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Wetland seed banks: implications in vegetation management

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Wetland seed banks: Implications in vegetation management

by

Parvaiz Akhtar Naim

A Dissertation Submitted to the

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

GENERAL INTRODUCTION

Managed properly, wetlands provide an excellent opportunity to attract a wide variety of waterfowl and other animals to an area. To maximize the production of food and shelter for wildlife it is imperative to understand the processes that control the vegetation in a wetland. Such knowledge will be helpful both in facilitating the progress of natural ecological processes, and reducing the cost of management.

Marsh managers have long used planned water level fluctuations in attempts to keep, or return, marshes to the point of maximum productivity primarily to provide better habitat for waterfowl (Kadlec, 1962; Harris and Marshall, 1963; Meeks, 1969).

Reviewing such previous studies Weller (1978) noted that marsh management was "poorly founded in theory and as a predictive science", and called for the development of management strategies based on natural successional patterns.

In nature, periodic droughts temporarily expose the marsh bottom. This allows the viable seeds buried in soil (seed bank) to germinate and subsequently revegetate the marsh (Weller and Spatcher, 1965; Weller and Fredrickson, 1974; van der Valk and Davis, 1978). An understanding of the seed bank, therefore, becomes a key to predicting vegetation changes in wetlands as they are drawn down, naturally or artificially (van der Valk and Davis, 1976, 1978, 1979; Leck and Graveline, 1979; Pederson, 1981, 1983; van der Valk, 1981, 1985). Studies in this direction have so far been confined to looking at the total number of seeds in a relatively large bulk of soil and do not portray the vertical distribution of seeds in a soil profile (Roberts, 1981).

Because the percentage of seed germination declines considerably with increase in soil depth, it is the viable seeds in the top 2 cm soil that will contribute most to the development of future vegetation of a marsh after a drawdown (Galinato and van der Valk, 1986).

If marsh managers are to develop management strategies based on the regenerative capacity of the seed bank, they must know what seeds are there in the soil, how these seeds are distributed horizontally and vertically, and what manipulations will result in the emergence of desired vegetation at minimum cost.

During the course of this study, I was interested in elucidating the processes responsible for the distribution pattern of propagules in a soil profile, and to develop a better understanding of the mechanisms that regulate the expression of seed bank species in the future vegetation. Finally, these informations were to be used in designing management strategies to encourage the establishment of desirable plant species (Martin and Uhler, 1939) in a marsh by taking appropriate soil ameliorative measures in conjunction with water level manipulations (Fredrickson and Taylor, 1982).

Explanation of dissertation format

This dissertation is subdivided into three papers, all in a format for publication in a technical journal. References cited in the general introduction are at the end of the dissertation. References cited within a section are at the end of each section.

The first paper describes seed bank characteristics. Interactions of possible forces that may influence the seed distribution pattern in the soil profile are discussed. The second paper is concerned with the response of seeds of various wetland species to diurnally fluctuating temperatures and depth of burial. Responses of various species to soil water matric potential changes are described in the third paper. Findings of this study are summarized in the Summary-Discussion section which is followed by a complete list of references cited in the General Introduction as well as in the Summary-Discussion.

PAPER 1. WETLAND SEED BANKS: SEED DISTRIBUTION PATTERN IN SOIL PROFILE

WETLAND SEED BANKS: SEED DISTRIBUTION PATTERN IN SOIL PROFILE

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ABSTRACT

Seed distribution in the top 6 cm soil profile was examined in a wetland of the Mingo National Wildlife Refuge, southeast Missouri, in 1984 and 1985.

Seventeen species (*Amaranthus tamariscinus*, *Ambrosia artemisiifolia*, *Bidens frondosa*, *Carex tribuloides*, *Cyperus esculentus*, *C. iria*, *C. ovularis*, *Digitaria filiformis*, *Diodia virginiana*, *Echinochloa crusgalli*, *Eleocharis obtusa*, *E. smallii*, *Hibiscus lasiocarpos*, *Ipomoea hederacea*, *Leersia oryzoides*, *Leptochloa panicoides*, *Ludwigia repens*, *Panicum dichotomiflorum*, *Polygonum hydropiperoides*, and *Xanthium pensylvanicum*) were represented in the seed bank in 1984; three more (*Carex tribuloides*, *Cyperus ovularis*, and *Hibiscus lasiocarpos*) were found in 1985. Composition of the seed bank, in general, was reflective of the surface vegetation.

Both quantitative and qualitative changes occurred in the seed bank during the study period. Seed quantities of seven species (*Amaranthus*, *Ambrosia*, *Carex*, *Cyperus ovularis*, *Diodia*, *Hibiscus*, and *Polygonum*) in 1985 were significantly different ($P<.05$) than those found in 1984. Also, significant differences ($P<.05$) were found in the number of seeds present at various depths in the soil, within the years; comparatively high number of seeds were found at 2-5 cm depth in 1984, and at 2-4 cm depth in 1985. Differences in the total number of seeds present in the top 6 cm soil were non-significant between the years.

No significant relationship could be established among the seed specific density, soil physical characteristics, and the depth of occurrence of various seeds in the soil profile.

INTRODUCTION

Since the revival of interest in wetland seed banks by van der Valk and Davis (1976), several studies have focused on understanding the nature of wetland seed banks. The common denominator in all these studies is the methodology as described by van der Valk and Davis (1976, 1978). It entails sampling a bulk of wetland substrate 4-5 cm deep, stirring, removal of detritus, tubers, and rhizomes, spreading the samples in containers and subjecting them to greenhouse conditions; various water levels are maintained in the samples in an effort to mimic flooded and/or drawdown conditions. Subsequently, seedlings are identified, counted, and removed. The number of species present and their abundance are recorded. This information is extrapolated to compare seed banks of different marshes or zones within a marsh. A typical study of this nature requires about three months of observation after the samples are placed in a greenhouse.

A different sampling approach was used by Leck and Graveline (1979). They removed blocks of marsh substrate and sliced them horizontally to obtain layers from 0-2, 4-6, and 8-10 cm depths; the rest of the procedure was similar to that of van der Valk and Davis (1976, 1978).

Gaudet (1977), while studying the formation of a papyrus swamp after a natural drawdown on Lake Naivasha, Kenya, took soil samples from 0, 10, and 20 cm depths, set them out in glass dishes on a shaded bench, and watered them daily with deionized water. Seedlings emerged only from the top soil layer, with one exception in which more seedlings came from samples collected from the 10 cm depth than those from the surface.

Thompson and Grime (1979) were content to remove only the top 3 cm soil profile. These samples were air-dried with the aid of an electric fan, passed through a 1 cm-mesh sieve to remove the coarsest plant material and stones, and spread in 2 cm deep layers on 2 cm of coarse sand. A 16 h day at 20°C and an 8 h night at 15°C was provided, with an assumption that it was "suitable for the germination of seeds of a wide variety of native species." They recognized, however, that the methodology did not give an accurate picture of the seed banks. Criticizing their own technique, van der Valk and Davis (1979) emphasized that such techniques were useful only as far as comparison of various wetland zones was concerned. Smith and Kadlec (1983) voiced the same concern, yet went ahead with similar technique for making predictions about vegetation changes (Smith and Kadlec, 1985).

It is apparent from the literature that various investigators worked with techniques with which they were not completely satisfied. Sampling methods were primarily borrowed from agricultural science and used in wetland studies without foundation. For instance, why were 3 cm (Thompson and Grime, 1979), 0-2, 4,6, 8-10 (Leck and Graveline, 1979), or 4-5 cm deep (van der Valk and Davis, 1978; Pederson, 1981) samples collected? Nevertheless, users of these methods have unanimously contended that a knowledge of wetland seed banks can be useful in wetland management. Wetland managers, on the other hand, have long relied upon methods developed through trial and error

(Weller, 1978). Discing, for instance, has been practiced on many drawdown surfaces to improve vegetation, but with various outcomes (Linde, 1969; Fredrickson and Taylor, 1982). This method of disturbing the soil profile down to about 15 cm assumes that it ameliorates soil conditions through increased aeration and release of nutrients, thus improving seed germination and subsequent seedling establishment (Dr. Leigh H. Fredrickson, Univ. Missouri, Columbia, MO, personal communication).

In view of the variety of sampling methods and management suggestions that are supposedly based on seed bank characteristics, a study was designed actually to examine the seed distribution in wetland soil, both in horizontal and vertical planes. Also, I was interested in finding the relation between the specific density of a seed and the depth of soil where it was abundant.

MATERIALS AND METHODS

Collection site

The 8,760 ha Mingo National Wildlife Refuge, south-east Missouri, lies in an ancient valley of the Mississippi River which now flows about 64 km east of the refuge. Most of the area has Waverly silt loam formed from loess soils eroded from the upland. The soil is generally low in fertility but rich in iron concretions, which occur throughout the subsurface (Krusekopf, 1966). Summers are hot and humid, and winters are mild. The area receives about 110 cm of precipitation annually.

My studies concentrated on the Moist Soil Unit 2 South (MSU2S). This is an 18 ha field in which rice was cultivated for 12 years until 1969. Since then it has been used for wetland plant production. A dike allows control of water level in the unit. Seasonal flooding encourages use of this unit by waterfowl, raccoons, and white-tailed deer. Artificial drawdowns during late spring are used to establish mudflat species in the unit.

Eleocharis obtusa (Willd.) Schultes and *Polygonum hydropiperoides* Michx. dominated vegetation in the unit from 1983 to 1985. After shallow discing and irrigation, details of which are described elsewhere (Naim, Fredrickson, and van der Valk, 1986), *Echinochloa crusgalli* (L.) Beauv. significantly increased in cover, and *Xanthium pensylvanicum* Wallr., which was confined to the south-east end of the study area during spring 1983, spread to the north-east end by summer 1984.

Preliminary study

Soil and water samples were collected from the study site in the summer of 1983. I placed these samples in a glass tank, making a 15 cm layer of soil inundated with about 30 cm of water.

Seeds of various species were made fluorescent by impregnating them with flavinoids. These seeds were then introduced gently on top of the water layer and their migration down to the soil was observed.

After the seeds had settled on the soil surface, the soil-water interface area was agitated with a mallard duck's beak. The idea was to simulate the tactile feeding action of a dabbling duck and observe its effect on the vertical distribution of the seeds in the soil. Ultraviolet light was used to track the settlement of the seeds relative to the soil particles.

Specific density of a seed

Seeds of eleven species were collected from the plants growing in the MSU2S. Displacement of water by a pre-weighed sample of seeds of a species was used to calculate the specific density of seeds.

Seed distribution in soil

Soil cores were extracted from the area making a figure of "W". A total of 50 samples, each 8 cm deep with 8 cm dia., were collected, each year, early in the spring. Ten groups of 5 cores each were made. Each soil core was sliced into 1 cm thick cross sections. For each group, the 5 slices were mixed to obtain a composite sample for a given depth. Seeds from such composite samples were separated by wet sieving, identified, checked for apparent viability (Roberts, 1981), and counted. Differences in the seeds between depths, years, and species, were tested for significance using the General Linear Model approach (SAS, 1982).

Soil analysis

A total of 25 soil cores were extracted from the area and sliced into 1 cm cross-sections, as described above. Soil sections from similar depths were pooled to get a composite sample. These samples were ground, air dried, passed through a 2 mm sieve, and analyzed for organic matter content, by loss on ignition (Nelson and Sommers, 1982), and particle size analysis, by the pipette method (Day, 1965); undisturbed soil samples were used to study bulk density (Blake, 1965).

RESULTS

Preliminary study

Use of fluorescent seeds in the glass tank made it possible to observe some of the factors responsible for the distribution of seeds in the soil profile. Some seeds sank deeper into the soil than others. I watched invertebrates as they crawled over and moved around the seeds. Smaller seeds appeared particularly affected by such activities, as some were lifted up while others got buried deeper into the soil.

Agitation of the soil-water interface disturbed the seeds and the top layer of soil. Within 10 minutes, some of the heavier seeds settled, thus getting buried into deeper layers of soil. Seeds of Eleocharis obtusa and E. smallii generally became attached either to each other, to plant debris, or to other seeds. Their distribution in the soil profile thus depended on the object(s) to which they became attached. Xanthium pensylvanicum burrs floated on top of water for the longest period of time, and after settlement stayed on the top layer of soil.

Specific density of a seed

Of the twenty species represented in the seed bank, seeds of eleven were selected for specific density measurements on the basis of their relative importance in the area. Of these, seeds of Ipomoea hederacea had the highest specific density (1.0047 g/cc), while those of Eleocharis obtusa were the least dense (0.3 g/cc) (Table 1.1).

TABLE 1.1. Specific density of seeds of various species

Species	Specific Density[a] (g/cc)
Eleocharis obtusa	0.300 ± 0.012
Diodia virginiana	0.308 ± 0.003
Leersia oryzoides	0.329 ± 0.019
Bidens frondosa	0.377 ± 0.015
Ludwigia repens	0.390 ± 0.012
Echinochloa crusgalli	0.471 ± 0.016
Xanthium pensylvanicum[b]	0.486 ± 0.023
Panicum dichotomiflorum	0.495 ± 0.002
Digitaria filiformis	0.502 ± 0.002
Polygonum hydropiperoides	0.653 ± 0.001
Ipomoea hederacea	1.005 ± 0.001

[a] Most seeds had some floral parts attached.

[b] Burrs were used.

Seeds of low specific density included those of Diodia virginiana, Leersia oryzoides, Bidens frondosa, and Ludwigia repens. In the medium range, specific density of Echinochloa crusgalli seeds was similar to those of Xanthium pensylvanicum (0.47 g/cc). Also, the specific density of seeds was similar for Panicum dichotomiflorum and Digitaria filiformis (0.5 g/cc). Seeds of Polygonum hydropiperoides showed a higher specific density (0.65 g/cc).

Seed distribution in soil

The distribution of seeds in the soil profile varied both spatially and annually. Significant differences ($P<.05$) were found in the number of seeds present at various depths in soil, within the years. Seeds of most of the species concentrated in the 2-5 cm deep layer of soil in 1984. In 1985, the highest concentrations of seeds were found at 2-4 cm depth.

On an average, there were 70,144 seeds m^{-2} of 17 species present in the top 6 cm soil in 1984 (Table 1.2). In general, seeds of *Amaranthus tamariscinus*, *Ambrosia artemisiifolia*, and *Cyperus esculentus* were found only at 3-4 cm depth. *Eleocharis smallii* seeds and *Xanthium pensylvanicum* burrs were confined to the top 2 cm soil, *Ludwigia repens* seeds to the top 1 cm, and *Polygonum hydropiperoides* seeds were present only at the 2-3 cm depth.

Seeds of other species showed a wider distribution in the soil profile. *Bidens frondosa* had the highest concentration of its seeds at the 2-3 cm depth, and *Cyperus iria*, *Eleocharis obtusa*, and *Panicum dichotomiflorum* at 3-4 cm. *Digitaria filiformis*, *Echinochloa crusgalli*, *Ipomoea hederacea*, and *Leersia oryzoides* had the highest concentration of their seeds at the 4-5 cm depth. The biggest reserves of *Diodia virginiana* and *Leptochloa panicoides* were found at 1-2 cm.

In 1985, the total number of seeds per square meter decreased to 62,059 (Table 1.3). This was, however, a non-significant decrease. Species that showed fewer seeds in 1985 than 1984 included *Cyperus*

TABLE 1.2. Average number of seeds m^{-2} in 1 cm deep layers from the surface down to 6 cm depth in the soil profile of Moist Soil Unit 2 South, Spring, 1984

SPECIES	SOIL DEPTH (cm)					
	0-1	1-2	2-3	3-4	4-5	5-6
Amaranthus tamariscinus	-	-	-	43	-	-
Ambrosia artemisiifolia	-	-	-	87	-	-
Bidens frondosa	175	438	614	394	263	131
Cyperus esculentus	-	-	-	263	-	-
Cyperus iria	307	701	2017	2192	745	701
Digitaria filiformis	263	921	1578	2763	3070	921
Diodia virginiana	-	394	131	350	219	-
Echinochloa crusgalli	87	-	219	614	1008	350
Eleocharis obtusa	1315	3859	9605	10877	9868	4035
Eleocharis smallii	131	131	-	-	-	-
Ipomoea hederacea	-	-	175	263	570	394
Leersia oryzoides	-	87	131	350	438	131
Leptochloa panicoides	87	219	-	-	43	-
Ludwigia repens	131	-	-	-	-	-
Panicum dichotomiflorum	307	745	1096	1403	1052	1052
Polygonum hydropiperoides	-	-	87	-	-	-
Xanthium pensylvanicum[a]	131	131	-	-	-	-

[a] In the case of *Xanthium*, burrs were counted.

iria, *Digitaria*, *Echinochloa*, *Eleocharis obtusa*, *Leptochloa*, and *Panicum*; the rest of the 11 species showed various amounts of increase in the number of their seeds. Of these, seed quantities of seven species (*Amaranthus*, *Ambrosia*, *Carex*, *Cyperus ovularis*, *Diodia*, *Hibiscus*, and *Polygonum*) in 1985 were significantly different (P<.05) than those found in 1984. Also, seeds of three new species were found in the soil, making the total number of species represented in the seed bank 20. These new species were *Carex tribuloides*, which had the highest concentration of its seeds at a depth of 1-2 cm, *Cyperus ovularis*, seeds of which were mostly concentrated at 4-5 cm, and *Hibiscus lasiocarpos*, seeds of which had their highest concentration at 3-5 cm.

All seed kinds were present in more than one layer of soil in 1985. *Amaranthus*, *Ambrosia*, *Cyperus esculentus*, *C. ovularis*, *Echinochloa*, *Ipomoea*, *Leptochloa*, and *Ludwigia* seeds were present in their highest concentrations at the 4-5 cm depth, whereas, seeds of *Bidens*, *Cyperus iria*, *Digitaria*, *Diodia*, *Eleocharis smallii*, and *Leersia* were found in large quantities at the 2-3 cm depth.

Eleocharis obtusa and *Polygonum* seeds exhibited their highest concentrations at 3-4 cm depth. The highest concentration of *Panicum* was found at 5-6 cm depth, whereas the burrs of *Xanthium* were largely confined to the top 1 cm soil.

TABLE 1.3. Average number of seeds (burrs for Xanthium) m^{-2} in 1 cm deep layers from the surface down to 6 cm depth in the soil profile of Moist Soil Unit 2 South, Spring, 1985

SPECIES	SOIL DEPTH (cm)					
	0-1	1-2	2-3	3-4	4-5	5-6
Amaranthus tamariscinus	87	131	87	43	175	87
Ambrosia artemisiifolia	-	-	-	87	131	-
Bidens frondosa	394	701	745	394	131	-
Carex tribuloides	43	131	43	87	87	-
Cyperus esculentus	-	-	-	-	263	219
Cyperus iria	263	1008	1228	833	394	657
Cyperus ovularis	-	-	-	-	219	87
Digitaria filiformis	526	438	2105	877	1754	1754
Diodia virginiana	701	789	833	350	219	219
Echinochloa crusgalli	-	87	131	526	570	131
Eleocharis obtusa	1666	4605	6052	7543	4385	3640
Eleocharis smallii	87	87	175	131	43	-
Hibiscus lasiocarpos	-	-	-	87	87	43
Ipomoea hederacea	-	219	307	394	438	175
Leersia oryzoides	-	219	438	263	394	175
Leptochloa panicoides	-	-	-	-	175	87
Ludwigia repens	-	175	-	-	219	87
Panicum dichotomiflorum	307	526	1184	1535	1622	1929
Polygonum hydropiperoides	-	-	219	307	263	87
Xanthium pensylvanicum	526	131	43	-	-	-

Soil physical analysis

Physical property data of the soil profile at the Moist Soil Unit 2 South are presented in Table 1.4 It appears that sand and organic matter contents decreased with increasing soil depth. Silt, clay, and bulk density, on the other hand, increased from top soil down to 3 cm depth.

TABLE 1.4. Physical properties of the soil profile at the Moist Soil Unit 2 South

Soil Depth (cm)	% Sand	% Silt	% Clay	Bulk Density (g/cc)	% O.M Loss on Ignition
0 - 1	35	52	13	1.14	2.8
1 - 2	25	57	18	1.23	2.5
2 - 3	24	60	16	1.34	2.1

DISCUSSION

My preliminary study indicated that the seed distribution in a soil profile may be influenced by a variety of factors. Invertebrates, for instance, may influence seed distribution during late summer and early fall, before the arrival of the migratory waterfowl. Observations I made in the field suggest, however, that activities of a host of other users of the habitat (e.g., frogs, toads, turtles, sirens, newts, snakes, fish, raccoons, and deer) may be more significant in this regard. Later in the fall, an influx of waterfowl imposes even larger scale disturbances of the soil-water interface. Seeds are dispersed in the water, along with soil, with various frequencies and intensities. Depending on their specific densities, various soil particles settle after a certain time period. I expected seeds to follow the same settlement pattern.

It seems, however, that the seed surface characteristics prevent settlement of the seeds in accordance with Stokes' Law (Hillel, 1982). More often than not, seeds of *Bidens*, *Echinochloa*, *Eleocharis obtusa*, *E. smallii*, and *Leersia*, and burrs of *Xanthium*, were found in clumps because of the presence of bristles on their surfaces. Further, the nature of the seed surface facilitated adherence to, or entanglement with, a variety of material, e.g., plant debris, apiphia, insects, invertebrates, and soil particles. In the case of *Digitaria*, *Ipomoea*, *Panicum*, and *Polygonum* seeds, the presence of perianth or husk appeared to have increased the seed floatation time (Staniforth and Cavers, 1976; Parker and Leck, 1985), thus affecting their settlement rate.

Within a plant population, not all the seeds are shed simultaneously. Therefore, all the seeds may not have the same time period available for settlement.

Conditions suitable for germination and emergence during a drawdown will partly deplete the seed bank. Subsequently, microsite environment (Hartgerink and Bazzaz, 1984), and competition (Harper, 1977; Grime, 1979), will largely determine the proportion of the seeds that will be successful in emerging as a component of the surface vegetation. Seed distribution pattern in the seed bank under the drawndown surface may be disturbed by the growth of roots. Later in summer, plants begin to shed seeds. Seeds that are not carried out of the area by various dispersal agents (Howe and Smallwood, 1982) will accumulate on the soil surface. Rain or water coming into the area from various sources may influence spatial distribution of these seeds as some may be washed down into depressions.

Under flooded conditions seeds that tend to float for comparatively longer periods of time, are likely to drift to the shore line. Here they become trapped in the litter and vegetation. Seeds with shorter floatation period will sink down to the soil-water interface. Here they will be acted upon by various users of the wetland habitat. Seeds that survive these disturbances will become part of the seed bank.

The relation between the specific density of a seed and the depth of its occurrence is not very obvious. I found poor correlation ($r=0.3$ $P<.03$) between the seed density of a species and the soil depth of its maximum concentration. Similarly, the soil physical characteristics (Table 1.4) do not appear to have any significant correlation with seed distribution. The seed distribution pattern, however, correlated well between the two years ($r=0.73$ $P<.0001$).

I do not know how much of the seed input in MSU2S came from the surrounding areas through wind, water, and wildlife. Also, the ages of seeds that I found in the soil profile are not known to me. It is likely, however, that I encountered seeds that have accumulated in the soil profile over several years. Also, it is likely that different seed lots were acted upon by various agents with various frequencies and intensities, thus resulting in the seemingly random distribution of these seeds in the soil profile.

Both quantitative and qualitative changes occurred in the seed bank during the study period (Table 1.2, 1.3). Like several other cases (e.g., van der Valk and Davis, 1978; Leck and Graveline, 1979; Thompson and Grime, 1979; van der Valk, 1981; Parker and Leck, 1985), my seed bank composition was reflective of the dominant surface vegetation. Nonetheless, the "fluctuation" and the "succession" (sensu van der Valk, 1981, 1985) that I found in the seed bank may not necessarily have any bearing on the surface vegetation (cf. Smith and Kadlec, 1985). Evidence to support such a notion comes from my field and laboratory investigations (see Paper 2), where seeds buried below 2 cm depth of soil showed significantly reduced germination (also see Galinato and van der Valk, 1986). Further, I feel that use of bulk soil in a seed bank study with the intent of predicting the future vegetation may not be a useful exercise. My methodology, on the other hand, provides a comparatively quick and more reliable way of assessing the abundance of seeds of various species and their location in the soil profile. If seeds of a desired species are not present in the top 2 cm of soil, then it may be necessary to use discing; this should bring the seeds closer to the soil surface, thus increasing their chances of germination and recruitment into the future vegetation.

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PAPER 2. SEED GERMINATION IN WETLAND SPECIES: RESPONSE TO DIURNALLY FLUCTUATING TEMPERATURES AND DEPTH OF BURIAL IN SOIL

SEED GERMINATION IN WETLAND SPECIES: RESPONSE TO DIURNALLY FLUCTUATING TEMPERATURES AND DEPTH OF BURIAL IN SOIL

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ABSTRACT

Germination behavior of Echinochloa crusgalli, Eleocharis obtusa, Polygonum hydropiperoides, and Xanthium pensylvanicum was studied at various diurnally fluctuating temperatures and depth of burial in soil using a two-way thermogradient plate. Emergence of the same four species during a drawdown was also observed in a seasonally flooded impoundment at the Mingo National Wildlife Refuge, southeast Missouri. Concomitant changes in the soil temperature profile also were recorded during the drawdown.

On the thermogradient plate, seeds failed to germinate when buried below 3 cm depth of soil; in the field, all the seedlings emerged from seeds buried at a maximum of 1.5 cm depth.

Seeds of Polygonum germinated best in a 19-21°C/11-12°C day/night temperature regime under a 12 h day/night cycle on the thermogradient plate; in the field, 50% of the total seedlings that emerged did so before soil temperatures reached 20°C. Eleocharis required 25-29°C/14-19°C day/night temperature regime for best germination; in the field, best germination occurred when day temperatures were above 20°C for about 3 h. However, most of the time soil temperature stayed below 15°C.

Temperature regimes of 25-32°C/15-20°C favored seed germination of Echinochloa, whereas, seeds of Xanthium germinated best at 27-33°C/16-20°C. Seeds of both these species germinated better in the field when soil temperatures over 25°C prevailed for less than 6 h in a day.

A general preference for higher germination temperatures on the thermogradient plate as compared to that in the field seems to be a result of different storage and germination environments. Apparently these seeds did not respond to a temperature continuum, which may have adaptive significance for these species in highly fluctuating soil temperature conditions. Overlapping temperature requirements for germination prevent elimination of *Xanthium* from the field by controlling soil temperature through changes in the drawdown dates.

INTRODUCTION

Seed bank studies in wetlands have been done primarily by subjecting wetland substrate samples to greenhouse conditions, observing the emergence of seedlings, and using these observations to speculate about the quality and quantity of the seed bank (e.g., van der Valk and Davis, 1978, 1979; Leck and Graveline, 1979; Smith and Kadlec, 1983, 1985). There is, however, a potential risk in such a procedure. As pointed out by van der Valk and Davis (1979) and Galinato and van der Valk (1986), lack of appropriate conditions for germination may result in a failure to detect certain taxa, or an under-estimation of their abundance. Such problems, they suggested, could be resolved by simulating drawdown conditions, or by exposing seed bank samples to a range of environmental conditions.

A range of environmental conditions often occurs in the field during a drawdown, particularly during a slow drawdown in which portions of the substrate are exposed at different dates during the growing season. A slow drawdown is recommended by Fredrickson and Taylor (1982) to allow seeds of waterfowl food species buried in the marsh substrate to germinate. Early and late spring drawdowns in such managed wetlands expose seeds in the soil to different temperature regimes. This could influence the recruitment of species during a drawdown, both quantitatively and qualitatively.

Diurnal fluctuations in temperature often have a significant influence on seed germination (Mayer and Poljakoff-Mayber, 1975; Thompson, Grime, and Mason, 1977). Using a specially designed incubator that allowed setting of various amplitudes of temperature fluctuations, Grime and Thompson (1976) found that seeds of wetland species were particularly responsive to temperature fluctuations. In a further study, Thompson and Grime (1983) opined that wetland species may have an adaptive mechanism which activates seed germination under increasing irradiance and falling water table during a drawdown.

Preliminary investigations that I conducted in the Mingo National Wildlife Refuge, southeast Missouri, revealed that most seedlings emerged during the first 4 weeks after a drawdown as water levels fell and soil temperature increased.

On the basis of these observations, I conducted both laboratory and field studies to examine germination of seeds, buried at different depths, under various alternating temperature regimes. In the laboratory, I used a two-way thermogradient plate, that had a temperature range of 10-40°C, to examine the germination behavior of seeds of four species that were abundant in a wetland of the Mingo National Wildlife Refuge. The field studies were conducted to examine the emergence of seedlings of the same four species in the field. The temperature profile of the soil in this unit was monitored at the same time.

MATERIALS AND METHODS

Collection site

The 8,760 ha Mingo National Wildlife Refuge, southeast Missouri, lies in an ancient valley of the Mississippi River which now flows about 64 Km east of the refuge. Most of the area has Waverly silt loam soil formed from loess eroded from the upland. The soil is generally low in fertility but rich in iron concretions which occur throughout the subsurface (Krusekopf, 1966). Summers are hot and humid and the winters are mild. The area receives about 110 cm of precipitation annually.

Moist Soil Unit 2 South (MSU2S) is an 18 ha field in which rice was cultivated for 12 years until 1969. Since then it has been used for moist soil plant production. A dike allows control of water level in the unit. Seasonal flooding encourages use of this unit by waterfowl, raccoons, and white-tailed deer. Artificial drawdowns during late spring are used to establish mudflat species in the unit.

Eleocharis obtusa (Willd.) Schultes and *Polygonum hydropiperoides* Michx. dominated vegetation in the unit from 1983 to 1985. After shallow discing and irrigation (described by Naim, Fredrickson, and van der Valk, 1986), *Echinochloa crusgalli* (L.) Beauv. significantly increased in cover, and individuals of *Xanthium pensylvanicum* Wallr., that were confined to the southeast end of the study area during spring 1983, spread to the north-east end by summer 1984. Seeds of these four species were collected from the plants in MSU2S during summer 1984.

Seed handling and storage

After collection seeds were placed in small cotton bags. These bags were soaked in marsh water. Soil removed from a spot where all four species were growing together was placed in polythene bags. The cotton bags containing seeds were then placed in the polythene bags containing soil. The polythene bags were kept on ice and transported to Ames, Iowa, where they were stored in a cold room at 4°C for about five months.

Preliminary seed germination trials

A two-way thermogradient plate, based on the design described by Larsen (1971), with a surface area of 86 X 86 cm was used in the laboratory study. A daily temperature regime consisted of a 12 h high temperature during day and a 12 h low temperature during night. A 10-40°C temperature gradient was maintained.

A large number of seeds of a species were spread evenly over a double layer of blotting paper. A 12 h light period was provided by fluorescent tubes, supplemented by sun-light for about 3 h from a large glass window to the east. Illumination at the surface ranged from 1,030 to 2,340 lux.

Type "T" (copper-constantan) thermocouples connected to a multichannel digital recording thermograph were used to regularly monitor temperature near the seeds. A series of one-week trials identified locations on the thermogradient plate where each species germinated best. These locations were used in the seed bed study.

Seed bed study

Soil samples collected from all the four zones of the study area were oven dried at 105°C, ground, passed through a 2mm mesh sieve, and thoroughly mixed together. This composite soil was then filled into 6 x 15 x 5 cm aluminum foil containers. Ten stratified seeds were planted at 1 cm depth intervals at each depth from 0-4 cm in the containers, and these were placed at various locations on the thermogradient plate, pre-selected by the preliminary seed germination trials. Since only one of the two seeds in a *Xanthium* bur germinates at a time (Thornton, 1935), a bur was treated as a seed. A thermocouple was inserted in the center of each seed cluster and temperature was monitored over a two week observation period for each species. Distilled water was added to the containers as needed to keep the soil moist. Germinated seeds were removed daily and observations were recorded as percent germination for each depth.

Soil temperature profile

A spot was chosen in the MSU2S where the four species under study had been growing the previous year (1984). After extracting a 6 cm deep by 8 cm dia. soil core, two type "T" thermocouples were inserted in opposite directions into the wall of the soil cavity at each 1 cm interval down to 6 cm depth. The soil core was placed carefully back in the hole after the installation of the thermocouples. Two such thermocouple stations were established about 2 meters apart. All thermocouples were connected to a data logger. Temperatures at each location were recorded at 3 h intervals throughout the entire month of

June, 1985, as the artificial drawdown progressed.

In situ Germination

Polygonum hydropiperoides and Ludwigia repens had already established a good cover in much of the unit prior to the commencement of my field observations. Remaining open areas (totaling approximately 100 m^2 in several patches) around the thermocouple stations were selected and marked for study. Observations were made daily on the emergence of seedlings of the four species under study. Each seedling was removed carefully to measure the depth at which its seed was buried. Since the open areas under observations were disturbed frequently as the seedlings were removed, which could have affected the germination of other seeds in the vicinity, no attempt was made to convert the data into seedlings or seeds per unit area.

RESULTS

Seed germination on the thermogradient plate

In general, a diurnal fluctuation of temperature with an amplitude of about 11°C appeared most favorable for seed germination of all four species tested. Temperature fluctuations above 15°C (except in the case of *Echinochloa*) or below 7°C reduced seed germination percentages. Fewer seeds germinated when spread on the soil surface, except in the case of *Eleocharis*. Highest germination occurred when seeds were buried at 1 cm depth in soil. A decline in the percentage and/or rate of germination was observed consistently with increasing depth of seed burial. Only the seeds of *Polygonum* and *Xanthium* could germinate from 3 cm depth. No seeds at 4 cm depth germinated within the 15-day observation period.

All the species studied, were tested for their responses to a wide range of temperatures. However, those results, where emergence was less than 30%, are not reported here.

Seeds of *Echinochloa* (Figure 2.1) germinated fastest when the diurnal fluctuations ranged from 10-12°C only when the day temperature ranged from 25-32°C and the night temperature from 15-20°C. Higher temperatures at night delayed the rate and reduced the percentage germination.

Eleocharis seeds did not show any germination within the observation period when buried below 1 cm depth in soil. Germination of seeds buried at 1 cm depth appeared to be delayed by 3-4 days as compared to those that were spread on the soil surface; the final

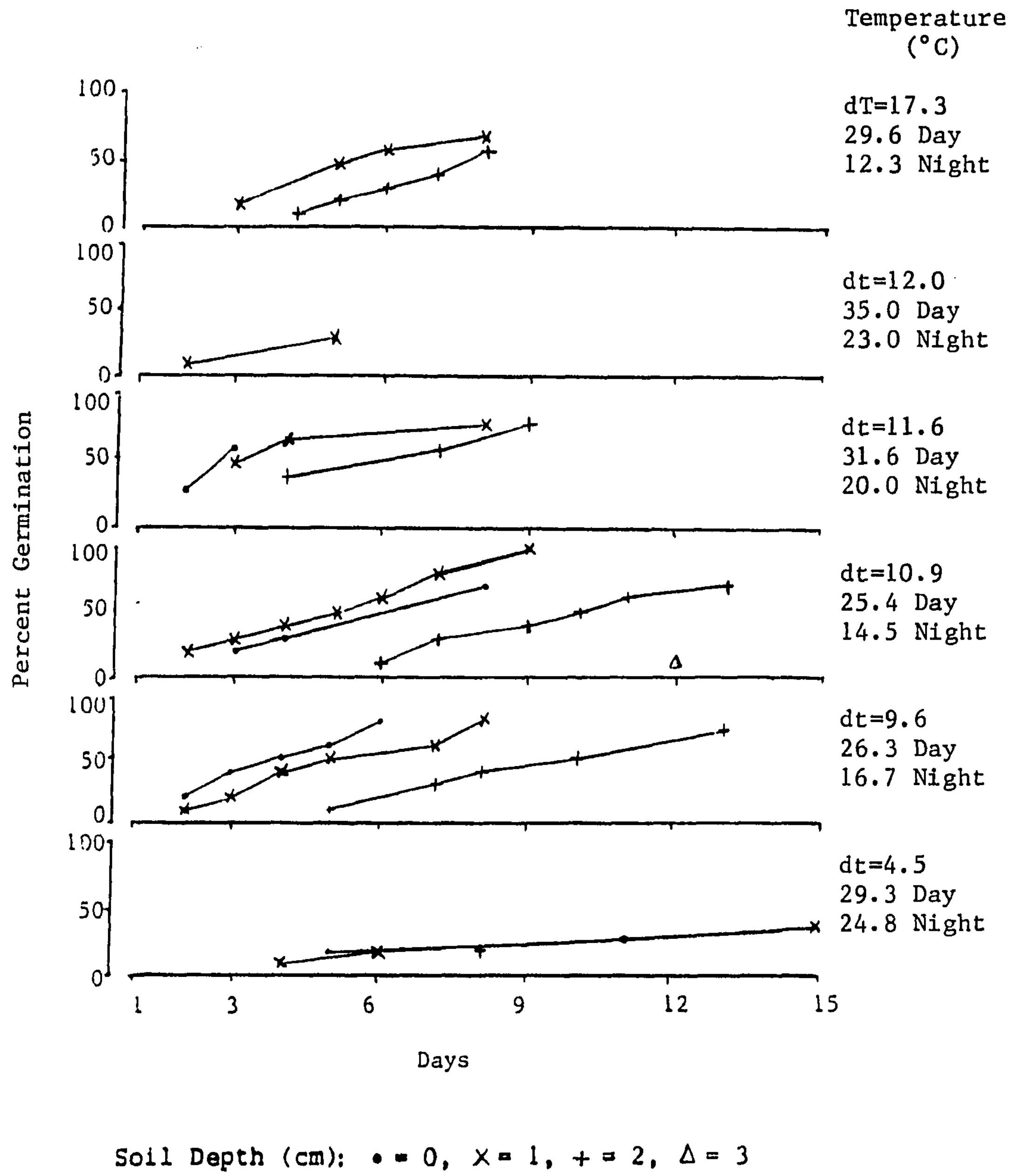


FIGURE 2.1. Percent germination of <u>Echinochloa crusgalli</u> seeds as influenced by various diurnal temperature fluctuations and depth of planting in soil (n=10/depth/trial)

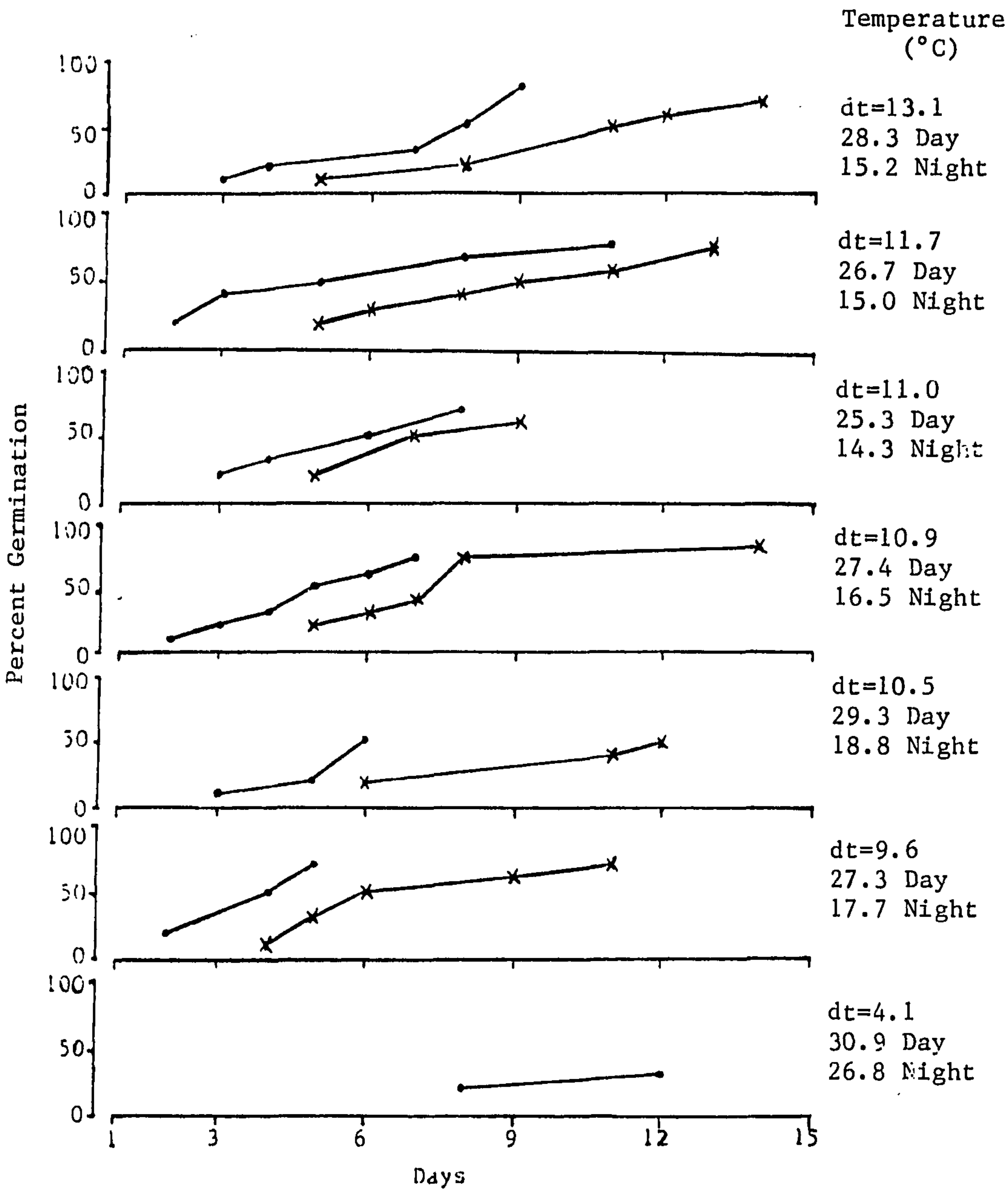
germination percentage was, however, similar at both depths (Figure 2.2). Day time temperatures of 25.3-28.3°C with 9.6-13.1°C lower temperatures at night time were conducive for seed germination.

Seeds of Polygonum did not germinate well on the surface (40% max.), or in 3 cm depth of soil (50% max.). Cooler day time temperatures (19-21°C) alternating with about 9°C lower night time temperatures were best for germination (Figure 2.3).

For germinating Xanthium seeds, higher day time temperature (29-33°C) alternating with about 9-14°C lower temperatures at night appeared best. No germination was seen in seeds spread on the surface or buried below 3 cm depth of soil (Figure 2.4).

Soil temperature profile

Average temperatures of the soil profile in the MSU2S are presented in Figure 2.5 The temperature in the top 6 cm layer of soil ranged from 4-23°C during the 1st week, 6-27°C during the 2nd, 8-28°C during the 3rd, and 14-34°C during the 4th week of June, 1985. In general, the soil surface was cooler than the lower layers. The lowest temperatures were registered in the morning from 07.00-10.00, whereas, the highest temperatures were recorded at 21.00. The greatest fluctuations in temperature occurred on the soil surface. During the first 2 weeks of June, soil temperature rose steadily. The maximum daily temperature leveled off during the 3rd week. My soil profile had become drier by the end of the 3rd week. This resulted in a higher maximum temperature on the surface than in the deeper profile during the 4th week.



Soil Depth (cm): • = 0, X = 1, + = 2, Δ = 3

FIGURE 2.2. Percent germination of *Eleocharis obtusa* seeds as influenced by various diurnal temperature fluctuations and depth of planting in soil (n=10/depth/trial)

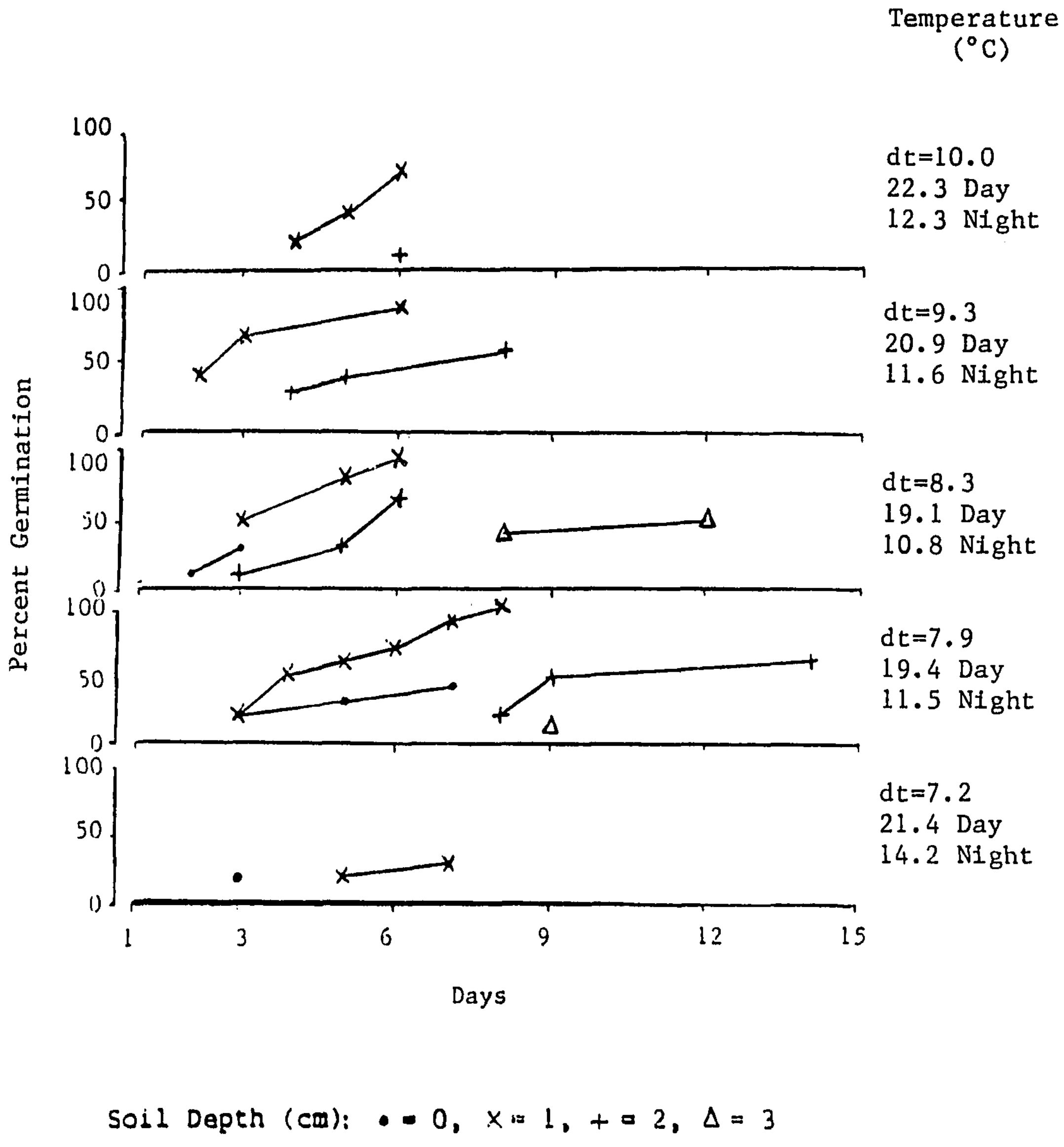
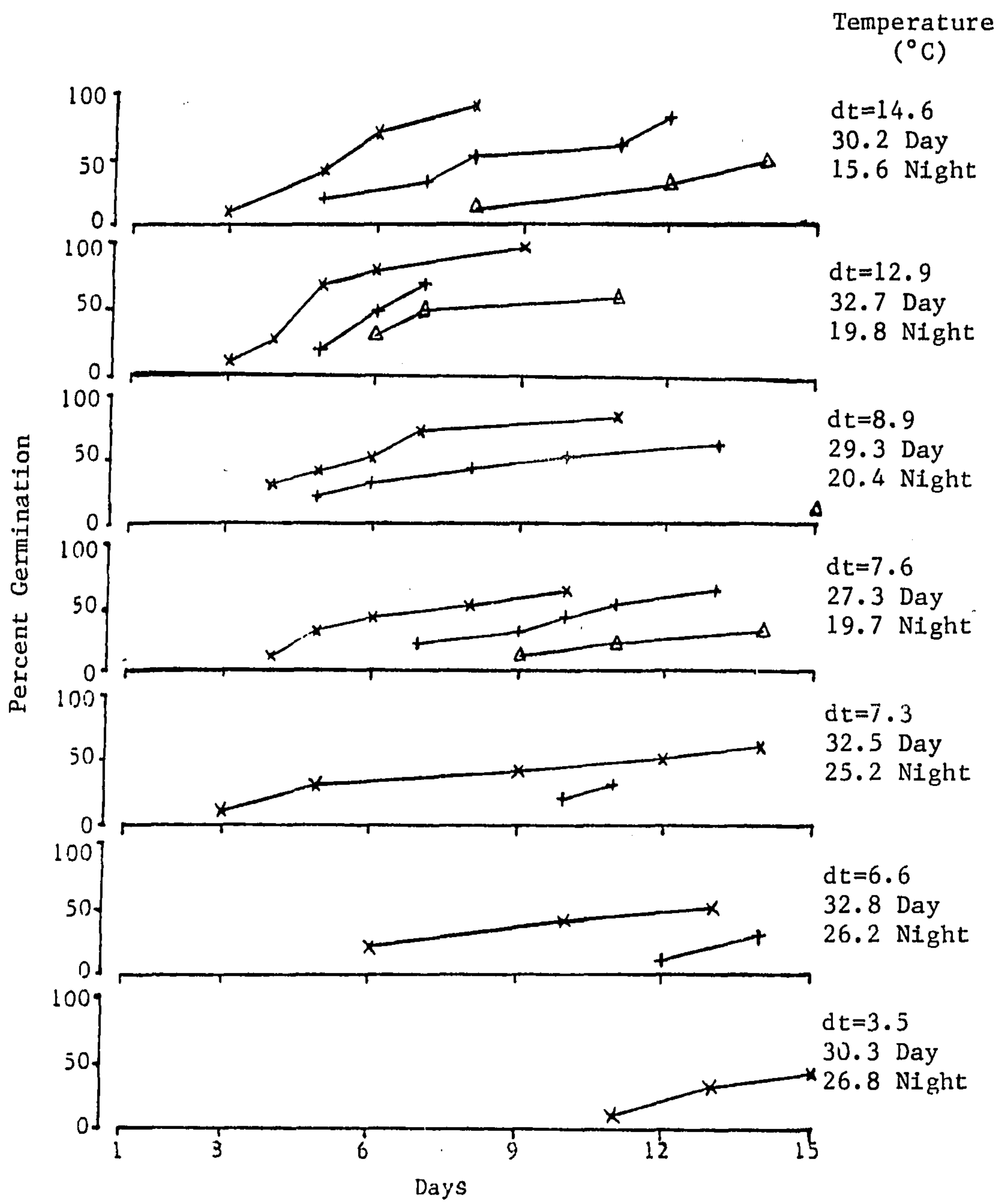


FIGURE 2.3. Percent germination of Polygonum hydropiperoides seeds as influenced by various diurnal temperature fluctuations and depth of planting in soil (n=10/depth/trial)



Soil Depth (cm): • = 0, X = 1, + = 2, Δ = 3

FIGURE 2.4. Percent germination of Xanthium pensylvanicum seeds as influenced by various diurnal temperature fluctuations and depth of planting in soil (n=10/depth/trial)

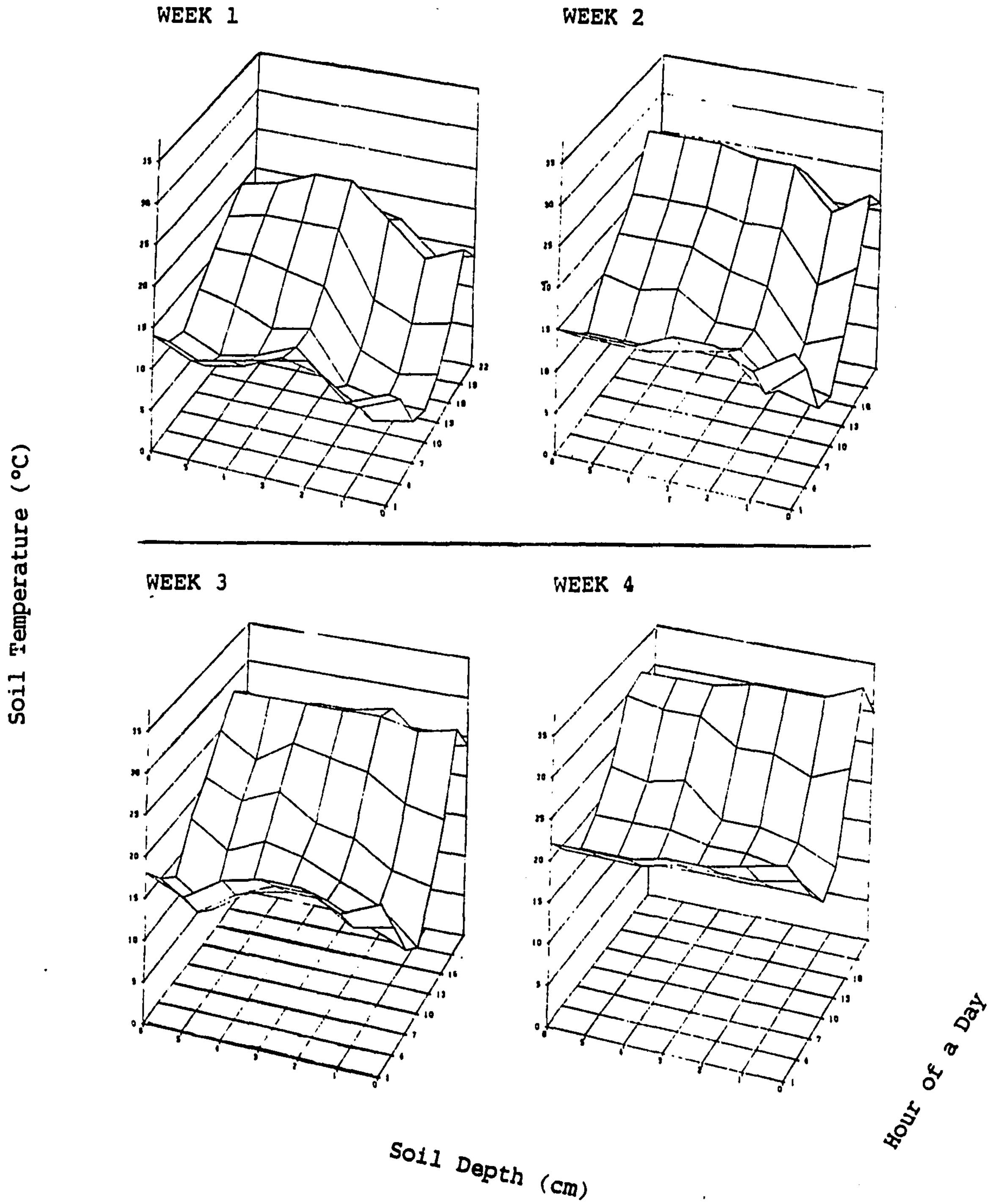


FIGURE 2.5. Average temperatures at seven depths in the soil profile during the 1st four weeks of an artificial slow drawdown in the Moist Soil Unit 2 South

The average difference between the minimum and maximum temperatures recorded on the soil surface for a day was about 13°C during the first week of drawdown. During the 2nd week, it increased to 18°C, while during the 3rd and 4th weeks the difference was as much as 20°C. Amplitude of temperature fluctuations in the soil layers deeper than 2 cm averaged 4-5°C less than that on the soil surface.

Field emergence

An increase in the number of seedlings in the area was observed as the month of June progressed and water standing on the marsh surface gradually receded (Figure 2.6). *Polygonum* seedlings were the first to appear on the marsh surface while there was no less than 2 cm standing water. Emergence of *Eleocharis* seedlings closely followed. Late in the 2nd week, seedlings of *Echinochloa* made their appearance followed by the seedlings of *Xanthium*. Most seedlings emerged from seeds buried at 0.1 to 1.5 cm.

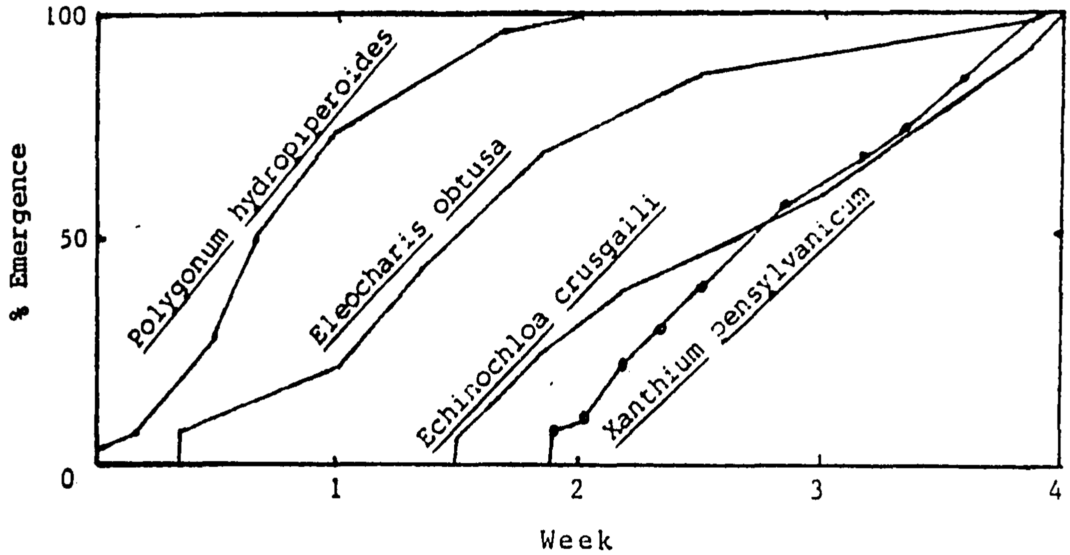


FIGURE 2.6. Relative percentage of seedlings emerging from natural seed bank during the first 4 weeks of an artificial slow drawdown in Moist Soil Unit 2 South

DISCUSSION

On the thermogradient plate, I found varied responses of seeds, both within and between species, to similar magnitudes of temperature fluctuations. Evidently, seeds were responding to the actual day and night temperatures as well as to simply the magnitude of the temperature fluctuations as suggested by Mayer and Poljakoff-Mayber (1975).

The optimum temperature for seed germination in Echinochloa has been suggested to range from 20 to 30°C (Arai and Miyahara, 1962; VanderZee and Kennedy, 1971). I found that the seeds of this species did not germinate well when day temperatures were lower than 25°C. However, in the field, I observed that 50% of the total number of seedlings emerged before temperatures above 20°C prevailed for at least 9 h per day; temperatures, in fact, remained below 15°C for most of this time. Differences between field and laboratory germination patterns may be due largely to differences in the environments to which seeds were exposed. I stratified seeds for approximately the natural length of time than did the workers mentioned above. This may have caused a shift in germination response to a higher temperature (Taylorson, 1982).

I observed no Echinochloa seedling emergence from seeds buried below 1.5 cm depth of soil in the field or below 3 cm depth of soil on the thermogradient plate. Siriwardana and Zimdahl (1984), however, were able to record 83% and 27% emergence from 4 and 8 cm depths of soil, respectively, after 7 days in a greenhouse study; temperature in their greenhouse ranged from 23-35°C. They stored their seeds at -20°C. Also, it is interesting to note that they germinated seeds in clay loam with a 7.5 pH, while my soil was silt loam with 6.5 pH. A clay loam should offer more resistance to seedling emergence than a silt loam (Hadas, 1982). Soil pH however, may be another factor that may have influenced seed germination.

Come and Thevenot (1982) suggested that imbibition depends on pH and temperature. The "Zwitter ions" present in the embryo show a minimum of imbibition at their isoelectric point. Imbibition increases with increasing pH differences on either side of this point. Further, imbibition proceeds more rapidly at higher temperatures. These factors may have played a role in my study. In the field I observed that the seeds of *Echinochloa* remained afloat for several days before settling in water. The pH of surface water during this period fluctuated in a range of 5 to 8.2 , while the water temperature went as high as 34°C. Such conditions may be responsible for seed germination in the field at lower temperatures than in the laboratory.

Day time temperatures below 25°C resulted in less than 30% seed germination on the thermogradient plate in *Eleocharis* seeds. In the field, however, seeds of this species germinated well when day time temperature rose above 20°C only for about 3 h. Most of the time, soil temperature remained below 15°C, a period during which 50% of the total number of seedlings emerged (Figures 2.5 and 2.6). I did not find any published work on germination behavior of this species.

On the thermogradient plate, Polygonum seeds germinated well when day time temperature was higher than 19°C while the night time temperature was below 12°C (Figure 2.3). These result do not agree with the findings of Justice (1944), who observed best germination in the seeds of this species in dark in a 30°C/20°C (8 h/16 h) temperature regime. Provision of light does not appear to be a factor in promoting germination at lower temperature in my study (cf. Thompson and Grime, 1983) since most of the seed germination occurred from 1 and 2 cm depths of soil where light could not have penetrated (Woolley and Stoller, 1978). In the field, emergence of Polygonum seedlings reached 50% of the total while the maximum temperature for a day never crossed the 20°C mark; temperature remained below 10°C during most of the time (Figures 2.5 and 2.6).

Katoh and Esashi (1975) observed seed germination in Xanthium when temperatures were above 25°C. Further increase in temperature up to 33°C increased seed germination. My thermogradient plate study corroborate their finding to some extent. On the other hand, I registered 50% of the total seedling emergence in the field when soil temperature above 25°C persisted for less than 6 h per day.

Results of my laboratory study were similar to that I observed in the field, as far as the responses of various species to a general range of temperatures is concerned. It is difficult, however, to compare my results with those of other workers, primarily because of different storage and germination facilities used, which affect the germination behavior of a species (Priestley, 1986). Further, difference in the seed source is probably a factor influencing the results since seed germination characteristics vary for a species from site to site due to genetic variations (Seneca, 1969; Silvertown, 1984), and/or varied environmental conditions during the seed development process (Evenari, Koller, and Gutterman, 1966; Kigel, Ofir, and Koller, 1977; Cresswell and Grime, 1981).

My soil temperature study essentially reflects thermal fluctuations in bare soil since I continuously removed seedlings from the area. This allowed a greater fluctuation of temperature on the soil surface (Figure 2.5). Seeds were present in the soil profile down to 6 cm (see Paper 1), however, the temperature fluctuations in soil below 1.5 cm depth may not have been high enough to stimulate seed germination (Scharringa, 1976; Thompson, Grime, and Mason, 1977).

Comparing the germination response in the field to that on the thermogradient plate, my results may have been influenced by not only the difference in storage and germination environments but also by differences in the age of seeds (Priestley, 1986). Seeds that germinated in the field may have included seeds from several previous years, while the seeds used in the thermogradient plate study were all of the same age.

The variation in germination under different environmental conditions in all the four species indicates the opportunistic nature of these species, allowing different portions of a species' seed bank to respond to various ranges of temperatures. This is likely to increase persistence of these species in an area (Silvertown, 1984).

For researchers, this may pose a problem. One set of experimental conditions may not be conducive to the germination of all portions of a seed bank (van der Valk and Davis, 1979). As a result, workers may underestimate the number of viable seeds of a species in seed bank studies.

Polygonum, *Echinochloa*, and *Eleocharis* are considered useful plants because their seeds are regularly consumed by waterfowl (Martin and Uhler, 1939), whereas, *Xanthium* is viewed as an undesirable species for waterfowl habitats (Fredrickson and Taylor, 1982). From a vegetation management perspective, both early and late spring drawdowns will allow emergence of *Polygonum* and *Eleocharis* because they can become established at low temperatures. Emergence of *Echinochloa* can be favored by a late spring drawdown when soil temperatures will be higher and favor the germination of seeds of this species. Seedlings of *Xanthium* will also emerge during a late spring drawdown because seeds of this species appear to have similar temperature requirements for germination (Figure 2.1 and 2.4). However, the timing of a drawdown *per se* can not be used easily to enhance or prevent the germination of one of these species, since their seed germination traits overlap so much (Figures 2.1 and 2.4). This problem can be overcome by reflooding the wetland to the point that *Xanthium* seedlings are submerged in water for 2-3 days. Fredrickson and Taylor (1982) found that this is a successful method for killing seedlings of this species without any noticeable effect on other plants.

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PAPER 3. EMERGENCE OF WETLAND SPECIES AT VARIOUS SOIL WATER MATRIC POTENTIALS

EMERGENCE OF WETLAND SPECIES AT VARIOUS SOIL WATER MATRIC POTENTIALS

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ABSTRACT

Fluctuations in soil water matric potential (ψ), and emergence of four dominating species namely Echinochloa crusgalli, Eleocharis obtusa Polygonum hydropiperoides and Xanthium pensylvanicum were monitored during the first 4 weeks of an artificial drawdown in the Moist Soil Unit 2 South, Mingo National Wildlife Refuge, Southeast Missouri.

Seeds of the same four species were subjected to a range of ψ in a greenhouse investigation, and the emergence behavior was recorded.

Soil physical analyses were performed including shear strength (τ) for 0-3 cm soil profile at various ψ.

Emergence of the species studied in the field commenced in the following order: Polygonum, Eleocharis, Echinochloa, and Xanthium. A -15 kPa seemed to be the critical ψ for this species below which no new seedlings emerged in the field. The greenhouse results revealed the critical ψ to be -10 kPa.

Eleocharis exhibited emergence over a wide range of ψ without much effect on the emergence rate. In the greenhouse study, however, the rate of emergence declined sharply as ψ approached -33 kPa.

Echinochloa appeared to have a bimodal response to decreasing ψ. Both in the field and in the greenhouse studies, emergence of this species was observed to be faster in the range of -10 kPa to -53 kPa, and -60 kPa to -80 kPa.

Lower ψ seemed to favor emergence of Xanthium. Comparatively higher rate of emergence was noted for this species in the range of -30 to -76 kPa ψ.

Of the top layers of soil analyzed, 1-2 cm layer offered significantly higher resistance to seed germination / emergence ($P<.001$) as compared to that by the 0-1 cm layer. The 2-3 cm layer appeared to impose the highest mechanical constraint on germination / emergence with a relatively insignificant decrease in ψ. Emergence of Xanthium was significantly affected ($r=-0.72$ $P<.04$) by τ. For all other species studied, emergence was better correlated with ψ than τ.

The results suggest that a slow drawdown is conducive to the emergence of desirable species.

INTRODUCTION

Artificial drawdowns, or natural seasonal water level recessions, facilitate emergence of mudflat species from seed banks. This increases plant biomass production and improves habitat condition for a variety of wildlife (Linde, 1969; Fredrickson and Taylor, 1982).

During a drawdown, lowering of water level causes several changes in the soil environment. These changes may include a decrease in the degree of pore saturation and thus increased soil aeration (Dasberg and Mendel, 1971), variation in the area of seed-soil contact that affects water uptake by seeds (Collis-George and Hector, 1966; Waggoner and Parlange, 1976; Hegarty, 1978; Rogers and Dubetz, 1980), and an increase in the mechanical strength of the soil matrix (Collis-George and Williams, 1968; Williams and Shaykewich, 1970; Benjamin and Cruse, 1985).

Seed germination, in general, decreases with a decrease in soil water matric potential (Collis-George and Sands, 1959; Harper and Benton, 1966; Hadas and Russo, 1974; Hegarty, 1978). Nonetheless, of all the changes caused by decrease in soil water potential, the increase in the mechanical strength of the soil matrix is considered to be the most effective deterrent to seed germination and emergence (Collis-George and Williams, 1968; Hadas, 1977; Royle and Hegarty, 1977; Voorhees, 1977; Hegarty and Royle, 1978). Seeds can imbibe water over a wide range of water potential. However, the mechanical constraint imposed by hardening soil inhibits or lowers the rate of germination and emergence (Hadas, 1977; Rogers and Dubetz, 1980).

Working on a managed wetland in the Mingo National Wildlife Refuge, Southeast Missouri, I designed a study to monitor seed germination behavior under artificial drawdown conditions. Soil water potential was recorded along with emergence of four dominating species in the field. In a greenhouse study, seeds of selected species were subjected to various levels of soil water matric potential. Emergence was correlated with the shear strength of soil. The main objective was to find a better strategy for artificial drawdown that may facilitate emergence and subsequent establishment of desirable vegetation in the area.

MATERIALS AND METHODS

Collection site

The 8,760 ha Mingo National Wildlife Refuge, south-east Missouri, lies in an ancient valley of the Mississippi River which now flows about 64 Km east of the refuge. Most of the area has Waverly silt loam formed from loess soils eroded from the upland. The soil is generally low in fertility but rich in iron concretions which occur throughout the subsurface (Krusekopf, 1966). Summers are hot and humid while the winters are mild. The area receives about 110 cm of precipitation annually.

Moist Soil Unit 2 South (MSU2S) is an 18 ha field in which rice was cultivated for 12 years until 1969. Since then it has been used for moist soil plant production. A dike allows control of the water level in the unit. Seasonal flooding encourages use of this unit by waterfowl, raccoons, and white-tailed deer. Artificial drawdowns during late spring are used to establish mudflat species in the unit.

Eleocharis obtusa (Willd.) Schultes and *Polygonum hydropiperoides* Michx. dominated vegetation in the unit from 1983 to 1985. After shallow discing and irrigation, details of which are described elsewhere (Naim, Fredrickson, and van der Valk, 1986), *Echinochloa crusgalli* (L.) Beauv. significantly increased in cover, and individuals of *Xanthium pensylvanicum* Wallr., that were confined to the south-east end of the study area during spring 1983, spread to the north-east end by summer 1984. Seeds of these four species were collected from the area during summer 1984. For convenience, only the generic names are used in the text to identify the species.

Soil collection and analysis

Twenty five soil cores (6 cm deep with 8 cm dia.) were extracted from the MSU2S. The top 3 cm soil of each core was sliced horizontally into 1 cm thick sections. Sections from the same depth were mixed together, oven-dried at 105°C for 24 h, ground, passed through a 2 mm sieve, and analyzed for organic matter content by loss on ignition (Nelson and Sommers, 1982), and particle size analysis (Day, 1965). For the determination of the soil water matric potential, water was added to these composite samples to make a thick slurry. The slurry was poured into rubber rings of 5 cm dia., placed on ceramic plates of various porosities, and subjected to air pressure ranging from 10 to 145 kPa using a pressure plate extractor (Richards, 1947). After 48 h soil samples were removed from the pressure chamber and immediately tested for shear strength as described below. Subsequently, water content of the samples were determined gravimetrically, and reported as the average of six samples on a volume basis.

Shear strength of soil   A fall-cone penetrometer (Geonor Model G-200, Eng. Lab. Equip. Inc., Houston, TX) was used for measuring soil shear strength. Each soil sample removed from the pressure plate was placed on a wooden block on the base of the fall-cone penetrometer frame. Measurements were taken, following Hansbo (1957), at the center of a sample. A cone weight of either 0.1 or 0.4 Kg with an apex angle of 30° was used. Shear strength value was calculated from tables presented in Hansbo (1957). Data from six samples were averaged for each soil water matric potential and soil depth.

In situ soil study To determine bulk density a depression was dug in the drawndown surface of the study area. A cork borer 11 cm long having a 1 cm internal diameter was inserted horizontally into the soil profile to extract soil samples from the top down to a 3 cm depth at 1 cm intervals. Five depressions were dug at random in the MSU2S. Soil was pushed out of the borer with a plunger. The first 1 cm of soil that appeared out of the other end of the borer as the plunger moved was discarded. The next 3 cm of soil was cut off with a sharp razor blade, and its water content was determined gravimetrically. Bulk density was calculated as a ratio of weight to volume (Blake, 1965).

Soil moisture tension

In the study area, three soil cores were extracted, creating holes of 8 cm dia. and 6 cm depths. Two pre-calibrated Bouyoucos gypsum blocks (Gardner, 1965) were inserted horizontally into the side walls of each hole. The arrangement was such that the blocks were placed at 0-2 cm depth in hole 1, at 1-3 cm in hole 2, and at 2-4 cm depth in hole 3 to avoid close contact between the blocks. The soil cores were emptied back into their respective holes after the installation of the blocks. Soil moisture tension was recorded using Model KS Moisture Detector (Delmhorst Instr. Co., Boonton, NJ) twice daily at 10 am and 7 pm (CST). There was about 1 cm deep water standing on the spot when the blocks were installed on June 6, 1985. As the month of June progressed water standing on the marsh surface gradually receded because of the artificial drawdown.

Greenhouse study

Top 3 cm samples of soil were collected from various sites in MSU2S where all the four dominant species studied were growing together. These samples were mixed together, oven-dried at 105°C, and passed through a 2 mm screen. Plastic flats (10 x 20 x 8 cm) were filled 5 cm deep with the composite soil. Seeds of Echinochloa, Eleocharis, Polygonum, and Xanthium were placed in soil about 1 mm below the surface. Twenty seeds of a species were planted per flat.

Five flats were maintained for each treatment in the greenhouse using a randomized complete block design. The treatments were the following soil water matric potentials (ψ): 0 (soil submerged under 1 cm water), -10, -20, -33, -40, -60, -80, -100, -120, and -140 kPa. The flats were weighed twice a day and a calculated amount of water was added to maintain soil at the predetermined water matric potentials. Seedlings were counted and removed daily. Analysis of variance was done to ascertain the response of seeds of different species to various levels of soil water matric potential.

RESULTS

Soil physical analysis

Physical property data of the soil profile at the Moist Soil Unit 2 South are presented in Table 3.1. Sand and organic matter decreased with increasing soil depth. Silt, clay, and bulk density, on the other hand, increased from top soil down to 3 cm depth.

TABLE 3.1. Physical properties of soil profile at the Moist Soil Unit 2 South, Mingo NWR

Soil Depth (cm)	% Sand	% Silt	% Clay	Bulk Density (g/cc)	% O.M Loss on Ignition
0 - 1	35	52	13	1.14	2.8
1 - 2	25	57	18	1.23	2.5
2 - 3	24	60	16	1.34	2.1

Large differences were observed in the shear strength (τ) for various depths of soil at any given soil water matric potential (Table 3.2). It is obvious that τ increased with decreasing soil water matric potential (ψ). The change in τ with decreasing ψ was dramatic, however, in soil at 2-3 cm depth. A seven times decrease in ψ appears to have caused a 6 fold increase in τ in the top 0-1 cm layer of soil, a 25 fold increase in the 1-2 cm layer, and a 62 fold increase in τ in the 2-3 cm layer of soil. The highest increase in τ (80 fold) was exhibited by the composite soil.

TABLE 3.2. Shear strength of soil layers at various ψ

	τ kPa			
ψ	Soil Depth (cm)			
kPa	0 - 1	1 - 2	2 - 3	0 - 3[a]
-20	8.26	10.40	17.70	9.50
-33	10.40	27.00	65.70	11.00
-40	12.90	31.90	111.00	14.80
-60	22.30	36.30	132.20	45.30
-80	27.70	44.30	326.50	71.10
-100	33.00	197.50	756.10	166.66
-120	36.30	206.60	1000.00	444.44
-140	48.30	250.00	1108.00	756.10

τ shear strength of soil.

ψ soil water matric potential.

[a] composite soil used in greenhouse study.

Soil water contents at various levels of ψ are presented in Table 3.3. A decrease in the volume of soil water content with decreasing ψ is evident. The top 0-1 cm layer of soil seems to hold comparatively more water at any given ψ. The 2-3 cm layer, on the other hand, appears to have the least water holding capacity. Soil water contents of the composite soil at various ψ were less than, yet close to, that of the 1-2 cm deep layer of soil.

TABLE 3.3. Soil water contents at various ψ

	Soil water content v/v			
ψ kPa	Soil Depth (cm) 0 - 1	1 - 2	2 - 3	0 - 3[a]
-20	0.400	0.379	0.306	0.378
-33	0.398	0.324	0.299	0.359
-40	0.369	0.319	0.235	0.312
-60	0.349	0.289	0.234	0.296
-80	0.297	0.260	0.207	0.290
-100	0.239	0.245	0.150	0.236
-120	0.231	0.244	0.138	0.213
-140	0.222	0.169	0.105	0.151

ψ soil water matric potential.

[a] composite soil used in greenhouse study.

Greenhouse study

Seeds of all the species studied germinated when the soil was kept submerged in water, except those of Xanthium. Soil water matric potential lower than -33 kPa, on the other hand, did not allow any emergence in Polygonum.

In submerged soil, emergence of Polygonum reached 85% in 12 days after planting, 50% of which was attained by the 4th day. A highly significant ($P<.001$) reduction in emergence occurred at ψ equal or less than -10 kPa (Figure 3.1).

Eleocharis seeds exhibited 57% emergence in 18 days under submerged condition. At -10 kPa ψ 85% emergence was recorded within the same period. A sharp decline in the total emergence as well as in the rate of emergence was observed when the soil was at -33 kPa ψ. Thereafter, emergence was low and delayed but apparently not affected by further decrease in ψ down to -140 kPa (Figure 3.2).

In the case of Echinochloa under submerged condition, 53% emergence had occurred by the 9th day of planting. The final count was 84% on the 18th day. A significant decrease ($P<.05$) was evident in the percent emergence under -10 kPa ψ. However, at -20 and -33 kPa ψ, the final emergence percentages were similar to that found in submerged condition. The rate of emergence showed a decline beginning from -33 kPa ψ, whereas at ψ equal or less than -40 kPa a gradual decrease in the percent emergence was discernible (Figure 3.3).

High ψ appeared less favorable for the emergence of Xanthium seeds. Percent emergence increased with decrease in ψ down to -100 kPa. A sharp decline in the rate and final percent emergence was observed with a further decrease in ψ (Figure 3.4). Emergence of Xanthium was significantly affected ($r=-0.72$ $P<.04$) by τ. For all other species studied, emergence was better correlated with ψ than τ.

Field observations

Initiation of emergence of various species commenced at different times during the first two weeks of drawdown. Figure 3.5 portrays the changes in the soil water matric potential in the top 0-2 cm layer of

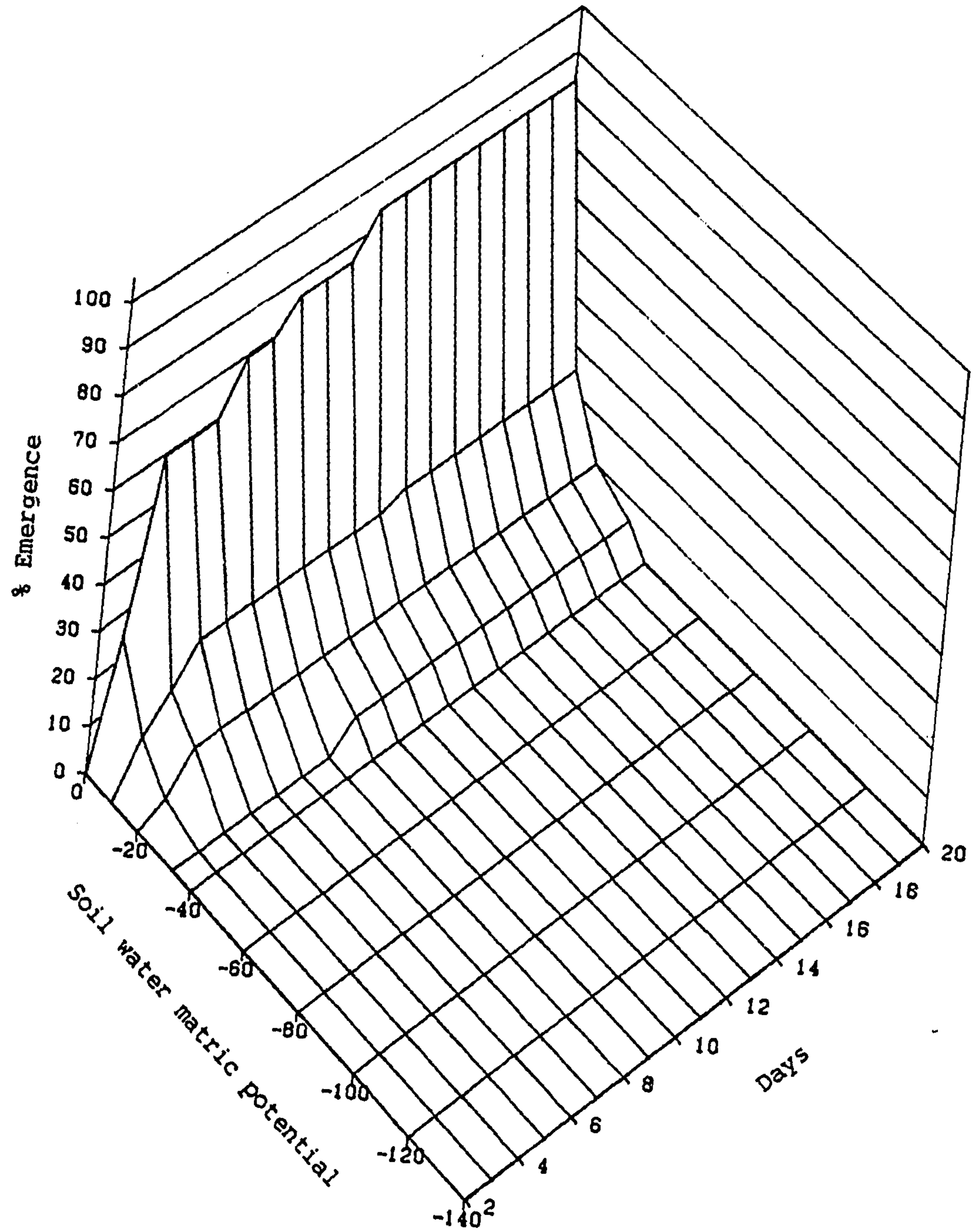

FIGURE 3.1. Emergence of Polygonum hydropiperoides at various levels of soil water matric potential

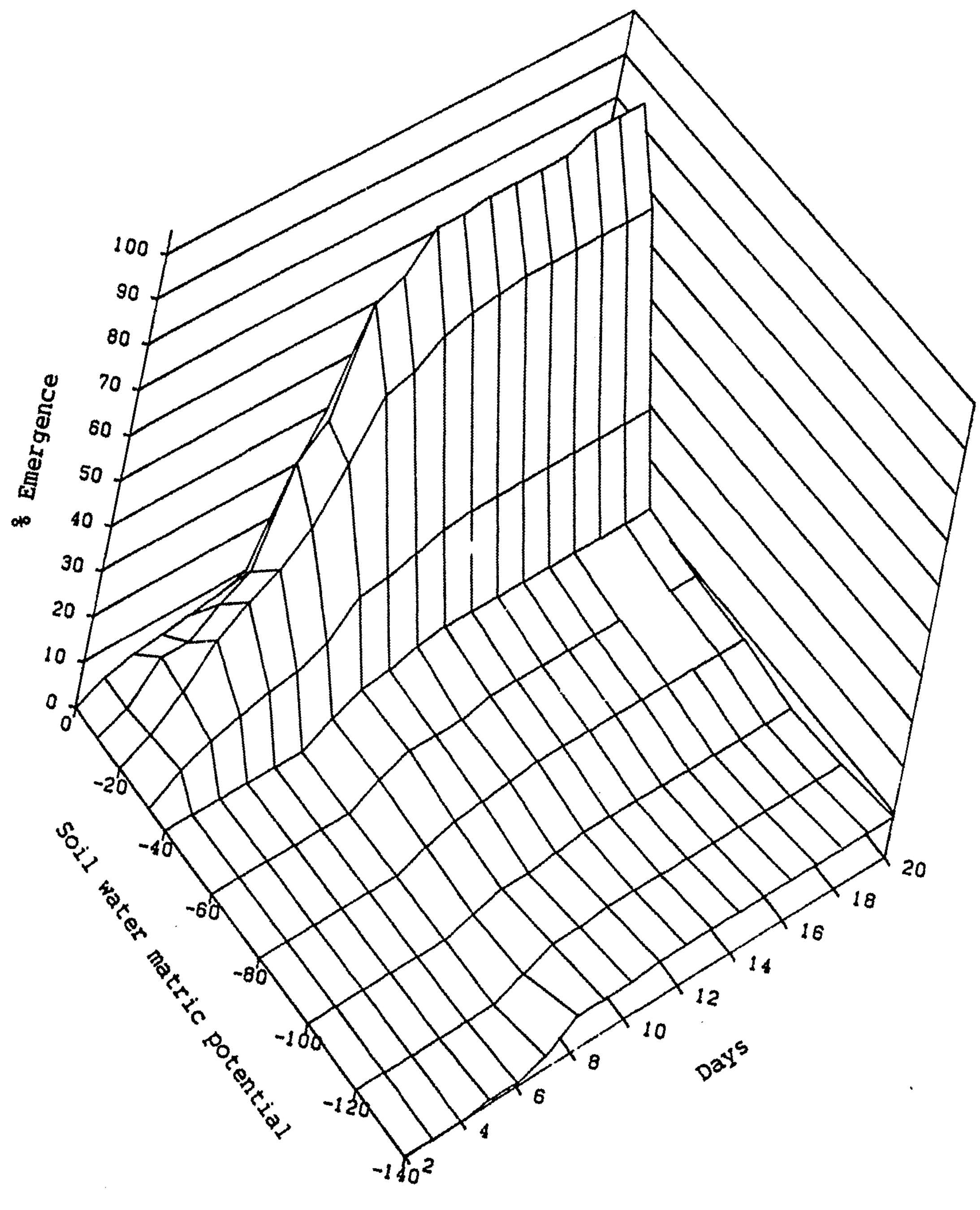

FIGURE 3.2. Emergence of Eleocharis obtusa at various levels of soil water matric potential

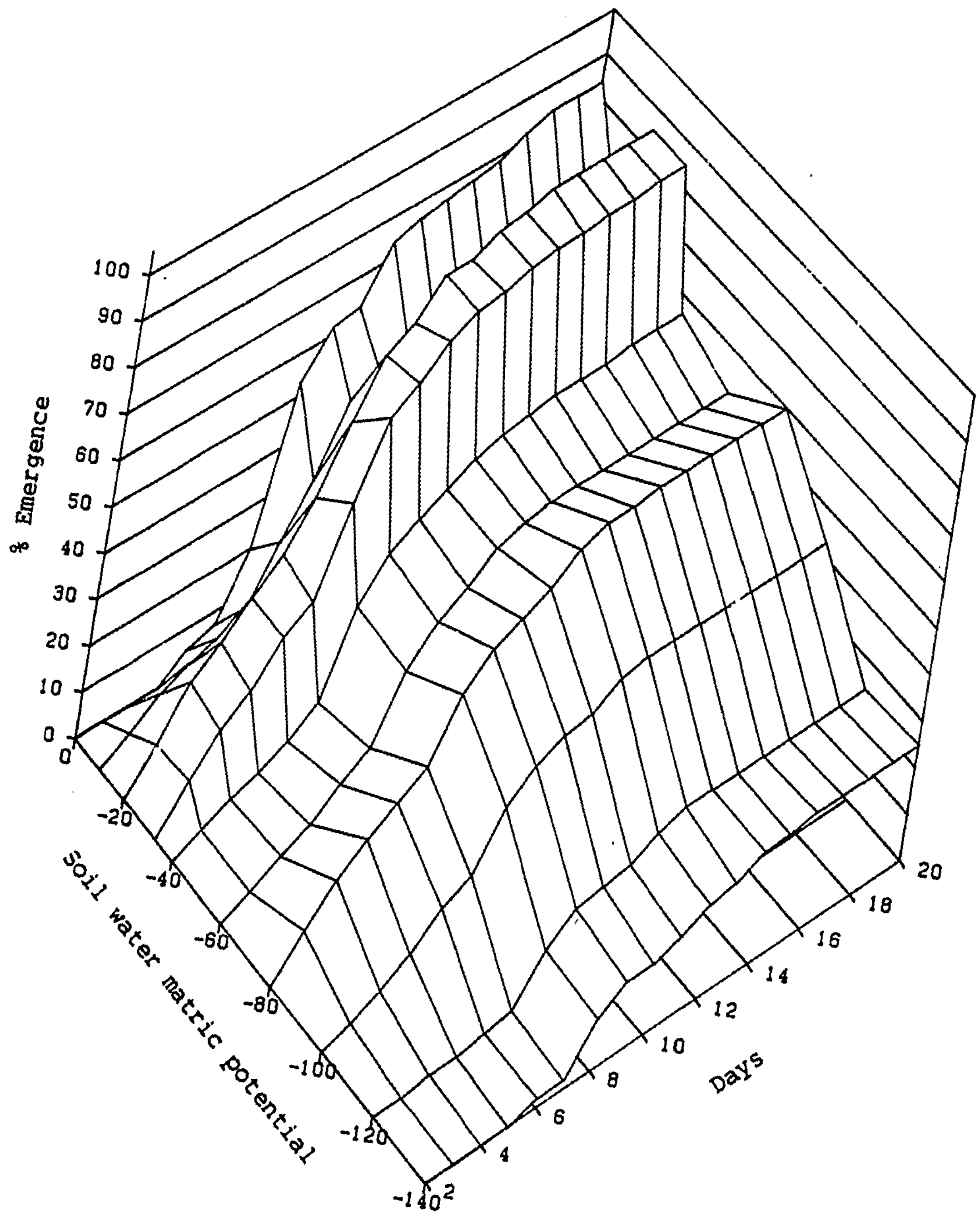

FIGURE 3.3. Emergence of Echinochloa crusgalli at various levels of soil water matric potential

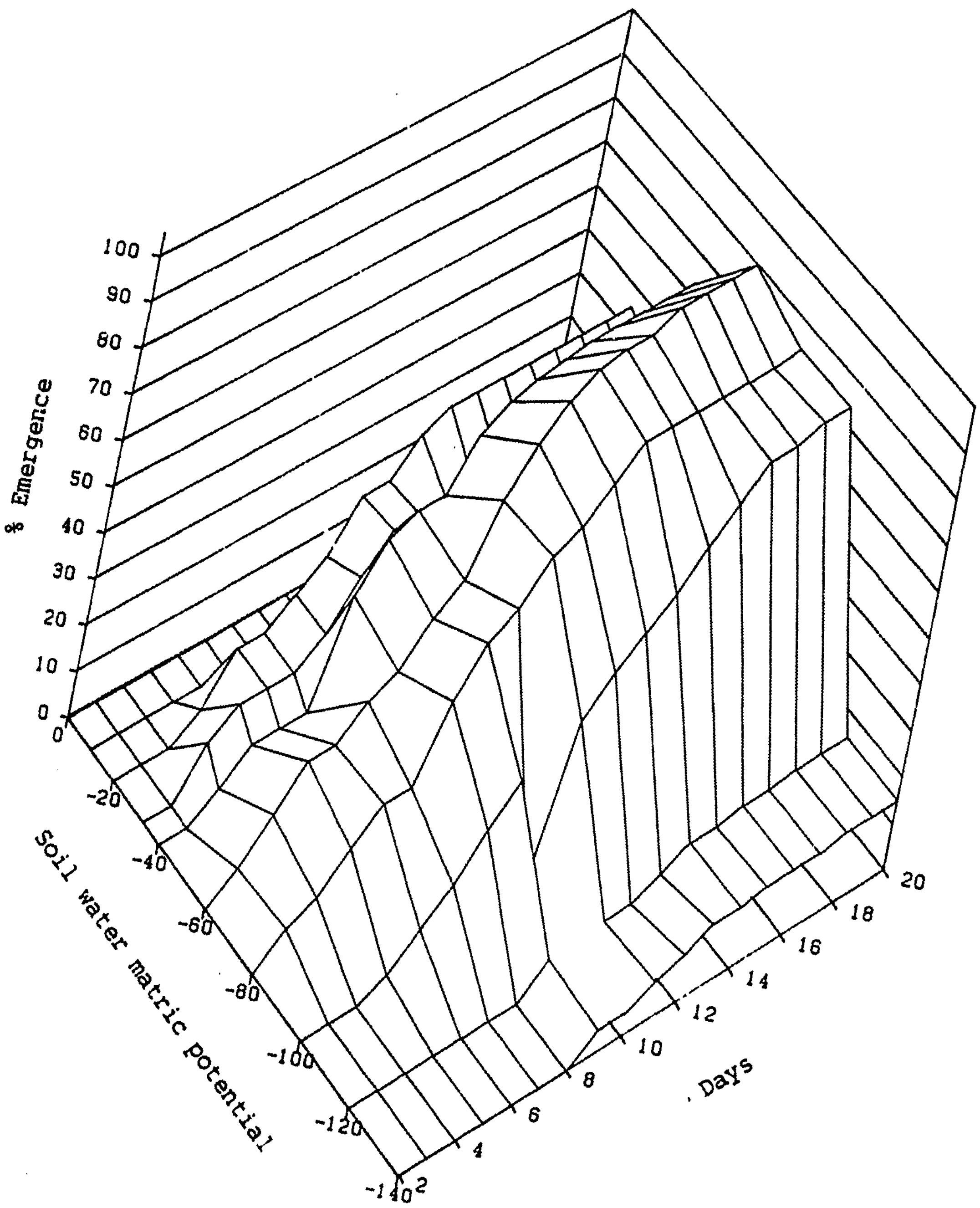

FIGURE 3.4. Emergence of _Xanthium pensylvanicum_ at various levels of soil water matric potential

soil, and the relative percentage of seedling emergence.

Polygonum seedlings were the first to make their appearance on the marsh surface. During this time, the soil was submerged under water. By the time standing water was drained from the marsh, half of the total number of seedlings had emerged. The soil was still saturated with water. No new seedlings of Polygonum were found as the ψ dropped below -15 kPa.

Emergence of Eleocharis seedlings also began while the marsh substrate was still inundated. The rate of emergence, however, was not as high as that of Polygonum. The emergence reached 50% of the total when the ψ was about -10 kPa. A gradual decrease was discernible in the rate of emergence as ψ dropped below -15 kPa. Nonetheless, the seedlings continued to make their appearance on the gradually drying marsh surface down to a ψ of -63 kPa.

Echinochloa seedlings emerged when the ψ was around -10 kPa. The emergence rate was high until it reached 50% of the total emergence. At this point, the ψ was about -40 kPa. Then the rate of emergence appeared to have slowed, while ψ was in the range of -40 kPa to -60 kPa. From a ψ of -60 kPa and less, the emergence rate picked up its momentum. I did not find any more seedlings of this species in the study area as the ψ approached -75 kPa.

Seedlings of Xanthium did not emerge until there was no free water standing on the soil surface. Once begun, the rate of emergence was high throughout the observation period. Half of the total number of seedlings had emerged as the ψ approached -53 kPa. A further decrease

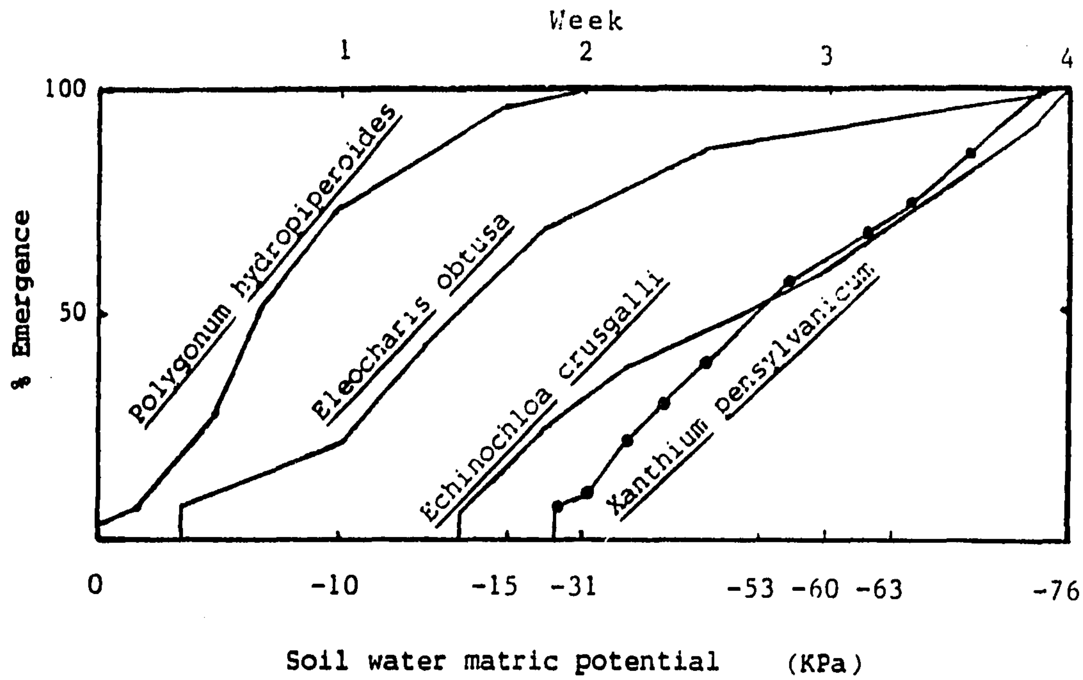

FIGURE 3.5. Changes in soil water matric potential at 0-2 cm depth, and relative percentage of seedling emergence during the first 4 weeks of drawdown

in ψ down to -76 kPa appeared to have little effect on the emergence of this species.

DISCUSSION

Seedling emergence in the field was from seeds that were buried in the soil down to 1.5 cm only. The soil physical analysis may explain such observations. It is apparent that the top soil layer (0-1 cm) had more sand and organic matter (Table 3.1), its water holding capacity was comparatively higher (Table 3.3), and it did not pose as high a mechanical resistance to germination and emergence (Table 3.2). A higher bulk density and comparatively much higher change in the shear strength of soil with a relatively much smaller change in ψ would seem to hamper the germination and emergence rates (Benjamin and Cruse, 1985).

The Moist Soil Unit 2 South contained a sizable seed bank that was distributed in the soil profile down to 5 cm (see Paper 1). The physical analysis of various layers of soil suggests, however, that seeds buried below 1 cm may not be able to germinate or emerge primarily due to a mechanical constraint imposed by the soil matrix.

My greenhouse study demonstrated a species specific behavior of seed germination and emergence to soil water matric potential (ψ). Of the four species studied, Polygonum was most intolerant of low ψ. A high rate of emergence was seen when ψ was 0, but this decreased sharply with a decrease in ψ. These results closely parallel my field observations, where Polygonum emerged on the marsh surface while ψ was less than -15 kPa. A sharp increase in the rate of emergence in the field during the middle of the first week of drawdown is attributable to an increase in the soil temperature (see Paper 2).

Under greenhouse conditions, emergence of Echinochloa was observed over the entire range of ψ tested. This observation is in agreement with the findings of Wiese and Davis (1967), and Wiese and Vandiver (1970). Emergence was greater when ψ was less than -40 kPa. From -40 to -80 kPa, the rate was lower, but then it increased at ψ of -80 kPa. A similar bimodal behavior was exhibited by this species in the field. Such polymorphism in germination and emergence behavior may have some survival value (Silvertown, 1984). In this way, all the viable seeds of a species do not germinate simultaneously but may be able to appear at various times during a drawdown, or occupy different microtopographical locations.

Eleocharis responded well to ψ less than -20 kPa in the greenhouse. Below ψ of -20 kPa, both the rate of emergence and total percent emergence were significantly reduced. In the field, on the other hand, Eleocharis behaved in quite a different manner (Figures 3.2 and 3.5). The rate and percentage of emergence appeared to be affected very little by a wide range of ψ. There does not seem to be a logical explanation for such varied behavior other than differences in the temperatures prevalent in the field and in the greenhouse. Other factors that may have influenced the seed responses include storage conditions, as well as the fact that seeds in the natural seed bank may have been of different ages, whereas seeds of the same age were used in my study.

Emergence of Xanthium in the greenhouse was best while ψ was in the range of -40 kPa to -80 kPa. My field data corroborate these observations. I terminated my field study before the marsh substrate could dry down to -80 kPa ψ, since emergence of three of the four species under study appeared to have reached a plateau. The greenhouse study, however, suggests that a reduction in the emergence rate and percentage would take place beyond -100 kPa ψ. Wiese and Vandiver (1970) found similar results.

Unlike other species studied, emergence in Xanthium was correlated better with τ than with ψ. It appears that the bur protects Xanthium seeds against the soil mechanical constraint to a large extent. This species thus invades marsh substrates when the soil has dried below the so-called field capacity. Once Xanthium makes its appearance on the drawdown surface of the marsh, its broad leaves can shade already emerged seedlings of Eleocharis and Echinochloa. Seedlings of Polygonum do not appear to be affected in similar manner, since early emergence facilitates this species' escape from competition (Ross and Harper, 1972; Hartgerink and Bazzaz, 1984). Further, the stem elongation rate seems to be faster in this species than in Xanthium.

My results imply that a slow drawdown is better than a fast one (Fredrickson and Taylor, 1982). This should allow sufficient time for desirable species (Martin and Uhler, 1939) to establish in the area before the substrate becomes dry enough to facilitate the emergence of Xanthium. Prolonged shallow inundation of the marsh substrate would encourage establishment of a good cover of Polygonum and Eleocharis, and keeping water contents in the marsh soil above the so-called field capacity should ensure a good stand of Echinochloa.

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SUMMARY-DISCUSSION

Studies were conducted at the Moist Soil Unit 2 South in the Mingo National Wildlife Refuge, Southeast Missouri during the summers of 1983-1985. Seed bank characteristics were examined, and emergence of mudflat species was monitored during an artificial drawdown. Seed germination / emergence of four dominating species (Echinochloa crusgalli, Eleocharis obtusa, Polygonum hydropiperoides, and Xanthium pensylvanicum) was investigated over a wide range of diurnally fluctuating soil temperatures using a two-way thermogradient plate. Further, emergence behavior of the same species was observed under various levels of soil water matric potential (ψ).

Seed distribution in soil profile

Both qualitative and quantitative changes occurred in the seed bank during the study period. The distribution pattern, however, did not change significantly. No relationship could be established among the seed specific density, soil physical characteristics, and the depth of occurrence of various seeds in the soil profile.

I found the number of seeds in the seed bank to gradually increase in the soil profile down to 4 cm depth and then sharply decline. It appears that all the investigations in the past that have used bulk of soil to make estimates of seed bank, overlooked the heterogeneity inherent in the vertical distribution of seeds in the soil profile. Work of Leck and Graveline (1979), Thompson and Grime (1979), Pederson (1981), and Smith and Kadlec (1983, 1985), for instance, failed to recognize the vertical distribution pattern of the seeds in the soil profile. Considering that it is mostly the seeds in the top 2 cm layer of soil that make the future vegetation of an area (Gaudet, 1977; Galinato and van der Valk, 1986), ignoring the vertical seed distribution pattern would seriously reduce the applicability of any seed bank study.

Response to temperature

Use of a two-way thermogradient plate allowed me to evaluate the response of seeds of the selected species to a very broad range of diurnally fluctuating temperature as compared to that used by Thompson and Grime (1983). I found seeds of Polygonum to prefer cooler temperatures as compared to the other species studied. Xanthium was on the other extreme of the range, while moderate temperatures facilitated the germination / emergence in Eleocharis and Echinochloa. Depth of seed burial affected germination / emergence of all the species to the extent that no emergence was observed from seeds buried below 3 cm depth of soil. Seeds of Xanthium were exception, however, the rate of germination / emergence was substantially reduced.

Germination polymorphism (Silvertown, 1984) was exhibited by all the species examined. This alludes to the occurrence of some adaptive mechanism(s) that may have evolved owing to the highly fluctuating environmental conditions in the area. Such adaptations are desirable in species useful to waterfowl (Martin and Uhler, 1939) or other wildlife in the refuge, nevertheless, it is equally undesirable in species classified as "unwanted" for wetlands (Fredrickson and Taylor, 1982). My results show that Xanthium does possess such features rendering it difficult to eliminate this species from the area.

Field and laboratory studies appeared to have good agreement as far as the general trend in the response of seed germination / emergence was concerned. Discrepancies in the specific temperature ranges and/or rates of germination / emergence may be due to differences in the storage conditions to which I subjected the seeds prior to laboratory study. Seeds in the field face lower temperatures with much higher diurnal fluctuations in addition to other physico-chemical dissimilarities.

Response to soil water matric potential

During the drawdown, Polygonum seedlings were the first to appear on the marsh substrate. It appears that this species prefers higher soil water potentials for germination / emergence. Initiation of a drawdown earlier in the spring should greatly increase its abundance in the marsh. A drawdown late in the spring may also bring about similar results as long as the soil temperature stays lower than 22°C.

Eleocharis seemed very much unaffected by lower soil water matric potentials down to -63 kPa. In the greenhouse, however, the critical soil water potential appeared to be - 33 kPa. This could be due to differences in the seed storage conditions as well as the age of the seeds. The greenhouse study used seeds of the same age while those that germinated from the natural seed bank in the field very likely belonged to different age groups.

Both field and greenhouse studies encountered a bimodal germination / emergence response of Echinochloa to various levels of soil water matric potential. Apparently, this behavior is not affected by temperature. Considering the micro-topographical heterogeneity that exists in the habitat, such behavior may have a survival value for this species.

Xanthium seeds germinated / emerged when the soil water matric potential had fallen below the so called field capacity. Such condition is an obvious result of a drawdown. Soil temperature during this period is usually high enough to be conducive for seed germination of this species. My results suggest that a slow drawdown may be a way to discourage this species from invading the marsh. Maintenance of soil water potential above the so-called field capacity will allow sufficient time, in addition to conditions suitable for germination / emergence, for desirable species to establish in the area. Later in the season, when the marsh substrate becomes drier, seedlings of the species useful for waterfowl will be big enough to escape shading by the late emerging broad-leaf seedlings of Xanthium.

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