Zonation, Competitive Displacement and Standing Crop of Northwest Iowa Fen Communities

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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, 1965; Misra, 1958; 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 innumerable, 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 Hudc, 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 Eckstaedt (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 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 inexpectans, 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 kalnii, 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 inexpectans at the Excelsior complex and by Phragmites communis and Helianthus grosseseratus at the Silver Lake fen (van der Valk, 1975).

METHODS

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

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

<table>
<thead>
<tr>
<th>Species</th>
<th>B¹</th>
<th>SM</th>
<th>D</th>
</tr>
</thead>
<tbody>
<tr>
<td>Calamagrostis inexpansa</td>
<td>21</td>
<td>0</td>
<td>12</td>
</tr>
<tr>
<td>Carex spp.</td>
<td>12</td>
<td>0.01</td>
<td>18</td>
</tr>
<tr>
<td>Eleocharis erythropoda</td>
<td>0.05</td>
<td>0.01</td>
<td>0</td>
</tr>
<tr>
<td>Eupatorium maculatum</td>
<td>3</td>
<td>0.6</td>
<td>3</td>
</tr>
<tr>
<td>Eupatorium perfoliatum</td>
<td>0.4</td>
<td>0.04</td>
<td>0</td>
</tr>
<tr>
<td>Juncus nodosus</td>
<td>4</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Lobelia kalmii</td>
<td>0.04</td>
<td>4.0</td>
<td>0.01</td>
</tr>
<tr>
<td>Lycoerus asper</td>
<td>4</td>
<td>0.04</td>
<td>12</td>
</tr>
<tr>
<td>Mentha arvensis</td>
<td>0</td>
<td>0</td>
<td>12</td>
</tr>
<tr>
<td>Muhlenbergia racemosa</td>
<td>0.6</td>
<td>0.7</td>
<td>0.3</td>
</tr>
<tr>
<td>Parnassia glauca</td>
<td>4</td>
<td>4</td>
<td>3</td>
</tr>
<tr>
<td>Rhynchospora capillacea</td>
<td>0.04</td>
<td>160</td>
<td>0.01</td>
</tr>
<tr>
<td>Scirpus acutus</td>
<td>0.4</td>
<td>0.01</td>
<td>10</td>
</tr>
<tr>
<td>Scirpus americanus</td>
<td>4</td>
<td>4</td>
<td>0.5</td>
</tr>
<tr>
<td>Triglochin maritima</td>
<td>0.3</td>
<td>24</td>
<td>6</td>
</tr>
<tr>
<td>Viola nephrophyllia</td>
<td>24</td>
<td>0.03</td>
<td>12</td>
</tr>
</tbody>
</table>

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

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

Each quadrat was 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.

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

Table 2. Above ground standing crop (g/m²) of the border, sedge mat and discharge zone communities of Iowan fens.

<table>
<thead>
<tr>
<th>Fen</th>
<th>Border Mean ± SD</th>
<th>Sedge Mat Mean ± SD</th>
<th>Discharge Mean ± SD</th>
</tr>
</thead>
<tbody>
<tr>
<td>E-2</td>
<td>435 ± 55</td>
<td>284 ± 24</td>
<td>716 ± 38</td>
</tr>
<tr>
<td>E-3</td>
<td>463 ± 40</td>
<td>192 ± 31</td>
<td>427 ± 39</td>
</tr>
<tr>
<td>E-4</td>
<td>410 ± 36</td>
<td>189 ± 30</td>
<td>484 ± 16</td>
</tr>
<tr>
<td>E-7</td>
<td>436 ± 28</td>
<td>183 ± 30</td>
<td>399 ± 18</td>
</tr>
<tr>
<td>E-9</td>
<td>391 ± 28</td>
<td>179 ± 39</td>
<td>450 ± 17</td>
</tr>
<tr>
<td>E-10</td>
<td>231 ± 32</td>
<td>191 ± 32</td>
<td>428 ± 99</td>
</tr>
<tr>
<td>E-11</td>
<td>370 ± 28</td>
<td>144 ± 45</td>
<td>266 ± 30</td>
</tr>
<tr>
<td>SLK</td>
<td>484 ± 28</td>
<td>237 ± 68</td>
<td>777 ± 356</td>
</tr>
<tr>
<td>Average</td>
<td>425 ± 113</td>
<td>197 ± 56</td>
<td>528 ± 228</td>
</tr>
<tr>
<td>Total # samples in a zone</td>
<td>23</td>
<td>58</td>
<td>18</td>
</tr>
</tbody>
</table>

¹SD — Standard deviation. ²E — Excelsior fen complex. ³SLK — Silver Lake fen. ⁴Only 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

<table>
<thead>
<tr>
<th>Source of Variation</th>
<th>df²</th>
<th>Sum of Squares</th>
</tr>
</thead>
<tbody>
<tr>
<td>LOC¹</td>
<td>1</td>
<td>231,378*</td>
</tr>
<tr>
<td>FEN (LOC)</td>
<td>6</td>
<td>267,697*</td>
</tr>
<tr>
<td>ZONE (FEN LOC)</td>
<td>16</td>
<td>2,042,586*</td>
</tr>
<tr>
<td>ERROR</td>
<td>75</td>
<td>697,656</td>
</tr>
<tr>
<td>CORRECTED TOTAL</td>
<td>98</td>
<td>3,239,317</td>
</tr>
</tbody>
</table>

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

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 characteristic of these fens (van der Valk, 1975) does not appear to be a result of the low nutrient content of the ground water (Holte, 1966). 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 fen 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 µhos at the Silver Lake fen and 1,300 to 1,500 µhos 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).

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Table 4 gives the average height, weight and differential growth indices of ten 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 fens 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 quadrant. 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 fen 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 µhos at the Silver Lake fen and 1,300 to 1,500 µhos 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).

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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 sedgemat 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 sedgemat species (Table 4). Butterly 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 and growing conditions. This zone is low in nutrients and also has anaerobic, organic soils. The border zone has a better nutrient status and growing conditions. This zone is low in nutrients and also has anaerobic, organic soils. The sedge mat zone, on the other hand, while having the highest nutrient status, suffers from a harsh environment characterized by low pH and high alkalinity.

ACKNOWLEDGEMENTS

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REFERENCES