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Well developed Iowa fens contain three distinct vegetation zones (border zone, sedge mat zone and discharge zone). On the average, the above ground standing crop of these zones is 425, 197 and 528 g/m² respectively. Species growing on these fens show three basic distributional patterns: (1) they grow in the border and discharge zones; (2) they grow primarily in the sedge mat zone or (3) they grow in all three zones. Individual plants of species growing in the border and/or discharge zone are on the average 1.6 to 2.7 times taller and weigh 1.8 to 5.4 times more than when they grow on the sedge mat zone. Species with primarily bimodal or ubiquitous distributions show the greatest decline in height and weight when found in the discharge zone. The three Iowa fen zones are a result of differences in environmental conditions, plus competitive displacement of the dominant sedge mat species from the border and discharge zones.

The relationship between various environmental factors and the distribution of both aquatic macrophyte species and communities has been extensively investigated (Pond, 1905; Misra, 1938; Moyle, 1945; Olsen, 1950; Spence, 1967; Seddon, 1972; Westlake, 1973; Britton, 1974; *inter alia*). However, wetland ecologists have paid remarkably little attention to biological factors (allelopathy, herbivory, disease, competition) and their effects on the distribution of aquatic macrophytes. The significance of allelopathy in wetlands is still unknown. Work by McNaughton (1968) on autoinhibition of *Typha* seed germination and later experimental work by Szczepanska (1971) and Szczepanski (1971) suggest that this might be a fruitful area for additional research. The best understood and studied biological factor is herbivory. Besides inumerable, scattered bits of anecdotal material, there have been a number of studies concerned with this topic (Lynch et al., 1947; Weller and Spatcher, 1965; Durska, 1970; Kvet and Hudec, 1971; Gill, 1974). Although some information on the diseases of aquatic macrophytes has been collected (see for example Durska, 1970), its significance in natural wetlands remains to be documented. Competitive interactions among macrophytes (with the exception of members of the Lemnaceae and other small free floating macrophytes) have also rarely been studied in the laboratory or in the field. Some experimental work on interspecific competition among helophytes has been published by Szczepanska and Szczepanski (1973). The only published account of competitive interactions among macrophytes under field conditions appears to be that of Buttery and Lambert (1965) who demonstrated that interspecific competition was responsible for the zonation of *Glyceria maxima* and *Phragmites communis* in a British fen.

This study was designed to determine if interspecific competition might be responsible for the zonation found in fens in northwest Iowa (van der Valk, 1975). These fens have three distinct vegetation zones: a more or less central discharge zone which is raised above the surface of the remainder of the fen, a sedge mat zone, and a border zone. It is the low stature of the plants in the sedge mat zone compared to the other two zones which makes this zonation so striking. The following information was collected during the course of the study:

(1) the floristic composition of all three vegetation zones in these fens;
(2) primary production of all three zones; and
(3) the weight and/or height of individuals of species growing on the sedge mat and off it in either of the other zones.

Study Sites

Iowa fens are relatively small (generally several thousand square meters) seepage areas on the sides of morainic hills where alkaline ground water reaches the surface because of the presence of sand lenses in an impermeable clay stratum (van der Valk 1975). There are only two known fen complexes remaining in northwestern Iowa, both in Dickinson County. The Silver Lake fen complex is located in the northwest corner of section 32, Silver Lake Township. This complex is an Iowa State Preserve and is protected from disturbance. The flora of this complex has been described by Anderson (1943), Conard (1952), Holte and Thorne (1962), Holte (1966), and van der Valk (1975). Only the large, main fen was included in this study, i.e., fen number one of Eickstaedt (1964). The second fen complex, the Excelsior fens, is located in the southwest corner of section 10 and the northwest corner of section 15, Excelsior Township. All seven well developed fens, i.e., having all three zones, in this complex were studied. These are fens, 2, 3, 4, 7, 9, 10 and 11 of Holte (1966). The flora of this complex has been studied by Holte and Thorne (1962), Holte (1966), and van der Valk (1975). All the Excelsior fens are located on privately owned pasture and are subject to grazing by cattle. This grazing is restricted normally to the border zone. However, in dry years cattle will venture out onto the unstable fen surface if all other forage has been eaten. During this study, grazing occurred only in the border zone. An examination of the floristic composition of the border zones at the Excelsior complex and the Silver Lake complex indicates that grazing has had no noticeable influence on the floristic composition of the border zone (van der Valk, 1975).

Calamagrostis inexpansa, Carex spp, *Scirpus americanus,* and *Viola nephrophylla* are the dominant species in the border zone (Table 1). The floristic composition of this zone can vary considerably both within and among fens. *Rhynchospora capillacea* is the dominant species of the sedge mat zone. Other species typically found in this zone are *Lobelia kalmii, Muhlenbergia racemosa, Parnassia glauca, Scirpus americanus,* and *Triglochin maritima.* The floristic composition of this zone is nearly constant from fen to fen. The discharge zone is dominated by *Carex* spp. and/or *Calamagrostis inexpansa* at the Excelsior complex and by *Phragmites communis* and *Helianthus grosseserratus* at the Silver Lake fen (van der Valk, 1975).

Methods

Each fen was sampled using a transect along which were placed at

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Table 1. *Importance values of all species found at three or more fens in at least one zone.*

Species	Zone B[1]	Zone SM	Zone D
Calamagrostis inexpansa	21	0	12
Carex spp.	12	0.01	18
Eleocharis erythropoda	0.05	0.01	0
Eupatorium maculatum	3	0.6	3
Eupatorium perfoliatum	0.4	0.04	0
Juncus nodosus	4	0.01	0
Lobelia kalmii	0.04	4.0	0.01
Lycopus asper	4	0.04	12
Mentha arvensis	0	0	12
Muhlenbergia racemosa	0.6	0.7	0.3
Parnassia glauca	4	4	3
Rhynchospora capillacea	0.04	160	0.01
Scirpus acutus	0.4	0.01	10
Scirpus americanus	4	4	0.5
Triglochin maritima	0.3	24	6
Viola nephrophylla	24	0.03	12

[1]B — Border zone; SM — Sedge Mat zone; and D — Discharge zone.

evenly spaced intervals 11 quadrats (20 x 50 cm). These transects were positioned so that they passed through all three zones and avoided areas in the border zone disturbed by grazing. At the Silver Lake fen two intersecting transects were used.

In each quadrat, the cover of each species was estimated using a cover-abundance scale (van der Valk and Bliss, 1971; van der Valk, 1975). For each zone, the importance value (IV) of each species was calculated using the following formula:

IV = zonal presence x average percent cover in that zone

where

IV = importance value of a species in a given zone; and

zonal presence = number of fens in which a species occurred in a given zone.

The maximum value of IV is 780, i.e., the species occurred in a particular zone at all eight fens with covers in the range of 95 to 100 percent.

Each quadrat was also clipped at ground level, and all dead material removed from each sample. These standing crop samples were oven dried at 80°C and weighed. All quadrats were harvested in late July and early August, 1974. A nested analysis of variance was applied to the standing crop data using the ANOVA procedure in Service (1972). In this analysis, fens were nested within sites or complexes and zones within fens.

At the Silver Lake fen, the above ground height of 10 to 15 randomly chosen individuals of all sedge mat species were measured on the sedge mat. Another 10 to 15 were measured in either the border or discharge zones. Ten individuals of many of these same species were also clipped at ground level on and off the mat. A differential growth index (DGI) was calculated for each species by dividing its average height or weight off the sedge mat by its average height or weight on the sedge mat.

For each standing crop sample harvested from the sedge mat zone, its potential standing crop (PSC) was calculated using the following equation:

$$PSC = SC \sum_{i=1}^{s} P_i \times DGI_i$$

where

SC = actual standing crop of a quadrat (g/m²)·

P_i = relative cover of the i^{th} species in the quadrat;

DGI = the differential growth index of the i^{th} species in the quadrat; and

s = the total number of species in the quadrat.

The nomenclature in this study follows Gleason and Cronquist (1963).

RESULTS

The importance values for all species found at three or more fens in at least one zone are given in Table 1. Fen species show three basic distributional patterns. *Calamagrostis inexpansa, Carex* spp, *Eupatorium maculatum, Lycopus asper* and *Viola nephrophylla* have a bimodal distribution and are found primarily in the border and discharge zones. According to Table 1, *Juncus nodosus, Mentha arvensis* and *Scirpus acutus* were found mainly in either the discharge or the border zones; this is a sampling artifact. Field observations indicate that these species also have a bimodal distribution. A second, smaller group of species are found mostly in the sedge mat zone: *Lobelia kalmii, Rhynchospora capillacea,* and *Triglochin maritima*. The third group of species are ubiquitous and are found more or less equally distributed in all three zones: *Parnassia glauca, Muhlenbergia racemosa,* and *Scirpus americanus*. The remaining species in Table 1 were encountered too infrequently (their importance values are less than 0.5) to gain any clear impression of their distributions. Table 1 also indicates that all sedge mat species were found in either the border or discharge zones and often in both. However, at least two species (*Calamagrostis inexpansa* and *Mentha arvensis*) never were found in the sedge mat zone (Table 1).

Table 2. *Above ground standing crop (g/m^2) of the border, sedge mat and discharge zone communities of Iowan fens.*

Fen	Border Mean	±SD[1]	Sedge Mat Mean	±SD	Discharge Mean	±SD
E-2[2]	435	112	284	62	716	221
E-3	463	119	192	29	427	143
E-4	430	115	189	50	484[3]	
E-7	436	41	183	30	399	18
E-9	391	46	179	35	450	117
E-10	231	88	191	32	428	99
E-11	370	64	144	45	266[3]	
SLK	484	124	237	68	777	356
Average	425	113	197	56	528	228
Total # samples in a zone	23		58		18	

[1]SD — Standard deviation.
[2]E — Excelsior fen complex.
SLK — Silver Lake fen.
[3]Only one sample.

The average standing crop data for the three zones are summarized in Table 2 and the analysis of variance of these data in Table 3. The sedge mat zone has a significantly lower average standing crop (197 g/m²) than that of the border (425 g/m²) or discharge zone (528 g/m²). The general standing crop pattern is discharge > border > sedge mat. However, at three fens at the Excelsior complex (3, 7, and 11), the pattern was border > discharge > sedge mat (Table 1). This reflects the variability of the standing crops of the discharge zone which ranged from 266 to 777 g/m². It is this variability which is responsible for the significant differences in standing crops among fens (Table 3). The ANOVA (Table 3) also shows that the average standing crop at the Excelsior fens was significantly lower than that at the Silver Lake fen. At the Excelsior fens the average above ground standing crops of the border, sedge mat and discharge zones are 394, 195, and 453 g/m² respectively while at the Silver Lake fen they are 484, 237, and 777 g/m² respectively.

Table 3. *Analysis of variance of the above ground standing crop data*

Source of Variation	df[2]	Sum of Squares
LOC[1]	1	231,378*
FEN (LOC)	6	267,697*
ZONE (FEN LOC)	16	2,042,586*
ERROR	75	697,656
CORRECTED TOTAL	98	3,239,317

[1]LOC — Silver Lake or Excelsior fen complex.
[2]df — Degrees of freedom.
*Significant at 95 percent level

Table 4. *Average height (cm), biomass (g/plant), and differential growth index (DGI) of species growing both on the sedge mat and off it in the discharge and/or border zone)*

Species	On Sedge Mat Mean	±SD[2]	Off Sedge Mat Mean	±SD	DGI[1]
		HEIGHT(cm)			
Eupatorium perfoliatum	33	5	80	10	2.4
Lobelia kalmii	25	3	40	8	1.6
Lycopus asper	22	6	60	11	2.7
Muhlenbergia racemosa	31	4	55	4	1.8
Parnassia glauca	14	2	32	3	2.3
Phragmites communis	98	20	221	28	2.3
Rhynchospora capillacea	17	4	30	5	1.8
Scirpus acutus	83	8	200	18	2.4
Scirpus americanus	47	8	119	13	2.5
Triglochin maritima	35	8	57	10	1.6
		WEIGHT(g/plant)			
Eupatorium perfoliatum	1.14	0.35	5.21	2.40	4.6
Lobelia kalmii	0.061	——[2]	0.13	——	2.1
Lycopus asper	0.28	——	1.95	——	7.0
Muhlenbergia racemosa	0.26	——	0.47	——	1.8
Scirpus americanus	0.30	——	1.63	——	5.4

[1]DGI — differential growth index.
[2]SD — standard deviation; not determined for weight samples because plants were weighted together, rather than individually.

Table 4 gives the average height, weight and differential growth indices of fen species from the Silver Lake fen. Preliminary measurements and field observations had shown that there was no detectable difference in the growth of species in the border and discharge zones. All species examined were much shorter and weighed less when they grew on the sedge mat. Their heights were 1.6 to 2.7 times greater off the mat than on it, and their weights 1.8 to 5.4 greater. Although no measurements are included in Table 4 from the Excelsior fen complex, a few spot measurements indicated that the DGI's from there would be similar to those from the Silver Lake fen, but that the absolute values of height and weight would be slightly smaller both on and off the mat. The data in Table 4 also show that height measurements always give an equal or lower differential growth index than weight measurements for the same species. For example, the DGI's for *Scirpus americanus* are 2.5 based on height and 5.4 based on weight. Plants with similar morphologies, e.g., *Muhlenbergia racemosa* and *Rhynchospora capillacea*, appear to have similar DGI's of 1.8 based on height (Table 4). Species with a bimodal or ubiquitous distribution among fen zones all have higher DGI's based on height (2.3 to 2.7) than species found primarily on the sedge mat (1.6 to 1.8).

The potential standing crop of the sedge mat zone, calculated using the DGI's of Table 4 and relative cover value to determine the contribution of each species to the standing crop, is on the average 397 ± 152 g/m². This is double its actual value of 197 ± 56 g/m². A t-test assuming unequal sample size and unequal variance (Steel and Torrey, 1960) indicates that there is no significant difference between the average potential standing crop of the sedge mat zone and that of the actual standing crop of the border zone (425 ± 113 g/m²). In making the potential standing crop calculations, there were a few, minor species for which no DGI's were available. In these cases, a DGI was used from Table 4 of a species which morphologically resembled the species on which no measurements had been taken. These minor species have virtually no impact on the potential standing crop values, since they never had a cover of more than one percent in any quadrat. The potential standing crop calculated is undoubtedly an underestimate, since some DGI's based on height measurements had to be used.

DISCUSSION

According to the literature *Carex*-dominated wet meadow communities, similar to those in the border and discharge zones, have standing crops ranging from 400 to 1,470 g/m² (Gorham, 1974). However, wet meadow communities under stress because of repeated flooding (van der Valk and Bliss, 1971) have standing crops as low as 133 to 394 g/m² (see also Jakrlova, 1967). The *Carex*-dominated discharge and border zones in Iowa fens have average standing crops (425 and 453 g/m² respectively) at the lower end of the range previously recorded. The *Phragmites communis*-dominated discharge zone at the Silver Lake fens also has a low standing crop (777 g/m²) compared to other *Phragmites* communities (see Dykyjova and Hradecka, 1973). These depressed standing crop values indicate that growing conditions are poor in Iowa fens (see Buttery *et al.*, 1965). The hard water characteristic of these fens (van der Valk, 1975) does not appear to be the major factor responsible for these low standing crops. Average standing crops at the Silver Lake fen are higher than at the Excelsior fens even though the water at the Silver Lake fen is harder; e.g., the conductivity is 2,600 μmhos at the Silver Lake fen and 1,300 to 1,500 μmhos at the Excelsior fens. These low standing crops are more likely to be a result of the low nutrient content of the ground water (Holte, 1966).

The sedge mat zone (Table 2, 3) has the lowest standing crop of the three fen zones. Two basic explanations for this are possible: (1) the species composition of this zone makes it inherently less productive; or (2) the sedge mat zone is the zone where the greatest environmental stress occurs in the fens. Although the sedge mat does have a very different species composition from the other two zones (Table 1; van der Valk, 1975), its lower standing crop is not a result of this floristic difference, since the potential standing crop of the sedge mat zone is as high as the border zone. The second explanation seems most likely; the low standing crops of the sedge mat zone are a result of poorer growing conditions. Individual sedge mat species all grow better off the mat (Table 4) and at least two species will not grow in this zone at all (Table 1). It would appear from Table 4 that all species growing on the fens are closer to their physiologically optimum growth conditions (*sensu* Ellenberg, 1953), i.e., the conditions under which individuals of a species reach optimum size, when they are growing in the border or discharge zones. However, the ecological optimum zone of certain species, i.e., the environmental conditions under which the species is found in its greatest abundance, does not correspond to their physiological optimum zone of growth in the fens. The dominant sedge mat species (*Rhynchospora capillacea, Triglochin maritima,* and *Lobelia kalmii*) all have been competitively displaced to the sedge mat zone from the border and discharge zones where individuals of these species have their best growth (Table 4). This displacement cannot be caused by allelopathic interactions, since all fen species have their best growth when growing together in the border or discharge zones (Table 4). The three fen zones, then, result from differences in environment, plus the competitive displacement of several species from the border and discharge zones including the sedge mat dominant, *Rhynchospora capillacea,* into the sedge mat zone. From the data collected, it is not possible to establish if border and discharge zone species are prevented from becoming established on the sedge mat in any numbers as a result of competition, the harsher environment or, most likely, a combination of the two. What is known is that the growth of discharge and border species is more inhibited in the sedge mat zone, than the growth of the dominant sedge mat species (Table 4). Buttery and Lambert (1965) report a similar case of competitive displacement in a British fen in which *Glyceria maxima* was outcompeted in favourable habitats by *Phragmites communis* and also in the most unfavorable sections of the fen gradient, while in the remainder of the fen *Glyceria* was able to outcompete *Phragmites*.

The nature of the environmental differences among the three fen zones in an Iowa fen have not been definitively established and are presently under investigation. However, environmental data collected by Holte (1966) suggests that the sedge mat zone has the poorest growing conditions. This zone is low in nutrients and also has anaerobic, organic soils. The border zone has a better nutrient status because of its proximity to the mineral soils surrounding the fen and the discharge zone has aerated soils because of its higher elevation (Table 1). Experimental work is in progress to modify the sedge mat zone environment by the addition of fertilizer and by raising its surface level artificially to study changes in species composition, if any, that these manipulations will cause. Holte's (1966) ideas about the environmental differences among the zones and the account of the origin of these zones given above is supported indirectly by the fact that small fens at the Excelsior complex (not included in this study) have no sedge mat zone. They are completely covered with border/discharge vegetation. In these small fens the influence of mineral soils from around the fen reaches to the discharge zone and the harsh environment required for a sedge mat is not present.

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