. Four major life history groups were then compiled based on similar life history types (Table 1). For example, all life history types that only germinated in standing water, regardless of their life-span,

were combined to form the open water group. Some life history groups, such as the mudflat annuals, consisted of only one life history type, AS-I.

Seed pool analyses

The effects of hydroperiod on wetland seed pool composition were investigated by making numerous comparisons of seed pool variables between and among wetlands P1 and P4. The major comparisons between (inter-wetland) and within wetlands (intra-wetland) were based on total seed density (no./m^2) and seed pool composition. Seed pool composition was measured in two contrasting ways. The first was a floristic (qualitative) evaluation of seed species based on their presence or absence in samples, not on their relative density. The terms seed flora or floristic composition will hereafter refer to this qualitative aspect of seed pool composition. Species were grouped in various ways to enable floristic comparisons, including by zones, whole wetlands and life history groups. The second aspect of composition involved calculations of a quantitative measure of abundance for each seed species (e.g., the relative densitites of individual species) and will be referred to as species composition. Quantitative estimates were also made for species in zones, wetlands as a whole and for life history groups.

Inter-annual comparisons of seed pool composition in wetland P1 were also made using similar seed pool variables including total seed density, species composition, floristics, plus an additional semi-quantitative measure, the rank-order of the species according to seed density.

Results

Comparison of emergence & separation methods

The seedling emergence and seed separation methods yielded similar estimates of wetland seed bank composition (Table 2). Comparison of the two methods using a coefficient of similarity (IS = 2c/a + b, Sorensen 1948) based on floristic composition indicated a high degree of similarity (IS = 0.61). Species composition was even more similar between methods (IS = 0.83), and the rank-order of species was significantly correlated (Spearman = 0.47, p = 0.01).

Only six uncommon species were present as seeds but not as seedlings; their relative densities ranged from only 0.11-0.54% (Table 2). After omitting rare species (one seed or seedling in either method), floristic similarity between the methods increased from 0.61 to 0.71.

Overall, more species germinated in the emergence method (24) than were isolated in the separation technique (18). Only *Utricularia vulgaris* failed to germinate well in the emergence flats; its seedlings were far less abundant (0.13%) than sound seeds (3.91%).

Conversely, the separation method tended to yield a higher absolute number of seeds per unit volume of soil. The amount of soil analyzed per sample in the separation procedure was 100 g. Soil in the emergence flats was approximately five times greater. After multiplying the number of seeds isolated (Table 2) by five, one sees that separated seeds for each species were usually far greater than emerged seedlings. In arable soil in Denmark, Jensen (1969) also found the greatest number of viable seeds in separation techniques and the greatest number of species from germination experiments in the greenhouse. Since the separation method offered few advantages in estimating seed bank composition, results reported hereafter are all based on the emergence experiments.

Inter-wetland comparisons

Similarity patterns

Overall, few statistically significant differences were found between P1 and P4 in their seed pool characteristics. For example, total (all species) seed density (no./m^2) did not differ between the wetlands (ANOVA, $p > 0.05$); density was 3250 in P1 (1985) and 3799 in P4 (Fig. 3). Differences in density were also small between the respective zones in each wetland, except in the SMEZ where a statistically significant difference was probably precluded by high variance (ANOVA, $p > 0.05$, Fig. 3).

The seed flora between wetlands was also highly similar ($IS = 0.88$, Fig. 4). The small and generally non-significant differences were due primarily to the presence or absence of rare species. The five species present in only one or the other wetland ranged

in relative abundance from only 0.04-0.33% (Table 3). Four of the five most common species in each wetland were the same (Tables 4, 5): *Chenopodium rubrum*, *Rumex maritimus*, *Scirpus* sp., and *Typha* sp.. The species present in the two emergent zones (DMEZ and SMEZ) were also nearly identical (Fig. 4).

The pattern for life history groups was similar to that of zones and whole wetlands. Floristic composition among most life history groups in the pooled and emergent zones was not strikingly different (Table 6). The meadow life history group was least similar between the wetlands with only 40% of the species in common (Table 6). All species in this life history group occurred infrequently, each comprising less than 0.33% of the emergence list in P1 and/or P4. Again, the small and generally insignificant differences found in life history groups were due to the sporadic appearance of uncommon and rare species.

Dissimilarity patterns

Few comparisons of seed pool composition differed statistically between the wetlands. Those that did included: 1) floristic composition in the OWZ, and 2) species composition by zone, whole wetland and life history groups. These differences are detailed below.

Floristic composition was strikingly different between the OWZ of P1 and P4 (Fig. 4 & Table 6). Only three species germinated in this zone in P4 (Table 5) while 12 species germinated in P1 (Table 4), including the three species found in P4. Of the nine species present in the OWZ of P1 but absent in the OWZ of P4 (Table 3), seven occurred in the nearby DMEZ and SMEZ of P4. Three of these species (*Scirpus* sp., *Typha* sp., and *Scolochloa festucacea*) occurred frequently in P4 emergent zone samples (Table 5), and

four (*Scirpus* sp., *Typha* sp., *Scolochloa festucacea*, and *Utricularia vulgaris*) were common components of the extant vegetation (Fig. 2). In fact, *Utricularia vulgaris* was the dominant plant in the P4 OWZ flora, despite its absence in the emergence flats.

The second major difference between wetland seed pools was in species composition (Fig. 5). The relative densities of seed species were dramatically different, although floristically the seed banks were nearly identical. For example, the three most abundant species in P1 were *Scirpus* sp. (48.5%), *Chenopodium rubrum* (26.7%), and *Typha* sp. (11.2%); these species were considerably less abundant in wetland P4: *Scirpus* sp. (2.5%), *Chenopodium rubrum* (16.0%), and *Typha* sp. (3.1%, Tables 4, 5). Therefore, similarity measures based on species composition were very low in the wetlands as a whole (IS = 0.31) and in the two emergent zones, DMEZ (IS = 0.28) and SMEZ (IS = 0.24, Fig. 5). The OWZ comparison was most similar (IS = 0.78), but the variability in this zone was high (Fig. 5).

The species that caused most of the above differences belonged primarily to two different life history groups (Fig. 6). The emergent life history group dominated the seed bank of P1, while the mudflat life history group dominated P4. Overall seed pool samples, mudflats comprised an average of 82% of the seed bank in P4 and only 52% in P1. Conversely, emergents accounted for 48% of all germinating seeds in P1 and only 17% in P4 (Fig. 6). These differences between life history groups were strongly significant ($p < 0.001$, multivariate repeated measures test, SAS 1982).

The differences between life history groups were primarily due to a shift in dominance of only a few species. For example, the two dominant species in P1 were the emergents *Scirpus* sp. and *Typha* sp.. The relative density of these emergents was 48.5% and 11.2%, respectively, in P1 and only 2.5% and 3.1%, respectively, in P4. Likewise, the two dominant species in P4 were the mudflat annuals *Rumex maritimus* and

Ranunculus sceleratus, which had a relative density of 51.7% and 23.0%, respectively, in P4 and only 5.8% and 1.2%, respectively, in P1 (Tables 4, 5).

The mean relative seed density of mudflat and emergent species also differed significantly between two of the three zones (Fig 6). A strong difference was observed in the DMEZ ($p < 0.001$, multivariate repeated measures test) where 86% of the seeds in P4 were mudflat annuals and 73% of the seeds in P1 were emergents. Statistical significance was more moderate in the OWZ ($p = 0.0224$, multivariate repeated measures test) since mudflat annuals dominated the OWZ seed banks of both wetlands (Fig. 6). The SMEZ comparison, however, was not significantly different for either group ($p = 0.10$ multivariate repeated measures test).

Inter-annual comparisons (wetland P1)

Similarity patterns

The 1985 and 1986 seed banks in P1 were similar for most comparisons. Species rank-order, total seed density, and floristic composition in both the pooled and individual zones generally did not differ between years. The rank-order of all species arranged by density was significantly correlated ($p < 0.01$). Spearman coefficients were high between the pooled zones (0.83) and between all individual zones (0.66, 0.77, and 0.81 for the OWZ, DMEZ, and SMEZ, respectively). Total seed density was generally similar between years, i.e., mean seed density was not significantly different (ANOVA,

$p > 0.05$, Fig. 3) between whole wetlands and for two of the three individual zones (OWZ and SMEZ).

Finally, floristic composition in P1 differed little between years ($IS = 0.80$, Fig. 7). For example, both yearly seed banks were dominated by *Chenopodium rubrum*, *Ranunculus sceleratus*, *Rumex maritimus*, *Scirpus* sp., and *Typha* sp. (Tables 4, 7). As was observed in the 1985 inter-wetland comparisons, the minor compositional differences between years were due to the sporadic appearance of rare species ($IS = 0.94$ when rare species were omitted versus 0.80 with rare species included--one plant in one sample in either year). The five species present only in 1985 had a total relative density of 0.26%, while the total relative density of the three species found only in the 1986 seed bank was even lower (0.07%, Table 3). Floristics were also similar between individual zones for each year (Fig. 7).

Floristic composition between years by life history group varied in similarity (Table 8). If a life history group was comprised of common species, such as the emergents, it changed little overall (Table 8). When life history groups were dissimilar between years (e.g., the mudflat annuals in the OWZ where 50% were in common or the meadow species in the DMEZ with 0% in common, Table 8), it was due to the sporadic presence of uncommon and rare species.

Dissimilarity patterns

Only two statistically significant differences occurred in the inter-annual seed pool comparisons. First, a marginal difference in total seed density was found in the DMEZ. Second, as in the inter-wetland seed pool comparisons, a primary difference occurred between years in species composition, particularly in the DMEZ.

Only in the DMEZ was total seed density in 1985 (2840 $\pm$486, mean $\pm$ standard error of the mean) significantly lower than in 1986 (9370 $\pm$2675, ANOVA, $p = 0.0497$, Fig. 3). The higher seed density in the 1986 DMEZ was almost exclusively due to a higher 1986 density of *Chenopodium rubrum* seedlings. The density of this species in the DMEZ increased by an order of magnitude from 673 seeds/m^2 in 1985 to 6397 seeds/m^2 in 1986 (Tables 4, 7). Extreme variation in the seed density of certain species between years is not unknown in wetlands (van der Valk & Davis 1979, Smith & Kadlec 1985). For example, *Leersia oryzoides* increased from 163 to 7800 seeds/m^2 over two sample years in a prairie glacial marsh in Iowa without an apparent change in vegetation (van der Valk & Davis 1979).

Moderate differences in species composition between years were observed in the wetland as a whole, life history groups, and in zones. For example, similarity coefficients based on species densities were relatively low (Fig. 8). Similarity was lowest in the DMEZ ($IS = 0.54$), but high variation indicates that none of these differences among zones were significant (Fig. 8). As previously described, the most striking change in density occurred in *Chenopodium rubrum*, which increased in relative abundance overall zones from 26.7% in 1985 to 61.7% in 1986 (Tables 4, 7).

As a result of the dramatic but marginally significant increase in *Chenopodium rubrum* in the DMEZ, as well as an increase in the other ubiquitous mudflat species in 1986, the mean relative density of the mudflat life history group was significantly greater in this zone (multivariate repeated measures test, $p = 0.02$, Fig. 5). Mudflat annuals comprised 61% of the 1986 DMEZ seed bank and only 27% in 1985 (Fig. 5). Overall zones, mudflat annuals in 1986 were also significantly greater in mean relative density (multivariate repeated measures test, $p = 0.03$). The number of mudflat annuals between years in the OWZ and the SMEZ was not significantly different for this life history group (multivariate repeated measures test, $p > 0.05$).

Intra-wetland comparisons

Similarity patterns

Comparisons of zones within each of wetlands P1 and P4 showed similarities in seed pool composition. In general, all three zones within a wetland were floristically similar, and no significant differences in total seed density were observed among the zones of P4.

As was observed in other prairie pothole marshes (van der Valk & Davis 1976, Pederson & van der Valk 1984), there was relatively little floristic variability among the zonal seed banks of wetland P1 (Table 9). The dominant species in this wetland (*Scirpus* sp., *Typha* sp., *Rumex maritimus*, *Ranunculus sceleratus*, and *Chenopodium rubrum*) in 1985 and 1986 were found in every zone (Tables 4, 7). The presence or absence of uncommon and rare species caused the small and generally insignificant differences between zones. Zonal comparisons in P4, however, yielded low similarity coefficients because of the paucity of species in its OWZ (Table 9). When floristic composition was compared between the two emergent zones (DMEZ-SMEZ) similarity was considerably higher (IS = 0.57).

The uniformity among zones in floristic composition (particularly in P1) indicates that most life history groups are rather ubiquitously distributed. This was especially true for the emergents, the open water species and the common mudflat annuals (Tables 6, 8). Exceptions included meadow and rare mudflat species. An increasing number of meadow species was found landward (Tables 6, 8). The DMEZ seed banks had fewer meadow species in general than the SMEZ, and this life history group was completely

absent in all the OWZ seed banks. The less frequently occurring mudflat species were primarily found in the OWZ and the DMEZ. In fact, any mudflat species which germinated from the SMEZ seed pool was present in every zone for that particular wetland and year.

The second seed pool variable which was similar across all zones in wetland P4 was total seed density. Open water and vegetated areas in this wetland showed no significant differences in mean density (Least Squares means separation procedure, $p > 0.05$, SAS 1982, Fig. 9). This pattern was also reported for prairie glacial marshes in Iowa (van der Valk & Davis 1976, 1978, 1979), where seed density in open water areas was equivalent to or exceeded seed density in vegetated zones.

Dissimilarity patterns

The only seed pool variables that differed among wetland zones were total seed density in P1 and species composition in both P1 and P4. Seed density (no./m^2) in all three P1 zones was significantly different in 1985 (Least Squares, $p > 0.05$, Fig. 9). Density (no./m^2) increased landward: OWZ = 1309, DMEZ = 2840, SMEZ = 9893 (Table 4, Fig. 3, 9). The OWZ for P1 (1986) was significantly lower in seed density than the emergent zones (DMEZ and SMEZ), which themselves were not significantly different (Figs. 3, 9). Low seed density in open water areas was also observed in deep lakes (Haag 1983, Keddy & Reznicek 1982, 1984) and larger, deeper inland marshes (Pederson 1981, Smith & Kadlec 1983).

Species composition also varied among wetland zones, particularly in the two dominant life history groups. In both wetlands and years, the mean relative density of the emergent life history group increased landward. Emergent seeds in the OWZ of P1

(1986) comprised only 20% of the total seed bank, increased to 39% in the DMEZ and then to 56% in the SMEZ (Fig. 6). Conversely, the mudflat annual portion of the seed bank decreased landward. This life history group comprised 76% of the OWZ in P1 (1985). Mudflat annual seeds were reduced to 27% in the DMEZ and 23% in the SMEZ (Fig. 6).

Discussion

Methods of seed bank estimation

Overall, the emergence method proved accurate in estimating wetland seed pools. This method yielded more species than the separation technique. Germination of seeds in the greenhouse was better for identifying uncommon and rare seed species because of the larger amount of soil used.

The emergence method, however, was weaker in assessing open water species because it may have failed to meet their germination requirements. Several environmental factors could have contributed to the low germination rates of open water species under the submerged treatment including excessively high water temperatures (Smith & Kadlec 1983), suspension of fine organic sediments in the standing water, and herbivorous invertebrates. In addition, open water species may germinate more readily in water deeper than prescribed in the emergence method (2-3 cm, van der Valk & Davis 1978). Muenscher (1936) used tap water 20-30 cm deep in laboratory germination

experiments of 21 species of *Potamogeton*, while 20-30 cm of water was recommended for field propagation of the same genus (Sharp 1939).

The open water species that was underestimated in this study, *Utricularia vulgaris*, was also relatively uncommon in other prairie marsh seed banks. *Utricularia vulgaris* had a relative abundance of 0.34% in the seed bank of Delta Marsh, Manitoba, Canada (Pederson 1981), and 0.04% in the seed pool of Eagle Lake, Iowa (van der Valk & Davis 1978). Since both studies used a similar emergence method, it may have been underestimated in these studies as well.

The reliability of the emergence technique differed among types of wetlands. In several other studies important wetland species were sometimes missed or their abundance underestimated (van der Valk & Davis 1978, Pederson 1981, Smith & Kadlec 1983). Conclusions that the emergence method was inaccurate were not based on systematic separation of seeds, however, but on a variety of other factors including: 1) a casual examination of apparently viable seeds of *Sparganium eurycarpum* and *Scirpus fluviatilis* compared to emerged seedlings (van der Valk & Davis 1978), 2) a low number of *Scirpus acutus* (Pederson 1981) and *Phragmites australis* (Smith & Kadlec 1983) seedlings compared to the number of seedlings for other marsh dominants, and 3) the low number of *Tamarix pentandra*, *Potamogeton crispus*, and *P. pectinatus* seedlings compared to a greater number of seedlings that germinated from a drawdown in the field (Smith & Kadlec 1983). Thus, at least an initial check of this method by systematic seed separation should be made to determine if the cause of underestimation is due to either a faulty emergence method or other factors.

The results of the present study support the conclusions found in agricultural seed banks. Jensen (1969) compared methods in arable soils in Denmark and concluded that a combination of laboratory and greenhouse procedures would give the best estimates of these seed banks.

General and annual seed pool trends

Results from seed pool comparisons of wetlands and years support some of the general observations made in other prairie marsh seed banks. For example, seed density in shallow glacial marshes is significantly greater than in natural terrestrial plant communities (van der Valk & Davis 1978, 1979) but less than agricultural systems (Jensen 1969, Kropac 1966). Seed density in wetland P1 (1309-9893 seeds/m^2) was greater than estimates in forests (0-3400 seeds/m^2, Moore & Wein 1977), but much less than arable fields (600-496,200 seeds/m^2, Jensen 1969). Caution should be used in comparing absolute seed density among types of ecosystems because of differences in methodology; the general relationships, however, are apparent in these data (van der Valk & Davis 1978).

In addition, my study clearly illustrates the extreme variability in seed density characteristic of other wetlands (van der Valk & Davis 1976, 1978, 1979, Smith & Kadlec 1983, 1985, Pederson 1981, Pederson & van der Valk 1984, Keddy & Reznicek 1982). Variation in total seed density as well as the densities of most individual species was apparent both within and between wetlands P1 and P4. It is probable that the major seed pool difference between years in P1 (i.e., the marginally significant increase in *Chenopodium rubrum* seedlings) also reflects the heterogeneous nature of seed distribution rather than a predictable or consistant annual trend. No known drawdown occurred between years in P1 and therefore, very few (if any) mudflat annual seeds should have been added to the seed pool. (Unavoidable variation in methodology, e.g., differences in greenhouse temperatures, between years may have contributed to the increased germination of this species as well.)

Effect of hydroperiod on seed pools

Floristic composition

The major question addressed in this study was whether seed pool composition significantly differed between two wetlands with the same general size, vegetation and water quality but with different hydroperiods. I found that the floristic composition of the seed banks in these wetlands was extremely similar, except in the OWZ. This suggests that the major factors that were similar between the wetlands, i.e., extant vegetation, salinity, size, climate and location, generally were more influential than hydroperiod in shaping seed flora.

The seed banks of both wetlands were also similar in open water species. This was surprising because the major difference between the wetlands in the extant vegetation was the open water group (Fig. 2). Two factors may have contributed to the similarity in open water species. First, P1 and P4 were close in proximity (200 m, Fig. 1), and feeding waterfowl could easily transport seeds between the marshes. The fruits of *Potamogeton pectinatus*, for example, are one of the most abundant and important wild-duck foods in North Dakota (Metcalf 1931). In addition, seeds of open water species may have been present in the seed pool from a time when water levels were higher in P4 and environmental conditions supported open water species (Rabinowitz 1981).

The floristic similarities found between the seed banks of P1 and P4 did not match trends observed among the seed banks of eight prairie marshes in Iowa (van der Valk & Davis 1976). They found an average Sorensen similarity coefficient between wetland

zones of only 0.24-0.28. The eight marshes, however, ranged dramatically in size, distance from one another and extant vegetation (van der Valk & Davis 1976).

The primary floristic difference was the lower species diversity in the OWZ of P4 than in P1. The lower diversity in P4 was probably an artifact of sample size rather than a true difference in seed bank composition. Only two samples were collected in the OWZ of P4 (versus 12 samples in P1) because of its small size. Further, many of the common seed bank species that were lacking in the OWZ of P4 germinated in large quantities from the other zones in P4 which were sampled more intensively.

Finally, the relatively uniform floristic composition within the zones of each wetland, P1 and P4, is similar to the patterns observed in other northern inland marshes (Pederson 1981, van der Valk & Davis 1976, 1978, 1979, Smith & Kadlec 1983, 1985). Environmental factors in a wetland, including hydroperiod, apparently have little effect on seed pool floristic composition among the zones of a wetland. The seeds of most wetland species are water- or wind-dispersed (Sculthorpe 1967) and can potentially reach all areas in a marsh (van der Valk & Davis 1976, 1979, Pederson 1981).

Seed density

In contrast to floristic composition, two seed bank parameters, probably affected by hydroperiod, differed between the wetlands. First, the relative density of mudflat annual versus emergent seeds was significantly different between P1 and P4. Due to a shorter hydroperiod, greater and more frequent exposure of substrate occurs in P4. Short-lived annuals readily exploit this habitat (Harris & Marshall 1963, Merry & Slater 1978, Salisbury 1970), and can build up large pools of their seeds in P4 zones by wind and water dispersal (van der Valk & Davis 1978). In contrast, the longer hydroperiod

of P1 means that the primary input to the seed pool is from seeds of emergent species (van der Valk & Davis 1978).

Intra-wetland patterns revealed that mudflat annual seeds dominated the OWZ of both wetlands, despite their differences in hydroperiod. Mudflat annuals primarily colonize the OWZ during drawdown because this zone provides exposed substrate free of emergent vegetation and plant litter compared to the emergent zones. Thus, during drawdown millions of long-lived annual seeds are added directly to the OWZ seed pool (van der Valk & Davis 1978, Cook 1980). Van der Valk & Davis (1979) estimated that the annual seed production in a mature *Bidens cernua* stand was 555,750 seeds/m^2, and the estimated number of seeds per plant or flowering shoot of *Rumex* spp. was 13,000 to 98,250. In addition, the relative density of mudflat annual seeds decreased landward. Although some mudflat annual seeds get dispersed to emergent zones during drawdown, a thick mat of plant litter during drawdown inhibits their germination and establishment (van der Valk 1986).

A second seed bank parameter possibly affected by hydroperiod was the difference in seed density among the zones of a wetland. The larger, deeper wetland with a longer hydroperiod (i.e., P1), tended to accumulate significantly fewer seeds/unit area in its OWZ than in its emergent zones; P4 (a smaller, shallower wetland with a shorter hydroperiod) accumulated an equivalent seed density in these two areas. Low seed density in open water areas has been observed in deep lakes (Haag 1983, Keddy & Reznicek 1982, 1984) and large, deep inland marshes (Pederson 1981, Smith & Kadlec 1983). Conversely, seed density in open water and vegetated areas was comparable in a shallow prairie glacial marsh in Iowa (van der Valk & Davis 1976, 1978, 1979). The results of this study indicate that a more stable water regime produces a significantly lower seed density in open water areas, while wetlands with highly fluctuating water levels have a greater number of seeds in their open water areas (van der Valk 1981).

An additional factor lowering seed input in areas of open stable water could have been the lack of emergent vegetation to trap wind- and water-dispersed seeds (Smith & Kadlec 1983, 1985). Seeds may have been blown through the OWZ where they were then trapped against existing vegetation and litter and became incorporated into the seed banks of the emergent zones.

The results of this study clearly showed significant differences between seed pools of wetlands with different hydroperiods. Lack of replicate wetlands (i.e., pseudoreplication, Hurlbert 1984), make any conclusions attributing these differences solely to hydroperiod only tentative. However, as discussed above, results from other studies as well as an understanding of ecological processes lend support to the conclusion that hydroperiod influences seed bank composition in a predictable way.

If hydroperiod influences seed pool composition in semi-permanent wetlands as this study suggests, then a wetland's seed bank may be indicative of its hydroperiod. For example, a seed bank with 1) a high proportion of mudflat annual to emergent seeds, and 2) a high seed density in open water areas should indicate a wetland with a relatively short hydroperiod (e.g., P4). Since seed pools in prairie wetlands integrate environmental characteristics over time, estimating hydroperiod by sampling a seed pool may be much less difficult and less costly compared to long-term hydrologic monitoring. Use of seed bank composition to estimate (predict) hydroperiod may be most accurate when wetlands are similar in their major parameters (e.g., water quality, size, location, climate, extant flora).

Seed banks and model development

The results of this study lend insight as well as raise questions in the development of a predictive vegetation model. The potential flora in a wetland (i.e., the composition of the seed bank and current vegetation) was a major parameter in the van der Valk (1981) model of prairie marsh vegetation dynamics. This study showed that two slightly brackish, semi-permanent wetlands with differing cover proportions and hydroperiods had qualitatively similar seed banks (potential flora). Thus, they should respond similarly to the same changes in environment.

There are several other factors, however, that could complicate the problem and lead to inaccurate predictions. Seed recruitment and germination conditions, including the presence of pre-existing vegetation and its corresponding litter (van der Valk 1986), soil moisture (van der Valk 1986), salinity, temperature and light (Galinato & van der Valk 1986) influence the potential flora. In addition, biological factors such as competition, allelopathy, predation and pathogens may also shape the developing plant community (van der Valk 1981, 1986). Any or all of these factors may differ between (and even within) wetlands over time. To improve the accuracy of the van der Valk (1981) conceptual model it may be necessary to include some of these additional factors.

Quantification of the conceptual model is also a major objective in current ecological research on prairie marshes (van der Valk 1981). This study showed several important quantitative differences between the seed pools of wetlands with different hydroperiods, some of which may be important in model development. For example, the difference in the relative density of mudflat annual seeds between the wetlands should be reflected in the vegetation composition during the drawdown phase of a simulation

model. During the other stages of the wetland cycle, these mudflat species primarily persist only as seeds in the soil.

A second difference was found in the absolute number of seeds for most species and overall. These differences, however, may not be a critical component in a general quantitative model. Given such large numbers of seeds, it is likely that intra- and interspecific competition, pathogens, herbivores and other biological factors will eliminate all but a few of the germinating seedlings. The number of seeds that form the mature plant community (i.e., threshold levels) may be more important in model development. In addition, most wetland species establish by vegetative reproduction (Sculthorpe 1967), possibly decreasing the importance of absolute seed numbers. In general, much more information is needed on the threshold seed levels of species and on the autogenic aspects present in maturing vegetation.

Finally, extreme variation in the relative densities of seed species was observed between and within wetlands and years. This heterogeneous distribution of seeds may make the development of an accurate quantitative model for a generalized wetland type (e.g., slightly brackish, semi-permanent) more difficult. A detailed understanding of wetland seed banks remains critical to the success of any quantitative model.

Conclusions

1. The seedling emergence method was accurate in assessing wetland seed bank composition and proved to be superior and more time efficient in estimating uncommon species because of the large volume of soil that can be used. Providing conditions in the submerged treatment that are more conducive to the germination of open water species would significantly improve the method.

2. Two slightly brackish, semi-permanent prairie wetlands, which differed in hydroperiod and relative width of zones, had similar seed flora (i.e., presence/absence of species). The only exception occurred in the OWZ, and this was probably due to a small sample size.

3. Hydroperiod may have influenced the relative density of mudflat annual and emergent seeds in the seed pool. In general, the seed pool of the semi-permanent wetland with a shorter hydroperiod and more frequent drawdowns (P4) had more mudflat seeds than emergents. Conversely, a wetland with a longer hydroperiod (less frequent drawdowns)

had a seed pool dominated by seeds of emergent species. In addition, the relative densities of individual species were extremely variable between wetlands.

4. Floristic composition (presence/absence) was relatively homogeneous across the zones of a wetland. Since most aquatic and emergent seeds are water- and wind-dispersed, they are able to reach all areas in a marsh. Species composition (i.e., relative densities), however, differed among wetland zones.

5. Total seed density patterns differed among wetland zones. In the wetland exhibiting a shorter hydroperiod (P4), total seed density was approximately equal in all zones. Conversely, seed density in open water areas was significantly lower than in emergent zones in the wetland with a longer hydroperiod (P1). The large relatively stable open water area of this wetland probably experienced smaller seed inputs and trapped fewer seeds than landward emergent zones.

6. The two seed bank parameters possibly influenced by hydroperiod, i.e., the relative density of mudflat versus emergent seeds and the spatial distribution of all seeds may be useful in: 1) predicting seed bank composition based on a given hydroperiod, or 2) determining an unknown hydroperiod from characteristics of its seed bank. The latter may save both time and money compared to long-term hydrologic monitoring.

7. Without a change in mature vegetation, no major differences in floristic patterns were observed between years. As in inter- and intra-wetland trends, the extreme variability in species densities was apparent between years. The most striking example was the difference in the relative density of *Chenopodium rubrum* seeds.

8. To develop an accurate quantitative model of vegetation dynamics in prairie marshes, the following areas of wetland ecology in particular need further attention: environmental and biological factors affecting recruitment of seeds from the seed pool, and the number of seedlings needed to establish new areas of mature vegetation.

Figures and Tables

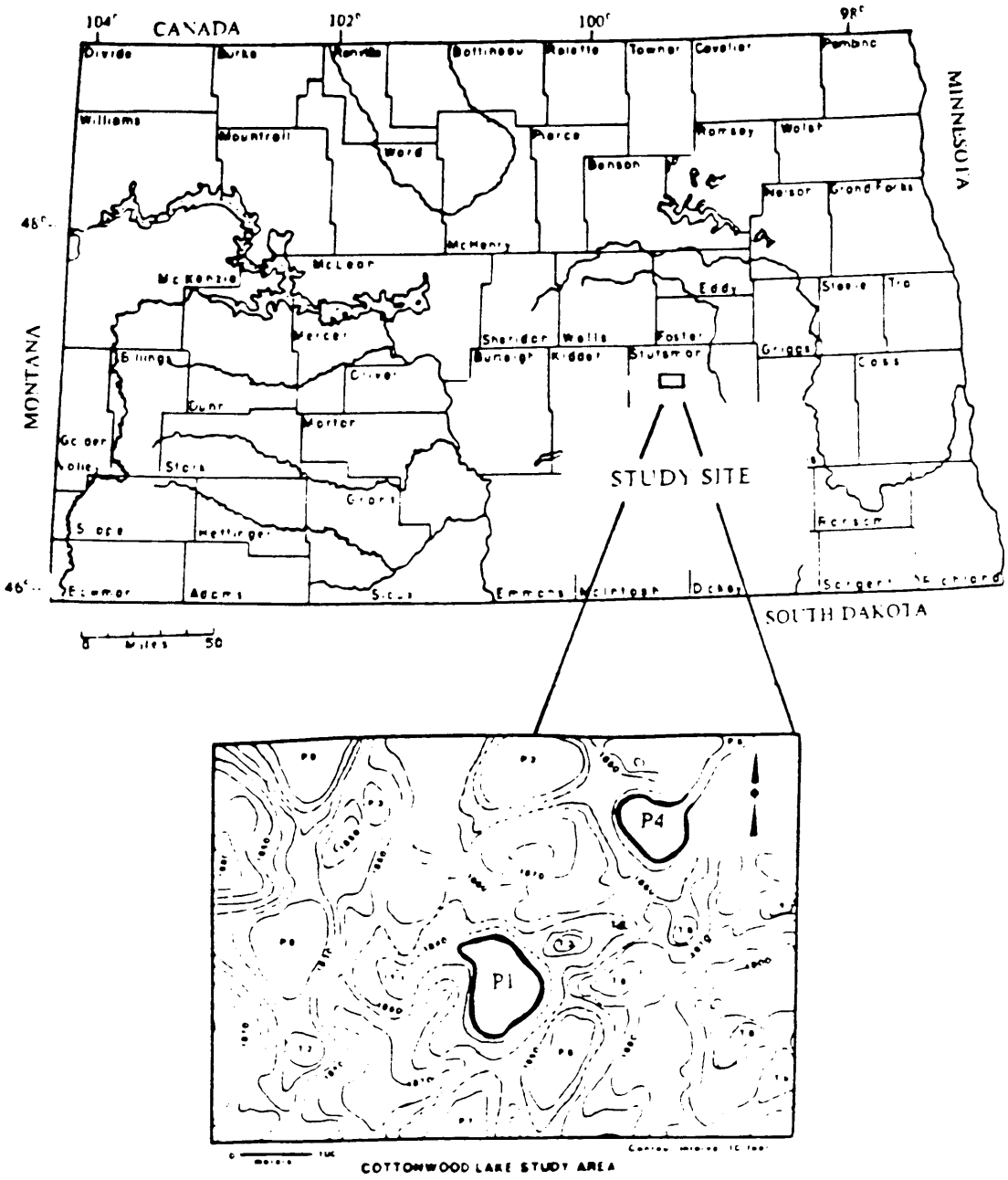
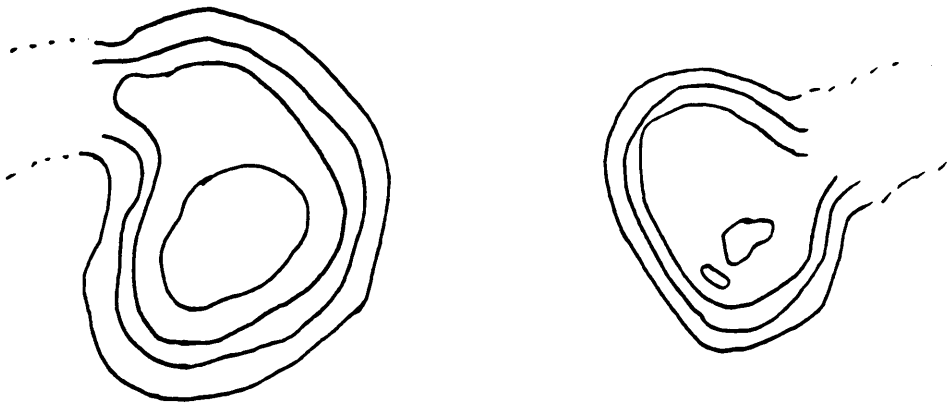


Figure 1. Location of semi-permanent wetlands P1 and P4: Cottonwood Lake Area, Stutsman County, North Dakota.



WETLAND P1 WETLAND P4

Zones from center landward: Open water zone (OWZ), Deep marsh emergent zone (DMEZ), Shallow marsh emergent zone (SMEZ), Wet-meadow zone (WMZ).

OWZ:	*Lemna minor* *Lemna trisulca* *Utricularia vulgaris* *Potamogeton pectinatus* *Myriophyllum exalbescens*	*Lemna minor* *Lemna trisulca* *Utricularia vulgaris*
DMEZ:	*Typha* spp. *Scirpus acutus*	*Typha* spp. *Scirpus acutus* *Scholochloa festucacea*
SMEZ:	*Scirpus acutus* *Carex atherodes* *Spartina pectinata* *Eleocharis* spp. *Calamagrostis canadensis*	*Scirpus acutus* *Carex atherodes* *Spartina pectinata* *Eleocharis* spp. *Calamagrostis canadensis*
WMZ:	*Sonchus arvensis* *Cirsium arvense* *Agropyron repens* *Poa palustris* *Juncus balticus* *Teucrium occidentale* *Potentilla anserina* *Hordeum jubatum*	*Sonchus arvensis* *Cirsium arvense* *Agropyron repens* *Poa palustris* *Juncus balticus* *Teucrium occidentale* *Potentilla anserina* *Hordeum jubatum*

Figure 2. Concentric wetland zones and dominant vegetation: wetlands P1 and P4, July 1985.

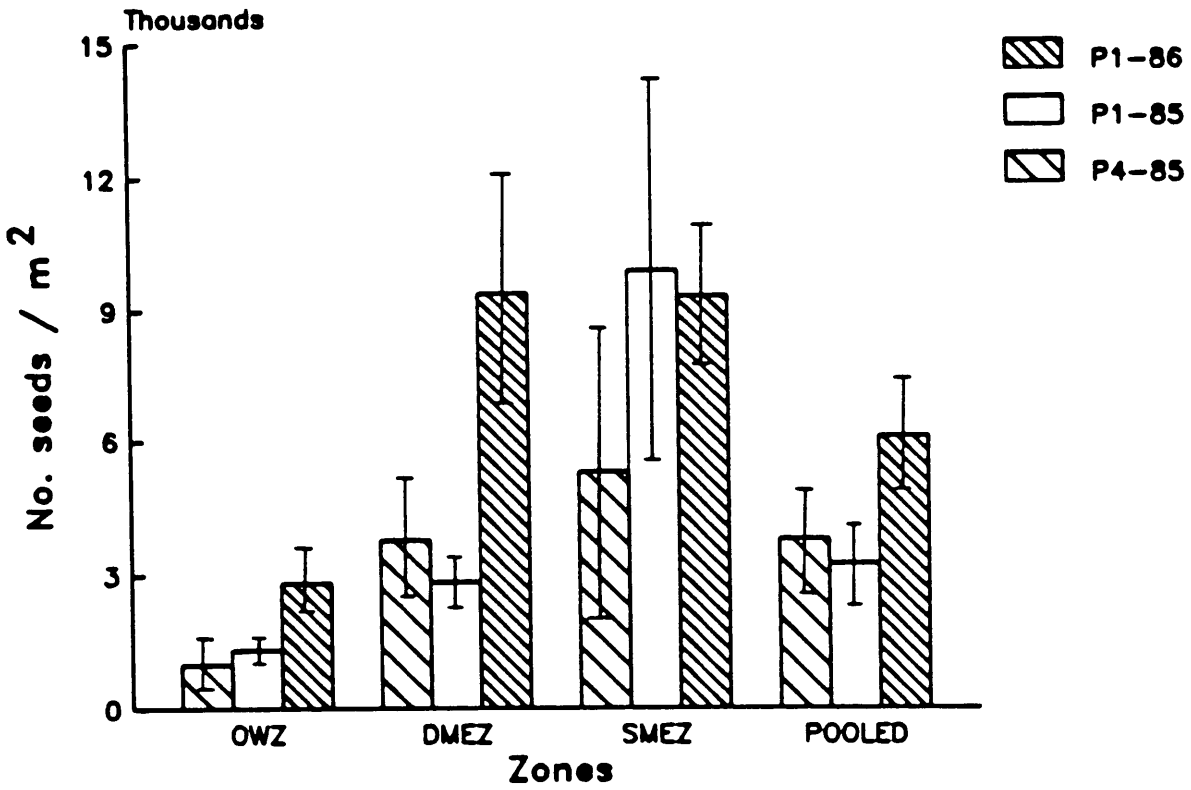


Figure 3. Mean number of seeds/m^2 for wetlands and years: P1 (1985 and 1986) and P4 (1985), individual and pooled zones, emergence method. Bars represent standard error of the mean. OWZ = open water zone; DMEZ = deep marsh emergent zone; SMEZ = shallow marsh emergent zone.

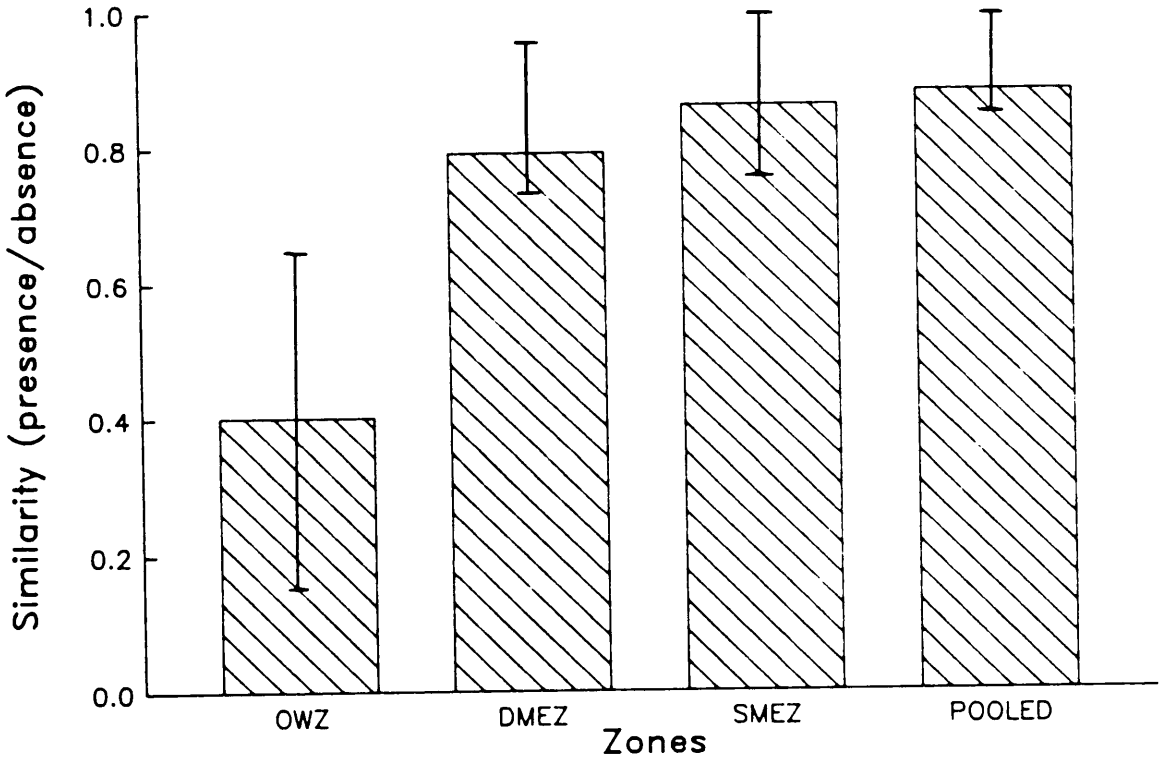


Figure 4. Index of similarity (presence/absence) between wetlands (1985): overall and by zone, emergence method (Sorensen 1948). Bars represent 95% confidence intervals around the mean coefficient as computed by the bootstrap statistical procedure (Smith 1985). Confidence intervals are not symmetric because points plotted represent overall coefficients calculated from pooled samples within a zone. OWZ = open water zone; DMEZ = deep marsh emergent zone; SMEZ = shallow marsh emergent zone.

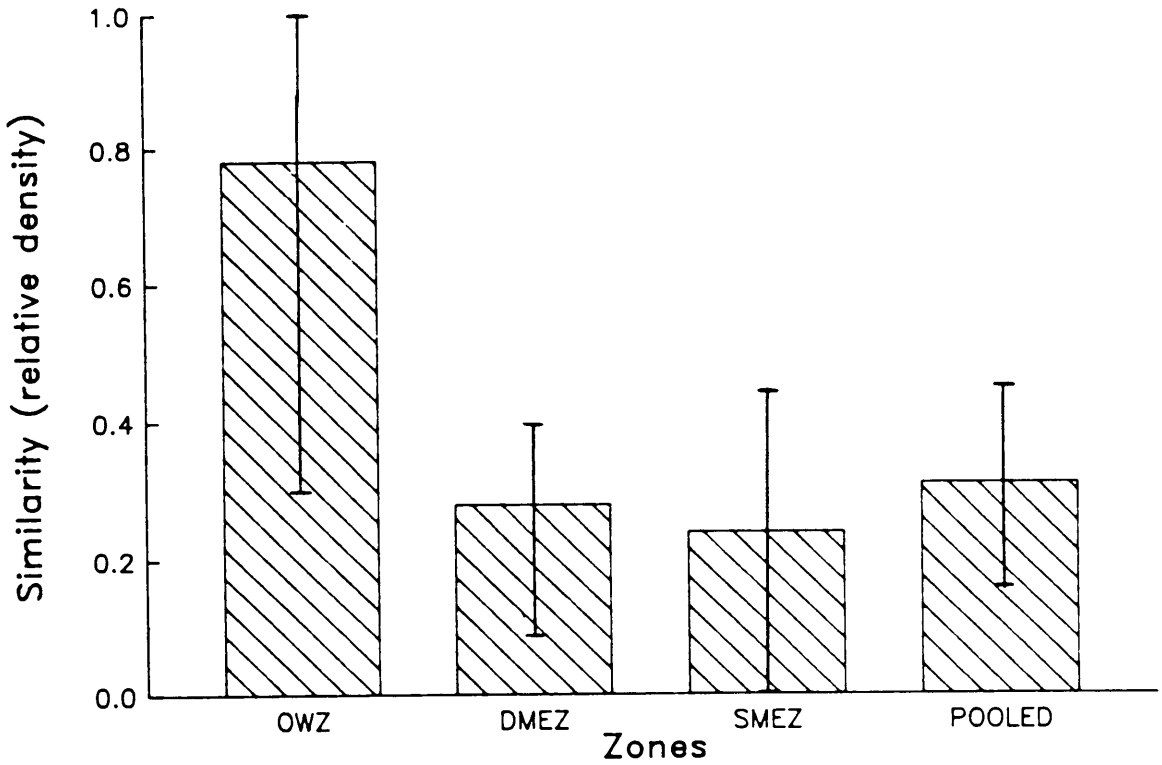
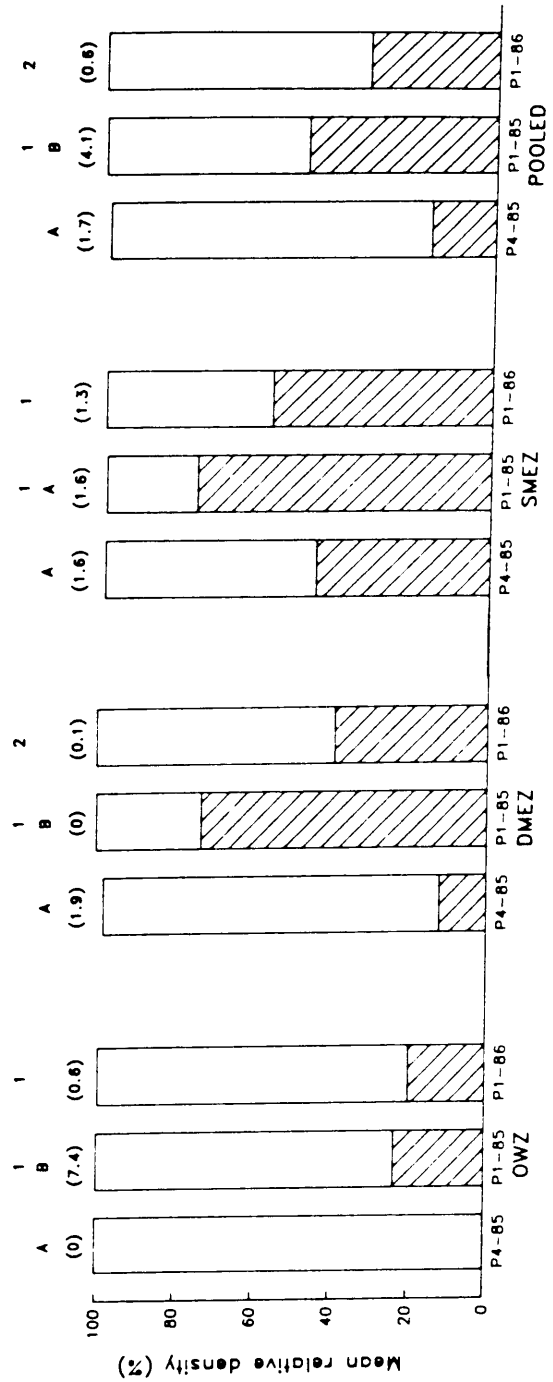


Figure 5. Index of similarity (relative density) between wetlands (1985): overall and by zone, emergence method (Sorensen 1948). Bars represent 95% confidence intervals around the mean coefficient as computed by the bootstrap statistical procedure (Smith 1985). Confidence intervals are not symmetric because points plotted represent overall coefficients calculated from pooled samples within a zone. OWZ = open water zone; DMEZ = deep marsh emergent zone; SMEZ = shallow marsh emergent zone.

Figure 6. Mean relative density of life history groups for wetlands and years: P4 (1985) and P1 (1985 & 1986), emergence method. Bar height indicates the mean relative density of mudflat annual and emergent groups. The small proportion of open water and meadow life history groups were combined and their mean relative density is given in ( ) at tops of bars. Mean relative densities of emergent and mudflat groups were compared between wetlands and years using a multivariate repeated measures test (SAS 1982). Significant differences *between wetlands* for pooled and individual zones are indicated by different *letters*. Significant differences *between years* (P1) for pooled and individual zones are indicated by different *numbers*. OWZ = open water zone; DMEZ = deep marsh emergent zone; SMEZ = shallow marsh emergent zone.


Mean relative density (%)
100
80
60
40
20
0
OWZ
DMEZ
SMEZ
POOLED
A (0) P4-85
1 B (7.4) P1-85
1 1 (0.6) P1-86
A (1.9) P4-85
1 B (0) P1-85
1 2 (0.1) P1-86
A (1.6) P4-85
1 A (1.6) P1-85
1 1 (1.3) P1-86
A (1.7) P4-85
1 B (4.1) P1-85
1 2 (0.6) P1-86

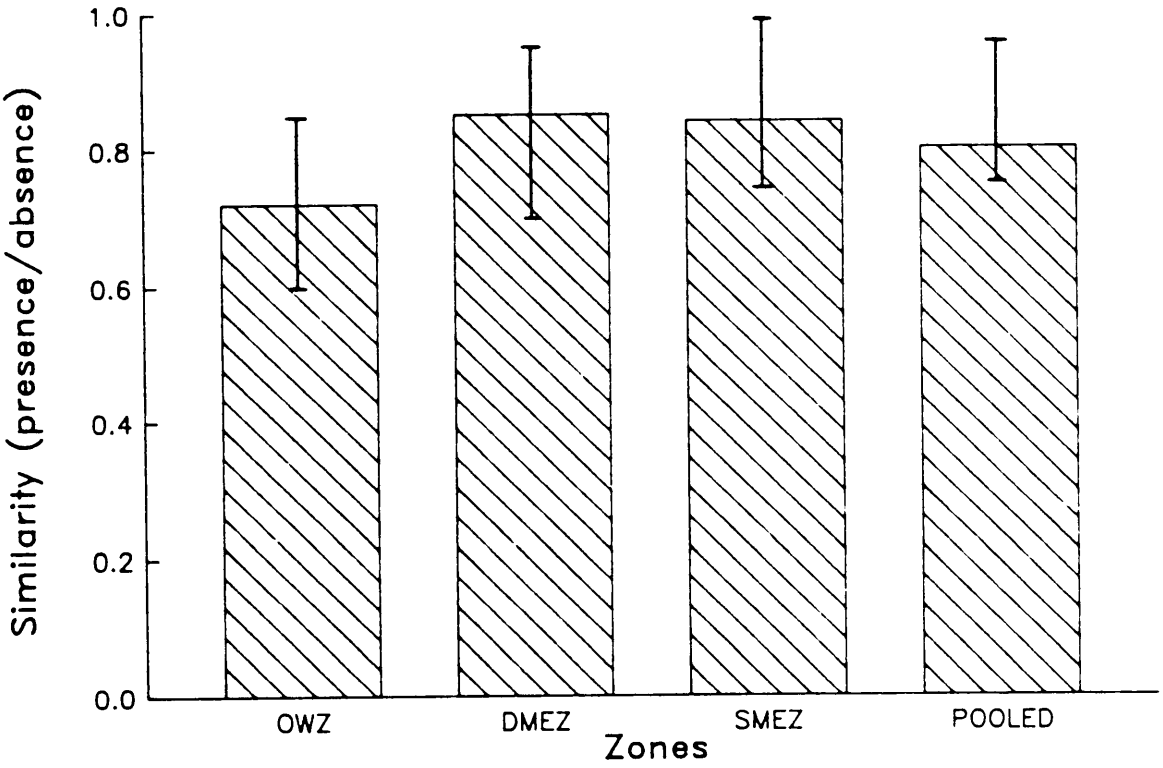


Figure 7. Index of similarity (presence/absence) between years (P1): overall and by zone, emergence method (Sorensen 1948). Bars represent 95% confidence intervals around the mean coefficient as computed by the bootstrap statistical procedure (Smith 1985). Confidence intervals are not symmetric because points plotted represent overall coefficients calculated from pooled samples within a zone. OWZ = open water zone; DMEZ = deep marsh emergent zone; SMEZ = shallow marsh emergent zone.

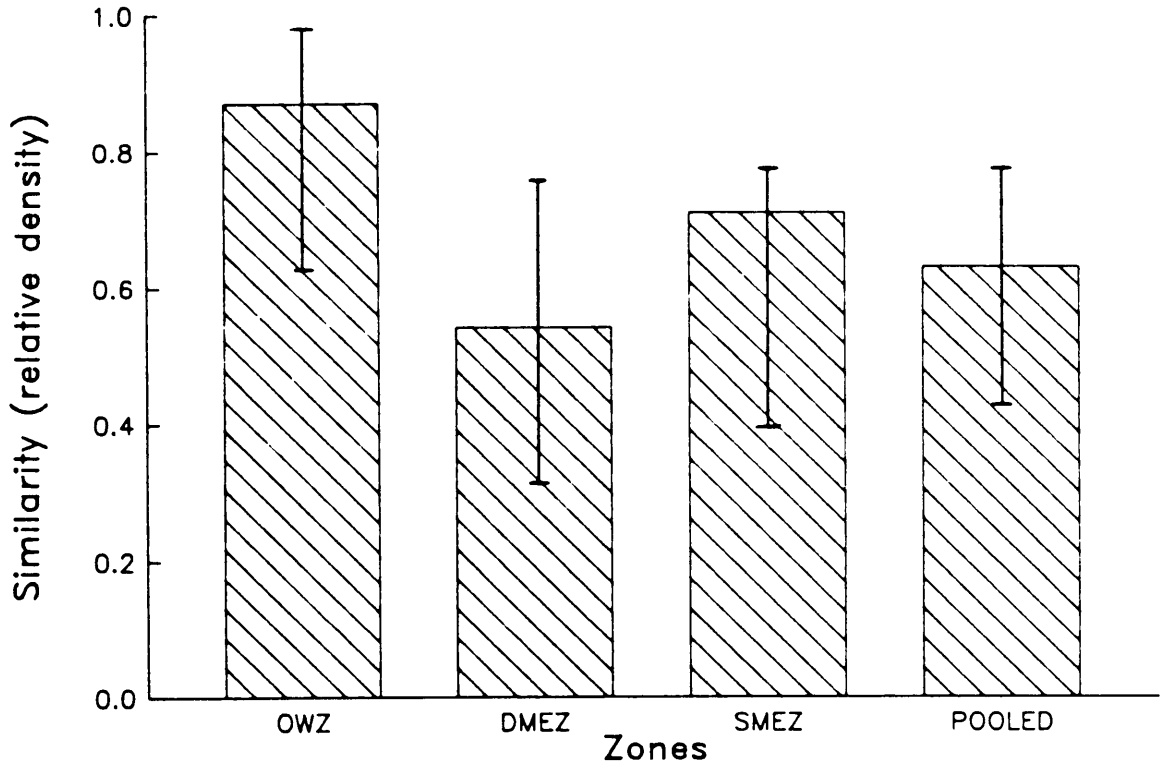


Figure 8. Index of similarity (relative density) between years (P1): overall and by zone, emergence method (Sorensen 1948). Bars represent 95% confidence intervals around the mean coefficient as computed by the bootstrap statistical procedure (Smith 1985). Confidence intervals are not symmetric because points plotted represent overall coefficients calculated from pooled samples within a zone. OWZ = open water zone; DMEZ = deep marsh emergent zone; SMEZ = shallow marsh emergent zone.

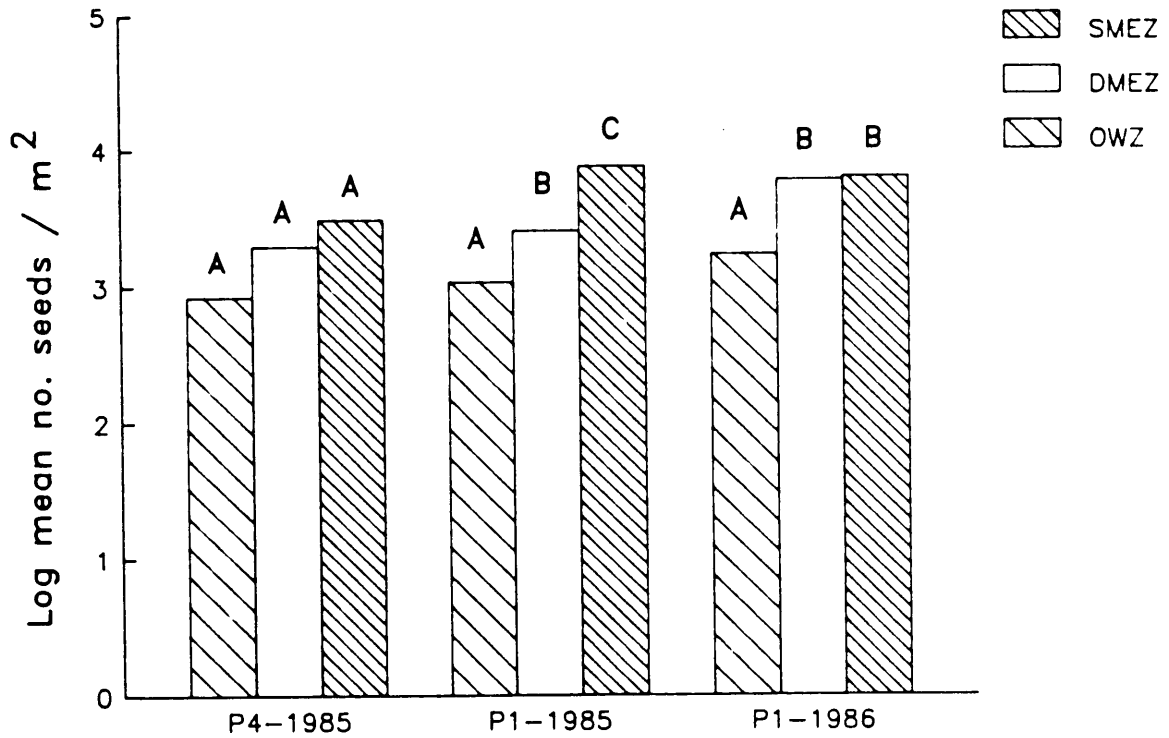


Figure 9. Log mean number of seeds/m², intra-wetland comparisons: P1 (1985 & 1986) and P4 (1985), emergence method. Different letters show significant differences *among the zones within each wetland.* Data were log transformed to meet the assumptions of the SAS (1982) general linear models parametric procedures. OWZ = open water zone; DMEZ = deep marsh emergent zone; SMEZ = shallow marsh emergent zone.

Table 1: Species comprising each life history group (after van der Valk 1981).

Life History Groups			
Open Water A/P/VS-II*	Mudflat AS-I(all)*	Meadow PS-I(all)*	Emergent VS-I,II(all)*
Potamogeton pectinatus (V)	*Arctium minus*	*Cirsium arvense*	*Carex* sp.
Utricularia vulgaris (A)	*Chenopodium rubrum*	*Epilobium ciliatum*	*Eleocharis* sp.
Zannichellia palustris (V)	*Conyza canadensis*	*Potentilla* sp.	*Juncus* sp.
	Euphorbia maculata	Lamiaceae	*Juncus torreyi*
	Polygonum pensylvanicum	*Mentha arvensis*	*Scirpus maritimus*
	Potentilla rivalis	*Potentilla anserina*	*Scolochloa festucacea*
	Ranunculus sceleratus	*Potentilla norvegica*	*Typha* sp.
	Rumex acetosella	*Sonchus arvensis*	*Scirpus acutus/validus***
	Rumex maritimus		
	Solanum ptycanthum		

* A = annual; P = perennial with limited life-span; V = vegetatively reproducing perennial without a limited life-span; S = seed pool species; I = only germinates free of standing water; II = germinates in standing water.

**Identification between *S. acutus* and *S. validus* could not be confirmed based on vegetative characteristics.

Table 2: Number of emerged seedlings and seeds isolated and their relative densities for the sixteen 1985 field samples. Species are arranged in order of decreasing density of emerged seedlings.

	Method			
	Emergence**		Separation	
Species	Seedlings emerged	Relative density(%)	Seeds isolated	Relative density(%)
Scirpus acutus/validus + +	672	43.78	315	34.24
Chenopodium rubrum	372	24.24	243	26.41
Typha sp.	168	10.95	180	19.57
Rumex maritimus	132	8.60	92	10.00
Ranunculus sceleratus	77	5.02	29	3.15
Eleocharis palustris +	42	2.74	5	0.54
Juncus sp.	26	1.69	0	0.00
Scolochloa festucacea	14	0.91	2	0.22
Scirpus maritimus	12	0.78	3	0.33
Cirsium arvense	5	0.33	0	0.00
Sonchus arvensis	4	0.26	0	0.00
*Carex atherodes** +	2	0.13	1	0.11
Juncus torreyi	2	0.13	0	0.00
Utricularia vulgaris	2	0.13	36	3.91
*Euphorbia maculata**	1	0.07	0	0.00
*Polygonum pensylvanicum**	1	0.07	0	0.00
Lamiaceae*	1	0.07	0	0.00
*Potentilla norvegica**	1	0.07	0	0.00
Potamogeton pectinatus	0	0.00	2	0.22
Potentilla rivalis	0	0.00	4	0.44
*Mentha arvensis**	0	0.00	1	0.11
*Zannichellia palustris**	0	0.00	1	0.11
Unknown A	0	0.00	5	0.54
Unknown B*	0	0.00	1	0.11
Lemna sp.	present	--	present	--
TOTAL	1535	100	920	100

**Combines seedlings from the drawdown and submerged treatments.
*Rare species: only one seed or seedling in either method.
+ Species identification was not confirmed for the emergence seedlings.
+ + Identification between *S. acutus* and *S. validus* could not be confirmed based on vegetative characteristics.

Table 3: Differences in seed banks between wetlands (P1 and P4) and between years (P1), emergence method. Species are arranged by decreasing relative density. OWZ = open water zone.

Inter-wetland

Species present only in P1	Relative density(%)
Cirsium arvense	0.24
Arctium minus	0.04
Conyza canadensis	0.04

Species present only in P4	Relative density(%)
Potentilla norvegica	0.33
Potentilla anserina	0.04

Species present only in P1 (OWZ)	Relative density(%) in OWZ
*Scirpus acutus/validus**	48.46
Typha sp.	11.24
Scirpus maritimus	1.11
Scolochloa festucacea	0.75
Utricularia vulgaris	0.12
Polygonum pensylvanicum	0.08
Arctium minus	0.04
Conzya canadensis	0.04
Rumex acetosella	0.04

Inter-annual, P1

Species present only in 1985	Relative density(%)
Juncus torreyi	0.10
Arctium minus	0.04
Conyza canadensis	0.04
Euphorbia maculata	0.04
Rumex acetosella	0.04

Species present only in 1986	Relative density(%)
Potentilla sp.	0.03
Epilobium ciliatum	0.02
Solanum ptycanthum sp.	0.02

*Identification between *S. acutus* and *S. validus* could not be confirmed based on vegetative characteristics.

Table 4: Mean number of plants per square meter and standard error of the mean for each zone in wetland P1 for the combined treatments, 1985 emergence method. Species are arranged by decreasing relative density.

Species	Open Water n = 12 $\bar{x}$	Open Water n = 12 SE	Deep Emergent** n = 8 $\bar{x}$	Deep Emergent** n = 8 SE	Shallow Emergent + n = 4 $\bar{x}$	Shallow Emergent + n = 4 SE	Relative density (%)	Frequency (%)
Scirpus acutus/validus + +	152	63	1435	439	6278	4147	48.46	83.3
Chenopodium rubrum	959	243	673	155	989	423	26.73	100.0
Typha sp.	115	27	575	168	897	418	11.24	87.5
Rumex maritimus	66	11	170	66	804	524	5.76	70.8
Eleocharis sp.	0	0	178	*	740	222	2.12	12.5
Juncus sp.	0	0	59	*	962	*	1.31	8.3
Ranunculus sceleratus	37	7	53	17	173	75	1.20	50.0
Scirpus maritimus	70	23	133	104	37	*	1.11	45.8
Scolochloa festucacea	54	9	49	20	111	*	0.75	41.7
Cirsium arvense	0	0	0	0	185	*	0.24	4.2
Sonchus arvensis	0	0	0	0	74	0	0.19	8.3
Carex sp.	0	0	30	0	37	*	0.16	16.7
Unknown (died before identified)	30	*	0	0	37	0	0.14	12.5
Utricularia vulgaris	30	0	0	0	37	*	0.12	12.5
Zannichellia palustris	0	0	89	*	0	0	0.11	4.2
Juncus torreyi	0	0	0	0	74	*	0.10	4.2
Polygonum pensylvanicum	30	*	30	*	0	0	0.08	8.3
Lamiaceae	0	0	0	0	37	*	0.05	4.2
Arctium minus	30	*	0	0	0	0	0.04	4.2
Conyza canadensis	30	*	0	0	0	0	0.04	4.2
Euphorbia maculata	0	0	30	*	0	0	0.04	4.2
Rumex acetosella	30	*	0	0	0	0	0.04	4.2
All species combined	1309	256	2840	486	9893	4290		

* appeared in only one sample

**Deep emergent zone combines samples from *Typha* and *Scirpus* zones

+ 20% of the original sample was removed for use in the separation procedures; conversion factor was slightly different than for other zones.

+ + Identification between *S. acutus* and *S. validus* could not be confirmed based on vegetative characteristics.

Table 5: Mean number of plants per square meter and standard error of the mean for each zone in wetland P4 for the combined treatments, 1985 emergence method. Species are arranged by decreasing relative density.

Species	Open Water n = 2		Deep Emergent** n = 18		Shallow Emergent + n = 4		Relative density (%)	Frequency (%)
	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE		
Rumex maritimus	296	*	2881	1516	247	118	51.69	83.3
Ranunculus sceleratus	59	*	337	144	3892	3229	23.04	87.5
Chenopodium rubrum	799	740	747	159	86	12	15.96	91.7
Typha sp.	0	0	70	14	472	136	3.14	75.0
Scirpus acutus/validus + +	0	0	116	58	333	133	2.49	58.3
Juncus sp.	0	0	40	10	333	130	1.23	25.0
Scolochloa festucacea	0	0	55	12	37	0	0.65	50.0
Carex sp.	0	0	44	7	49	12	0.45	37.5
Potentilla norvegica	0	0	59	23	0	0	0.33	20.8
Zannichellia palustris	0	0	266	*	0	0	0.29	4.2
Eleocharis sp.	0	0	0	0	65	18	0.28	16.7
Juncus torreyi	0	0	59	30	0	0	0.13	8.3
Potentilla anserina	0	0	0	0	37	*	0.04	4.2
Scirpus maritimus	0	0	0	0	37	*	0.04	4.2
Sonchus arvensis	0	0	0	0	37	*	0.04	4.2
Utricularia vulgaris	0	0	0	0	37	*	0.04	4.2
Euphorbia maculata	0	0	30	*	0	0	0.03	4.2
Lamiaceae	0	0	30	*	0	0	0.03	4.2
Polygonum pensylvanicum	0	0	30	*	0	0	0.03	4.2
Rumex acetosella	0	0	30	*	0	0	0.03	4.2
Unknown (died before identified)	30	*	0	0	0	0	0.03	4.2
All species combined	992	547	3780	1416	5289	3423		

* appeared in only one sample

**Deep emergent zone combines samples from *Typha*, *Scirpus* and *Scolochloa* zones

\+ 20% of the original sample was removed for use in the separation procedures; conversion factor was slightly different than for other zones.

\+ + Identification between *S. acutus* and *S. validus* could not be confirmed based on vegetative characteristics.

Table 6: Percent species in common for each life history group between wetlands (1985), emergence method. Numbers in ( ) indicate the number of species in P1 and P4, respectively. OWZ = open water zone; DMEZ = deep marsh emergent zone; SMEZ = shallow marsh emergent zone.

	Life History groups			
Zones	Emergent	Mudflat annual	Meadow	Open water
OWZ	0 (4,0)	43 (7,3)	0 (0,0)	0 (1,0)
DMEZ	63 (7,6)	83 (5,6)	0 (0,2)	100 (1,1)
SMEZ	88 (8,7)	100 (3,3)	25 (3,2)	100 (1,1)
POOLED	100 (8,8)	75 (8,6)	40 (3,4)	100 (2,2)

Table 7: Mean number of plants per square meter and standard error of the mean for each zone in wetland P1 for the combined treatments, 1986 emergence method. Species are arranged by decreasing relative density.

Species	Open Water n = 24		Deep Emergent** n = 16		Shallow Emergent + n = 8		Relative density (%)	Frequency (%)
	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE		
Chenopodium rubrum	2402	616	6397	2708	2893	532	61.73	97.9
Scirpus acutus/validus + +	92	18	1949	807	3708	963	18.55	66.7
Typha sp.	169	34	760	140	1232	208	8.04	81.25
Rumex maritimus	119	35	579	247	481	151	4.03	66.7
Ranunculus sceleratus	74	15	169	69	868	149	3.16	52.1
Scirpus maritimus	174	46	177	133	0	0	1.20	41.7
Eleocharis sp.	0	0	221	67	278	93	1.12	27.1
Juncus sp.	44	*	88	44	183	38	0.52	20.8
Scolochloa festucacea	81	17	55	11	111	66	0.49	37.5
Carex sp.	44	*	125	35	115	30	0.47	25.0
Sonchus arvensis	0	0	133	*	106	18	0.23	12.5
Utricularia vulgaris	59	15	44	*	44	*	0.15	16.7
Cirsium arvense	0	0	0	0	66	13	0.09	8.3
Polygonum pensylvanicum	66	22	44	0	44	*	0.09	10.4
Zannichellia palustris	133	*	0	0	0	0	0.05	2.1
Lamiaceae	0	0	0	0	88	*	0.03	2.1
Potentilla sp.	0	0	0	0	44	*	0.03	4.2
Epilobium ciliatum	0	0	0	0	44	*	0.02	2.1
Solanum ptycanthum	44	*	0	0	0	0	0.02	2.1
Unknown (died before identified)	44	*	0	0	0	0	0.02	2.1
All species combined	2818	648	9370	2675	9306	1604		

* appeared in only one sample

**Deep emergent zone combines samples from *Typha* and *Scirpus* zones

+ 20% of the original sample was removed for use in the separation procedures; conversion factor was slightly different than for other zones.

+ + Identification between *S. acutus* and *S. validus* could not be confirmed based on vegetative characteristics.

Table 8: Percent species in common for each life history group between years (P1), emergence method. Numbers in ( ) indicate the number of species in 1985 and 1986, respectively. OWZ = open water zone; DMEZ = deep marsh emergent zone; SMEZ = shallow marsh emergent zone.

	Life History groups			
Zones	Emergent	Mudflat annual	Meadow	Open water
OWZ	67 (4,6)	50 (7,5)	0 (0,0)	50 (1,2)
DMEZ	100 (7,7)	80 (5,4)	0 (0,1)	0 (1,1)
SMEZ	75 (8,6)	75 (3,4)	60 (3,5)	100 (1,1)
POOLED	88 (8,7)	44 (8,5)	60 (3,5)	100 (2,2)

Table 9: Sorensen (1948) index of similarity (presence/absence) comparing the zones within a wetland, emergence method. OWZ = open water zone; DMEZ = deep marsh emergent zone; SMEZ = shallow marsh emergent zone.

	P4-1985	P1-1985	P1-1986
OWZ-DMEZ	0.33	0.64	0.85
DMEZ-SMEZ	0.57	0.71	0.83
OWZ-SMEZ	0.38	0.59	0.69

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