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Vegetation Patterns in and among Pannes (Calcareous Intradunal Ponds) at the Indiana Dunes National Lakeshore, Indiana

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ABSTRACT: The relationships between plant species composition and dispersion, water chemistry and water depth/depth to water table were studied in five calcareous intradunal ponds (pannes) bordering the southern tip of Lake Michigan. The panne systems contained eight plant species threatened and endangered in Indiana. The aquatic zone was dominated by *Chara*, the pond edge by *Rhynchospora capillacea*, *Juncus balticus* and *Utricularia cornuta*, and the area surrounding the pond by *Hypericum kalmianum*. The water chemistry was typical of hardwater ponds in the area, probably affecting species composition but not species dispersion within the pannes. A significant correlation between the first axis scores from a reciprocal-averaging ordination and water depth/depth to water was demonstrated. Panne species are fitted to a model based on hydrology proposed by van der Laan for dune-slack vegetation in the Netherlands.

INTRODUCTION

There is a series of intradunal ponds (pannes) just inland from the beach dunes at the Indiana Dunes National Lakeshore. These pannes differ in origin, age and plant species composition from numerous interdunal ponds found farther inland in older dune systems. The pannes now provide habitat for plant species found nowhere else in Indiana. Depressions which support the pannes were scoured out by wind around the turn of the century when Lake Michigan and groundwater levels were relatively low. When lake levels rose in the 1930s, the water table also rose and was exposed in the base of the depressions. These shallow ponds (< 1m in depth) are normally perennial and the water is well-buffered with bicarbonates.

Pannes are associated with dune systems along the E coast of Lake Michigan, along the southern shore of Lake Huron, and in one known location on Lake Superior. The number of plant species these have in common with the pannes at Indiana Dunes decreases as distance from them increases (Chapman, 1982). Similar systems called "dune slacks" are associated with marine dune systems in the Netherlands (van der Laan, 1979; Londo, 1974), North Wales (Onyekwelu, 1972), North Devon (Willis *et al.* 1959), England (Bevercombe *et al.*, 1973) and New South Wales (Timms, 1982). Research on Great Lakes pannes has been limited to qualitative descriptions of vegetation (Chapman, 1982; Wilhelm, 1980), a study of primary production and ecosystem metabolism in one panne in Michigan (Barko *et al.*, 1977), and a study of Fowler's toad (Breden, 1979).

The goal of this study was to characterize the habitat and vegetation of five pannes and to quantify the dispersion of plant species along an elevation/water depth gradient.

METHODS

Study site. — This study was conducted in the West Beach Unit of the Indiana Dunes National Lakeshore, located between Gary and Michigan City, Indiana, at approximately 87° long and 42° lat. Just inland from the second row of beach dunes is a series of blowout depressions which contain nine pannes, ranging in size from several square meters to about 1 hectare. Although variable in morphology, the pannes can be characterized by a steep N bank of sparsely vegetated sand and a more gradual southern slope with a N-flowing seep zone. At the edge of the intradunal ponds, the vegetation changes

abruptly from the xeric dune vegetation to concentric bands of wetland vegetation. Five of the pannes were randomly selected for study.

Water chemistry.—Analyses for specific conductance, *pH*, alkalinity, total hardness, calcium, magnesium, potassium, total dissolved phosphorus, nitrate/nitrite and ammonium/organic nitrogen were performed on samples from all five pannes. At each panne, samples were taken from a 2.5-cm diam PVC drive point well screened 0.5 m beneath the surface in the seep zone to the S, from shallow (10 cm) waters adjacent to the seep zone, and from deeper (40-50 cm) waters farther into the pond. Samples were taken in April, July and October of 1983 prior to plant growth in the spring, during mid-season growth, and during plant senescence in the autumn, respectively.

Vegetation sampling.—Vegetation samples were taken in August 1983. The sampling scheme was designed to accommodate the irregular shape and variable size of the pannes and to concentrate sampling in and around the narrow band of vegetation at the pond edge. Other considerations were to eliminate sampling bias, to meet assumptions of randomness, and to allow relocation of transects for long-term monitoring of natural and anthropogenic change. Three transects were established on the N and S sides and two on the E and W sides of each panne (Fig. 1). Pannes are numbered from W to E. Ten 1 x 0.5 m plots were spaced from the pond edge (five into the pond and five away from the edge) at 0, 1, 3, 5 and 9 m for a total of 100 plots/panne. Cover of each species was estimated visually in each plot. Water depth was measured in aquatic plots and elevation above the pond level was measured with a hand level for terrestrial plots. Nomenclature follows Šwink and Wilhelm (1979).

Data analysis.—Vegetation data were summarized as importance values, calculated as the sum of relative frequency and relative mean cover, by panne. Species richness (mean no. of species/0.5m²) was calculated for each sample.

Indirect gradient analysis was done using reciprocal-averaging (RA) ordination because RA produces superimposable species and plot ordinations. Species were removed from the data set if their importance value for the particular panne or side was less than one. Cover values were neither transformed nor standardized. RA was used to examine composition gradients for each panne. To examine the relationship between plot ordination position and plot position along the moisture/topographic gradient, plot elevation

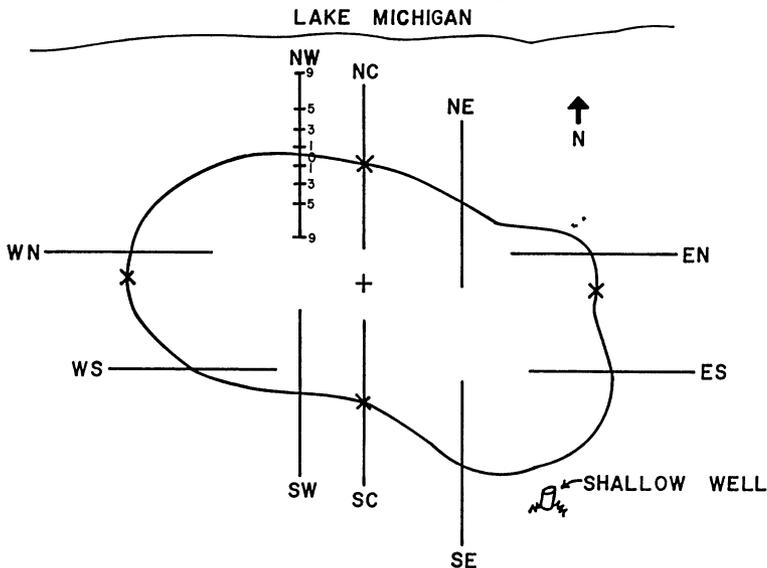


Fig. 1.—Diagrammatic representation of the vegetation sampling scheme

and water depth were combined to form an elevation variable. Elevation was transformed by adding 1 m to each value to make all values greater than 0. Product moment correlation coefficients were calculated relating elevation and log elevation to the first three ordination axes.

RESULTS AND DISCUSSION

Species composition and richness. — Seventy-four species were encountered in the 500 0.5 m plots sampled (54 panne species, 20 foredune species). Eight panne species are listed as endangered or threatened by the State of Indiana (Bacone and Hedge, 1980); eight species are restricted to the panne systems in the greater Chicago region (Swink and Wilhelm, 1979); nine species have known Atlantic Coastal Plain affinities, and five are considered Boreal relics. Some species are widespread on calcareous substrates, whereas others are widespread in wetlands. All pannes are dominated by the same species (Table 1). The area surrounding the pond that is normally not inundated is characterized by *Hypericum kalmianum*. *Rhynchospora capillacea*, *Juncus balticus* and *Utricularia cornuta* are dominant at the pond edge as well as in shallow water. *Chara* is the dominant aquatic species. Only 13 (17%) of the 74 taxa encountered were found in all five pannes.

ANOVA revealed significant differences among pannes [F(4,495) = 6.4, P < 0.0001] in species richness. Pannes 1 and 5 have significantly larger values for species richness per sample (mean 4.4 and 3.8 species per plot) than pannes 2, 3 and 4 (3.5, 3.2 and 3.0 species per plot). This parallels the total number of species in pannes 1-5, respectively, of 41, 29, 35, 34 and 47 species. This variation can be explained on the basis of morphology. Panne 1 has a large flat seep zone on the S side, providing a larger wetland habitat than found in pannes 2, 3 and 4. The undulating topography of the S side of panne 5 provides a more heterogeneous environment than the other pannes.

Water chemistry. — All of the waters analyzed from the pannes were of the calcium-magnesium bicarbonate water type (Back, 1961) (Table 2). They were mineralized,

TABLE 1. — Importance values (relative frequency + relative mean cover) for the most common species by panne at the Indiana Dunes National Lakeshore

		Panne				
		1	2	3	4	5
<i>Rhynchospora capillacea</i> Torr.	(RHCA)	25.5	56.9	36.4	34.8	10.9
<i>Utricularia cornuta</i> Michx.	(UTCO)	23.3	38.2	36.6	24.5	14.7
<i>Juncus balticus littoralis</i> Engelm.	(JUBA)	31.2	21.6	24.2	26.0	19.4
<i>Chara</i> species	(CHSP)	8.8	13.0	21.2	24.3	24.0
<i>Hypericum kalmianum</i> L.	(HYKA)	17.2	9.5	4.2	12.0	21.8
<i>Andropogon scoparius</i> Michx.	(ANSC)	6.9	5.0	4.5	6.9	14.7
<i>Eleocharis compressa</i> Sulliv.	(ELCO)	12.3	1.6	4.6	7.2	11.6
<i>Friglochin maritima</i> L.	(TRMA)	19.0	16.3	---	0.4	0.0
<i>Calamovilfa longifolia</i> (Hook.) Scribn.	(CALO)	1.5	3.4	4.0	14.7	8.7
<i>Aster linariifolius</i> L.	(ASLI)	7.3	4.4	0.4	6.1	4.0
<i>Carex viridula</i> Michx.	(CAVI)	4.8	1.6	7.2	4.3	4.2
<i>Eleocharis elliptica</i> Kunth.	(ELEL)	4.6	3.8	2.5	2.2	7.8
<i>Panicum implicatum</i> Scribn.	(PAIM)	3.1	3.4	3.2	4.5	4.1
<i>Aster ptarmicoides</i> (Nees) T. & G.	(ASPT)	3.0	0.3	6.6	3.8	2.9
<i>Najas flexilis</i> (Willd.) Rostk & Schmidt	(NAFL)	2.4	2.5	4.8	2.6	1.7
<i>Salix lucida</i> Muhl.	(SALU)	3.7	0.6	5.0	2.9	2.0
<i>Utricularia gibba</i> L.	(UTGI)	3.2	8.2	1.8	---	0.0
<i>Ammophila breviligulata</i> Fern.	(AMBR)	1.3	---	10.6	---	0.9
<i>Juncus scirpoides</i> Lam.	(JUSC)	2.6	0.9	---	---	4.6
<i>Potamogeton illinoensis</i> Morong	(POIL)	0.3	---	0.7	6.5	0.0
<i>P. gramineus</i> L.	(POGR)	---	0.9	1.6	1.4	3.2
<i>Equisetum</i> species	(EQSP)	---	---	---	0.4	6.3
<i>Vitis riparia</i> Michx.	(VIRI)	1.3	---	---	1.7	1.4

well-buffered waters with pH values usually well above neutral. These conditions are typical of groundwater-fed aquatic systems in the Indiana Dunes area (Arihood, 1975; Hendrickson and Wilcox, 1979; Hardy, 1981) and similar to those of older interdunal ponds in the park.

The water chemistry data were tested by ANOVA for differences among sites and seasons. The only significant spatial differences in water chemistry were in pH and nitrate/nitrite concentrations. Although not consistent, there was a trend toward lower pH values for samples taken from wells in the seep zone. Concentrations of nitrate/nitrite in the seep zone were consistently higher than in open water. Significant temporal variations were found for pH, ammonia/organic N, nitrate/nitrite, Mg, P and K. Most of these variations can be correlated to plant production and decomposition processes.

The calcareous water chemistry of the pannes probably influences what plant taxa occur there (Moyle, 1945). However, it is unlikely that water chemistry influences the distribution of species within the panne community because most of the variation is temporal rather than spatial.

Plot and species dispersion within pannes.—Species dispersion within pannes appears to be correlated with water depth and/or elevation above the water table (Fig. 2). This elevation gradient reflects a moisture gradient. RA ordination analysis of all five pannes studied showed a tight curvilinear ordination of plots and species on the first two ordination axes. Species ordinate along a gradient from typical dune taxa (*Ammophila breviligulata*, *Calamovilfa longifolia* and *Andropogon scoparius*), to species found in the transition zone between dunes and pannes (*Aster ptarmicoides* and *Salix lucida*), to species found at an elevation slightly above pond level (*Hypericum kalmianum* and *Panicum implicatum*), to a cluster of species found at or near average pond level (*Carex viridula*, *Eleocharis compressa* and *Rhynchospora capillacea*), to the true aquatics such as *Najas flexilis* and *Potamogeton gramineus*.

High correlations between Axis 1 and elevation/water depth lend further support to our interpretation. Correlation coefficients for all pannes are significant at the $P = 0.001$ level ($r^2 = 0.34-0.74$). This elevation gradient would be expected for most perennial pond systems. For example, our results have a good fit to a Bray-Curtis ordination analysis of dune slacks in the Netherlands by van der Laan (1979). He concluded that variation in vegetation in both space and time was related to differences in the groundwater regime. The same was true for dune slacks at Newborough Warren (Onyekwelu, 1972). Van der Laan proposed five vegetation zones related to hydrology.

TABLE 2.—Summary of water chemistry data from pannes. Mean values across all ponds, sites, and seasons (N = 45)

Parameter	Mean \pm SD	Variation* among seasons	Variation* among sites
pH	7.4 \pm 0.4	S	S
sp. conductance ($\mu\text{mhos L}^{-1}$)	409 \pm 96	NS	NS
mg/L			
Alkalinity	192 \pm 40	NS	NS
Total hardness as CaCO ₃	216 \pm 41	NS	NS
Calcium	67 \pm 16	NS	NS
Magnesium	11.7 \pm 5.4	S	NS
Potassium	0.81 \pm 0.39	S	NS
Nitrate and nitrite	0.42 \pm 0.57	S	S
Ammonium and organic N	0.52 \pm 0.50	S	NS
Total dissolved phosphorus	0.01 \pm 0.01	S	NS

*Significance of variation at the 0.05 level as determined by ANOVA

- Zone A: permanently inundated
- Zone B: periodically flooded
- Zone C: never flooded, permanently under the direct influence of groundwater, considerable fluctuations in water content of the soil
- Zone D: never flooded, permanently under the direct influence of groundwater, moderate fluctuations in water content of the soil
- Zone E: never flooded, considerable fluctuations in water content of the soil, periodically beyond the direct influence of groundwater

Zone A is here represented by the permanent portion of the pond and is generally habitat for the true aquatic plants (Fig. 2). Zone B is the zone between high and low pond levels. Therefore, species in this zone must be adapted to survive periodic inundation and water-saturated soils. This zone is where the dominant panne species are found (*Juncus balticus*, *Rhynchospora capillacea* and *Utricularia cornuta*). Zone C is rarely, if ever, flooded but most plants in this zone have roots penetrating groundwater. Zone D

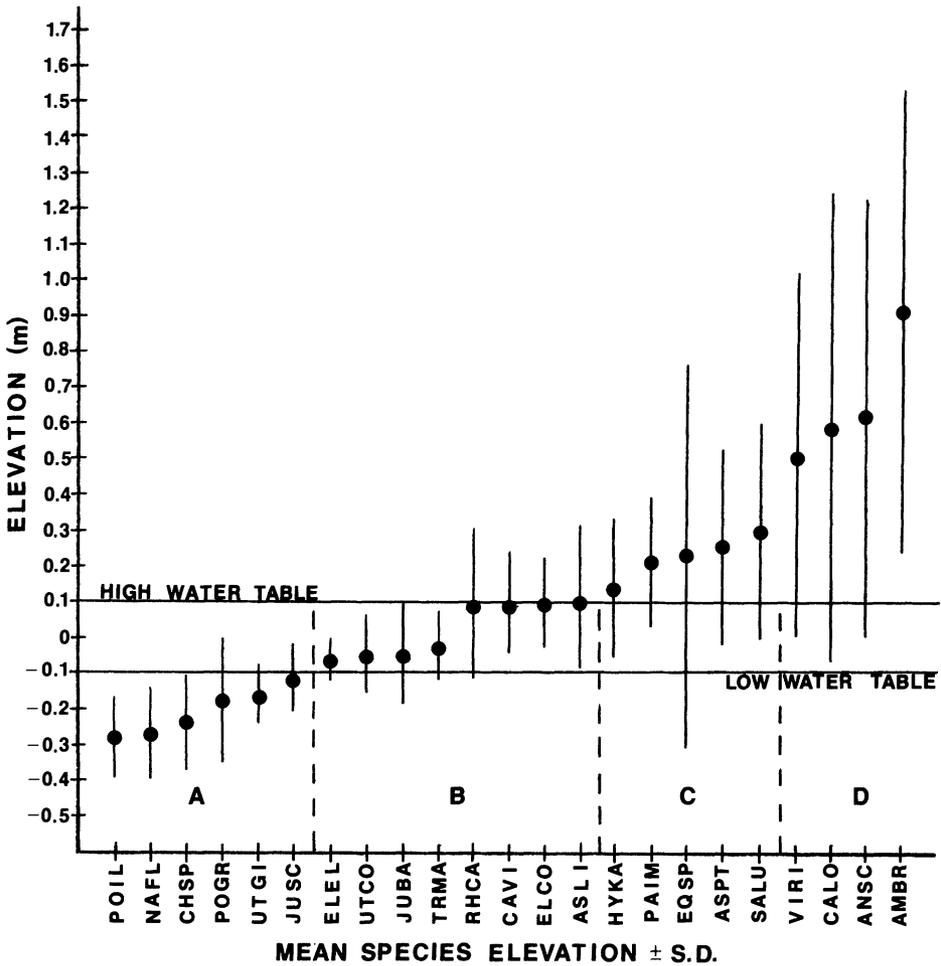


Fig. 2—Plot of mean species elevation in relation to pond level with a moisture gradient model, after van der Laan, 1979. (Species codes in Table 1)

is occupied by foredune species. Although these species are able to survive out of the influence of groundwater, the roots of the grasses most likely penetrate the groundwater table. Zone E was not represented in our sampling.

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