Disturbance effects on aquatic vegetation in regulated and unregulated lakes in northern Minnesota[1]

DOUGLAS A. WILCOX[2]
U.S. Fish and Wildlife Service, National Fisheries Research Center-Great Lakes, 1451 Green Road, Ann Arbor, MI 48105, U.S.A.

AND

JAMES E. MEEKER
Department of Botany, University of Wisconsin, Madison, WI 53706, U.S.A.

Received October 17, 1990

WILCOX, D. A., and MEEKER, J. E. 1991. Disturbance effects on aquatic vegetation in regulated and unregulated lakes in northern Minnesota. Can. J. Bot. **69**: 1542–1551.

The effects of water-level regulation on aquatic macrophyte communities were investigated by comparing two regulated lakes in northern Minnesota with a nearby unregulated lake. Natural annual fluctuations of about 1.8 m were replaced with fluctuations of 1.1 m and 2.7 m in the regulated lakes, and the timing of water-level changes was also altered. Quadrats were sampled along transects that followed depth contours representing different plant habitats in the unregulated lake. Ordinations showed that the macrophyte communities at all sampled depths of the regulated lakes differed from those in the unregulated lake. The unregulated lake supported structurally diverse plant communities at all depths. In the lake with reduced fluctuations, only four taxa were present along transects that were never dewatered; all were erect aquatics that extended through the entire water column. In the lake with increased fluctuations, rosette and mat-forming species dominated transects where drawdown occurred in early winter and disturbance resulted from ice formation in the sediments. The natural hydrologic regime at the unregulated lake resulted in intermediate disturbance and high diversity. There was either too little or too much disturbance from water-level fluctuations in the regulated lakes, both resulting in reduced structural diversity.

Key words: reservoirs, lake-level regulation, winter drawdown, aquatic vegetation, growth form, disturbance.

WILCOX, D. A., et MEEKER, J. E. 1991. Disturbance effects on aquatic vegetation in regulated and unregulated lakes in northern Minnesota. Can. J. Bot. **69** : 1542–1551.

En comparant deux lacs à niveau contrôlé avec un lac voisin non-contrôlé dans le nord du Minnesota, les auteurs ont étudié les effets du niveau de l'eau sur les communautés de macrophytes aquatiques. Des fluctuations annuelles d'environ 1,8 m font place à des fluctuations de 1,1 m et de 2,7 m dans les lacs à niveau contrôlé et la chronologie des variations est également modifiée. Les auteurs ont échantillonné des quadrats le long de transects qui suivent les courbes de niveau, représentant différents habitats du lac non-contrôlé. Les ordinations font voir que les communautés de macrophytes, à toutes les profondeurs échantillonnées dans le lac non-contrôlé, diffèrent de celles des lacs contrôlés. Le lac non-contrôlés comporte des communautés structurellement diverses à toutes les profondeurs. Dans le lac montrant des fluctuations réduites, seulement quatre taxons sont présents le long des transects où l'eau n'est jamais absente, i.e., toutes les plantes aquatiques dressées qui s'étendent sur toute la colonne d'eau. Dans le lac où la fluctuation est augmentée, les espèces qui forment des rosettes et des coussins dominent les transects où l'absence d'eau se fait au début de l'hiver et le dérangement provient de la formation de glace dans les sédiments. Le régime hydrologique naturel, dans le lac non-contrôlé, s'accompagne de dérangements intermédiaires et d'une forte diversité. Les fluctuations qui ont lieu dans les lacs contrôlés entraînent des dérangements soit trop faibles ou soit excessifs, ce qui entraîne dans les deux cas une diversité structurelle réduite.

Mots clés : réservoir, contrôle du niveau des lacs, baisse de niveau hivernal, végétation aquatique, forme de croissance, dérangement.

[Traduit par la rédaction]

Introduction

The responses of aquatic and wetland plant communities to differences in water depth are well known (Sculthorpe 1967; Spence 1982), but there have been few quantitative studies of macrophyte responses to the disturbance caused by altered hydrology in regulated systems, particularly in larger lakes (e.g., Nichols 1975; Nilsson 1981; Nilsson and Keddy 1988; Rorslett 1989). The emphasis has usually been on characterization and prediction of communities in reservoirs with large and varied water-level fluctuations. Little information is available about macrophyte responses in lake systems where water-level cycles have been closely regulated for many years and the amplitude has not been extreme. The occurrence of such systems that have no obvious expanses devoid of vegetation may lead to a misconception that natural plant communities are present. Since management for natural communities is one of the policies of the U.S. National Park Service, the present study was prompted by the desire to effect such management in a system of closely regulated lakes on Park Service lands (Kallemeyn et al. 1988).

We investigated the effects of water-level regulation on littoral macrophyte communities in two large lakes (Rainy and Namakan) in Voyageurs National Park, Minnesota, that are controlled by dams. We made comparisons with an unregulated lake (Lac La Croix) in nearby Boundary Waters Canoe Area to determine the effects of altered hydrologic regimes on plant communities. Our approach was to sample in each lake along each of several depth contours that represented specific

---

[1] Contribution No. 769 of the National Fisheries Research Center-Great Lakes, Ann Arbor, MI 48105, U.S.A.

[2] Author to whom correspondence should be addressed.

Printed in Canada / Imprimé au Canada

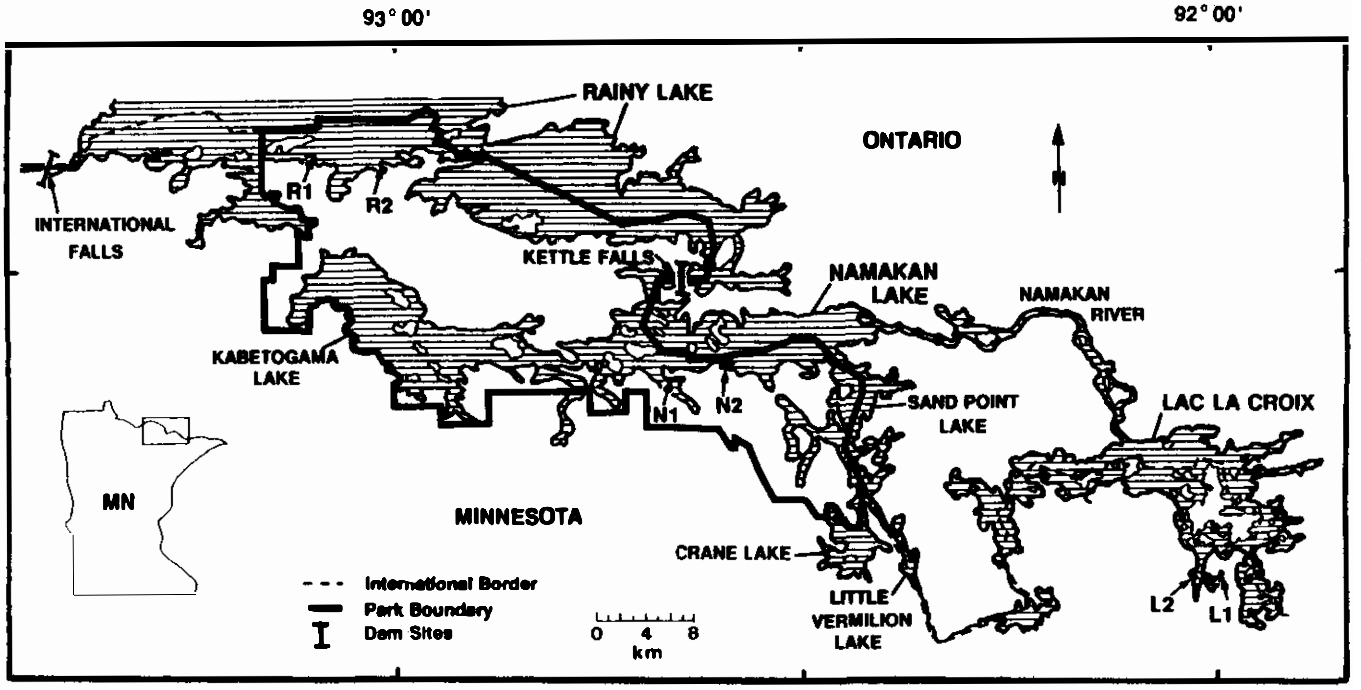

FIG. 1. Study area in northern Minnesota, showing the boundary of Voyageurs National Park and the major lakes, dam sites, and study sites. The international border and park boundary coincide from Rainy Lake to Little Vermilion Lake.

habitat types in the unregulated lake. We hypothesized that alteration of the timing and depth of flooding in the regulated lakes would favor species that can tolerate both drawdown during spring and flooding for long periods during the growing season. A more structurally diverse community would be expected in the unregulated lake because of greater natural habitat variation.

Study area

Voyageurs National Park is situated on the United States – Canadian border in the state of Minnesota (Fig. 1). There are 30 lakes in the park, 4 of which contribute 96% of the 34 400 ha lake surface area in the park. The large lakes are in a chain and are regulated by several dams across the Rainy River. The largest of the lakes is Rainy Lake, which has a total surface area of 89 357 ha, with approximately 14 600 ha in the park. The water-level control structure is a hydroelectric dam that was constructed in 1909 across the outlet at International Falls, Minnesota, and Fort Francis, Ontario. Namakan Reservoir is upriver from Rainy Lake and consists of Namakan, Kabetogama, Sand Point, Crane, and Little Vermilion lakes. The first three lakes are at least partially within the park and have a within-park surface area of 18 410 ha. Water levels were originally controlled by natural rock sills at the outlet of Namakan Lake at Kettle Falls. Two dams constructed at this outlet in 1914 are now used to regulate water levels.

The dams and lake levels of Rainy and Namakan lakes are regulated by the International Joint Commission because the lakes cross the U.S.–Canadian border. As part of its water management program in place since 1970, the Commission has set acceptable high and low limits (termed rule curves) for water levels throughout the year (Fig. 2). Although modeling has shown that the mean annual fluctuations of water levels under natural conditions would be 1.9 m for Rainy Lake and 1.8 m for Namakan Lake, regulation results in mean annual fluctuations of 1.1 m and 2.7 m, respectively (Flug 1986). However, the rule curves allow for annual fluctuations as small as 0.6 m on Rainy Lake and as great as 3.0 m on Namakan Lake. The lakes are regulated to reach peak levels in late June or early July, rather than after the spring runoff as much as a month earlier. The water levels are then held stable throughout the summer and allowed to decline gradually through autumn and winter, as opposed to a gradual decline that would naturally begin immediately after the peak.

Lac La Croix, in Boundary Waters Canoe Area, is a natural lake upriver from Rainy Lake and the lakes of Namakan Reservoir that is similar to those waters in most aspects, except that the water level is not regulated. The mean annual fluctuation of the water level is about 1.6 m (Fig. 2). The level peaks in late May or early June and then declines gradually until spring runoff begins during the following April. In addition, the degree of variability in annual water-level regimes differs from that in the regulated lakes because the rule curves reduce the variability in Rainy Lake and Namakan Reservoir. Although both Rainy and Namakan lakes deviate from the guidelines as much as 19% of the time, the extremes may be greater at Lac La Croix, where year-to-year seasonal variation ranges from 0.3 m to 3.0 m. The study lakes all have medium water clarity and moderate alkalinity (Kepner and Stottlemyer 1988; Minnesota Department of Natural Resources, unpublished data).

Two study sites were selected at each of Rainy Lake, Namakan Lake, and Lac La Croix (Fig. 1) following a reconnaissance flight in a small aircraft and inspections by boat. Much of the shoreline in these lakes consists of steeply sloping granitic bedrock, so site selections depended heavily on geology and basin morphology. Sites with similar basin size, geometry, and orientation were chosen to reduce variability due to disturbance from wind and waves. Since sampling was planned at certain altitudes (water depths), there was also a requirement that each site have depths of at least 2 m. All sites had veneers of loosely consolidated, mixed organic sediment above a fine-grained, consolidated clay substrate. Each site included some anomalous areas, most often small pockets of rocky or gravelly substrate; they could not be avoided but were equally frequent at all sites. At Rainy Lake, the sites selected were just east of Dove Bay (R1) and at Alder Creek (R2); at Namakan Lake, they were at Sheen Point (N1) and Deep Slu (N2); at Lac La Croix, they were at the east (L1) and west (L2) sides of Lady Boot Bay (Fig. 1).

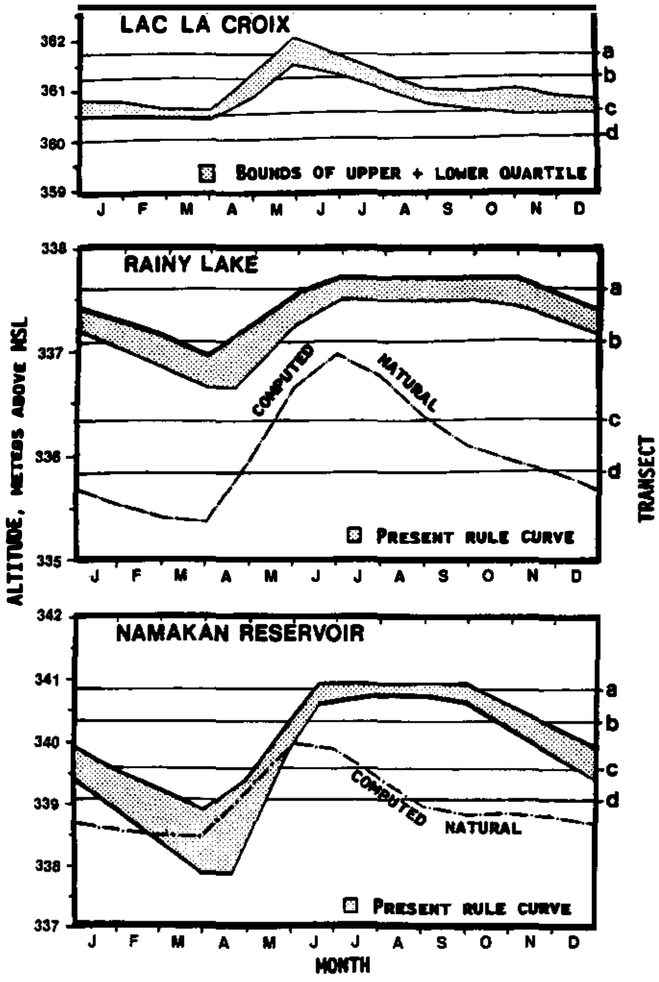

FIG. 2. Water-level regimes for Lac La Croix, Rainy Lake, and Namakan Reservoir, showing bounds of variation, computed natural water levels, and altitudes of study transects (adapted from Flug 1986).

Methods

Four transects were sampled at each study site in 1987 (see Fig. 2). The transects were established nearly parallel to the shoreline at altitudes relative to mean annual high water (MHW) and varied in length, depending on basin morphology. The altitudes (bathymetric contours described as depth from MHW) were selected to represent specific habitat types in the unregulated control lake, Lac La Croix. Sampling at these same altitudes on the regulated lakes enabled us to show the effects of altered hydrologic regimes on plant communities.

The four transects at each site were labeled *a* to *d*, resulting in site–transect designations such as Rl*a*, N2*b*, N2*c*, and Ll*d*. The altitudes of the transects and the respective habitats in Lac La Croix (along with comparisons for the other lakes) follows.

a. 0.0 m: shoreline zone

In Lac La Croix, the shoreline zone is minimally flooded at the peak water level in late May to early June but is soon dewatered and remains so throughout the growing season. Moist-soil species that cannot tolerate prolonged inundation should be dominant. In Rainy and Namakan lakes, this zone is usually flooded in June and remains minimally flooded throughout the growing season, as drawdown does not begin until early to mid-autumn. In some years, when water levels in these lakes are in the lower range of the rule curve, dewatered conditions are similar to those in Lac La Croix.

b. 0.5 m: amphibious zone

In Lac La Croix, the amphibious zone is flooded in May, remains so during the early part of the growing season, and then is dewatered in mid-July. It should contain plants, such as emergents, that are capable of existing in both aquatic and terrestrial habitats. In Rainy and Namakan lakes, this zone is usually flooded in May or June, remains so throughout the growing season, and then undergoes gradual drawdown, becoming dry in November in Namakan Lake and in February in Rainy Lake. Water levels in Rainy Lake were unusually low in 1987, causing this transect to be dewatered during the early growing season when it would usually be flooded.

c. 1.25 m: submersed zone

In Lac La Croix, the submersed zone is flooded in April and remains so throughout the growing season; it is often dewatered again in February. It should contain aquatic species that can tolerate late-winter drawdown. In Rainy Lake, this zone is always submersed; in Namakan Lake, it is dry in early spring and flooded in May. In both of these lakes, the zone remains at a depth of 1.25 m throughout the growing season and then undergoes gradual drawdown.

d. 1.75 m: deep-water zone

In Lac La Croix, the deep-water zone is inundated throughout almost all years. It should contain aquatic species capable of tolerating deep water and may be at the depth limit for growth of some species. In Rainy Lake, this zone is always submersed; in Namakan Lake, it is dry in early spring and then flooded in April or May. In both of these lakes, this zone remains at a depth of 1.75 m throughout the growing season and then undergoes gradual drawdown.

Twenty 1 × 1 m sampling quadrats were randomly selected on each of the four transects at each of the six sites. At each quadrat, we identified plant species present and estimated percent cover for each. In water too deep to wade, we sampled from a canoe, using a diving mask to aid underwater vision. Taxa present in only small amounts (less than 1% cover) were systematically recorded as 0.5%. Since plants may occupy space in different strata, cover estimates for each quadrat could exceed 100%. Plant names used conform to the nomenclature of Voss (1972, 1985) where possible. Taxa not included there are named according to Gleason and Cronquist (1963).

We summarized the vegetation data by lake and by transect, using summary statistics, Sorenson's index (Mueller-Dombois and Ellenberg 1974), and ordination. Importance values (IV) were calculated as the sum of relative frequency and relative mean cover of each taxon on each transect. The IV vs. transect matrix was analyzed by detrended correspondence analysis (DCA) (McCune 1987) to give ordinations of both transects and species. Since the purpose of the ordination was to assess general community patterns rather than occurrences of rare species, the total number of taxa used in the ordination was reduced from 109 to 69 by dropping the taxa found in less than 1% of the total number of quadrats.

To assess the effects of water-level regulation on the structure of the macrophyte communities, we used general structural characteristics to separate the 30 most important taxa (total IV) found in the study into six groups: erect terrestrials, thin-stem emergents, mat formers, low rosettes, low-growth aquatics, and erect aquatics. The IV of the selected species were totalled by transect for each lake. The four erect terrestrial species were subsequently excluded from further discussion because they were similar among lakes and did not generally provide aquatic habitat since they were not in the water. For similar reasons, the shoreline transects (*a*) were also excluded. The remaining five groups and 26 taxa that we assessed follow. The thin-stem emergents were *Carex lacustris, Carex rostrata, Eleocharis obtusa, Eleocharis smallii, Glyceria borealis, Polygonum lapathifolium*, and *Scirpus cyperinus*. The mat-formers were *Elatine minima, Eleocharis acicularis*, and *Ranunculus reptans*. The low rosettes were *Isoetes echinospora, Sagittaria* spp., and *Tillaea aquatica*. The low-growth aquatics were *Chara* spp., *Najas flexilis, Nitella* spp., *Potamogeton robbinsii*, and *Potamogeton spirillis*. The erect aquatics were *Bidens beckii, Myriophyllum* spp., *Nymphaea odorata, Potamogeton* *amplifolius, Potamogeton foliosus, Potamogeton richardsonii, Sparganium fluctuans,* and *Vallisneria americana.*

Results and discussion

Floristics

A total of 109 taxa were sampled across all transects at all lakes (Table 1). Species richness in Rainy Lake was slightly greater (76 taxa) than in either Namakan Lake (72 taxa) or Lac La Croix (65 taxa); however, not all of the increased number of taxa were natural components of the system. There were four non-native taxa in both Rainy and Namakan lakes and only one in Lac La Croix. Of the 109 total taxa, 20 were unique to Rainy Lake, 12 to Namakan Lake, and 11 to Lac La Croix. The presence of many of the taxa unique to Rainy Lake may have been in response to the unusually low water in early to mid-summer in 1987. These taxa include a number of Cyperaceae, such as *Carex sychnocephala, Carex crawfordii, Cyperus aristatus, Cyperus strigosus, Fimbristylis autumnalis,* and *Hemicarpha micrantha.* Species found only at the Namakan Lake sites included three shoreline grasses, *Glyceria grandis, Glyceria canadensis,* and *Poa pratensis*, which apparently can exploit the drawdown that occurs in the lake each year (Nilsson and Keddy 1988). Species encountered only at Lac La Croix included emergents such as *Carex stricta, Carex viridula, Equisetum fluviatile,* and *Juncus effusus.* In addition, *Sagittaria* differentiated beyond the rosette stage and identifiable as *Sagittaria latifolia* was found only at Lac La Croix.

Northern wild rice, *Zizania palustris,* was conspicuously absent in the samples from both Namakan Lake and Lac La Croix. In Lac La Croix, however, viable stands of wild rice were observed in wetlands adjacent to those sampled, and the species seems to be locally abundant elsewhere in the lake. Northern wild rice does not grow well in areas with wide water-level fluctuations (Nichols 1975) and is intolerant of both low water levels and flooding (Thomas and Stewart 1969; Pip and Stepaniuk 1988). Low water levels cause seeds to desiccate, and rising water levels force too much energy to be directed into shoot elongation. Wild rice is nearly absent from Namakan Lake, being restricted to a few plants near river mouths (L. Kallemeyn, personal communication).

The species that were unique to a lake were not dominant on any of the transects; however, some of the taxa that were dominant in Lac La Croix were rare or missing in the flora sampled in the other lakes. *Thelypteris palustris* was not found in Rainy Lake and was rare in Namakan Lake. This fern requires a wet soil habitat (Swink and Wilhelm 1979), which does not occur at the shoreline of the regulated lakes that are typically flooded throughout the summer. *Glyceria borealis* is favored by drawdown (Nichols 1975); it was not common at Rainy Lake, where the drawdown was less than at the other lakes. *Bidens beckii* was not found along any of the transects in Namakan Lake, and *Nymphaea odorata* and *Chara* were not collected in Rainy Lake. The observed distribution of these taxa may be an artifact of selected sampling sites, or it may relate to physical environment requirements or competitive interactions.

Species similarities among lakes

What is the species pool available for colonization in each of the three lakes? If the available species were different among the three lakes, any demonstrable differences in plant communities might not be attributable to the differences in water-level regimes. For this analysis, we assumed that if a species was sampled in a lake, it was likely that seeds or propagules of that species were available for future colonization. Sorenson's index, computed by using all species sampled in the lakes, showed the species pools to be similar. The similarity values were 61% between Rainy Lake and Lac La Croix, 66% between Rainy Lake and Namakan Lake, and 70% between Lac La Croix and Namakan Lake. These values compare with similarities of 75% for sedge meadows in Wisconsin and Cook County, Illinois (Curtis 1959) and 52% for temporary pools in buttonbush swamps in Ohio (Tyrrell 1987). The greatest similarity was between Namakan Lake and Lac La Croix, the lakes with the greatest ranges in water-level fluctuation. Rainy and Namakan lakes were next most similar; both were flooded throughout the growing season. The three lakes are connected by a river, making dispersal easy, and they shared a high percentage of species; therefore, it is reasonable that differences in communities at various depths were a result of different water-level regimes rather than of different species pools.

Comparison of lakes by transect

The aquatic plant communities in Lac La Croix, Rainy Lake, and Namakan Lake differed from each other, particularly at the greater depths sampled. In contrast, the two study sites in each lake were similar to each other; they seemed to adequately represent each lake. The DCA ordination (Fig. 3) showed that the transects at any given water depth in an individual lake had closely similar plant communities (e.g., R1*b* and R2*b*). With the exception of the *c* and *d* transects of Lac La Croix, the plant communities within each lake were shown to differ with depth because the transect pairs plotted apart from each other (e.g., R1*a*–R2*a*, R1*b*–R2*b*, R1*c*–R2*c*, and R1*d*–R2*d*). The plant communities at a given depth were shown to differ among the lakes, since these transect pairs plotted apart from each other (e.g., R1*b*–R2*b*, N1*b*–N2*b*, and L1*b*–L2*b*). These differences were less profound at the shoreline (*a* transects) than at greater depths (*c* and *d* transects). The ordination provides evidence that lakes with similar species pools but different hydrologic regimes develop different plant communities. Using different methods, Nichols (1975) drew similar conclusions in a study of 20 sites in Wisconsin flowages, as did Rorslett (1989) in a study of 17 hydrolakes in Norway.

In addition to the similarities and differences described above, the transect ordination scores suggest other, more subtle relations between transects and lakes. Axis 1 scores were closely correlated with water depth ($r^2 = 0.85, p < 0.0001$); scores were higher in shallow water transects. Since the ordination scores for each transect were determined by the scores for species that dominate them, Figs. 3 and 4 show shoreline transects and species to the right, amphibious transects and species in the middle, and aquatic transects and species to the left. The relations between transects and species can be explored by analyzing the IV in Table 1 and viewing the transect and species ordinations together.

Calamagrostis canadensis was a dominant species at the shoreline (transect *a*) of each lake. *Carex lacustris* and *Thelypteris palustris* were also dominant on the shoreline of Lac La Croix; *Scirpus cyperinus, C. rostrata,* and *Hypericum majus* were also prevalent at Rainy Lake; and *C. rostrata* was dominant and *C. lacustris* and *Lysimachia terrestris* were prevalent on the shoreline of Namakan Lake. Typically, all of

TABLE 1. Importance values (IV) of plant taxa found on transects *a*–*d* at sites 1 and

	L1				L2			
Species	*a*	*b*	*c*	*d*	*a*	*b*	*c*	*d*
Agrostis hyemalis (Walter) BSP.	1.7	.	.	.	0.4	.	.	.
Bidens beckii Torr.	.	0.5	3.0	1.2	.	5.6	20.8	.
Bidens cernua L.	.	.	.	.	.	.	.	.
Calamagrostis canadensis (Michaux) Beauv.	11.0	.	.	.	21.5	.	.	.
Campanula aparinoides Pursh.	0.8	.	.	.	2.2	.	.	.
Cardamine pensylvanica Willd.	.	.	.	.	0.4	.	.	.
Carex crawfordii Fern.	.	.	.	.	.	.	.	.
Carex hirta L.	.	.	.	.	.	.	.	.
Carex lacustris Willd.	22.5	.	.	.	15.5	.	.	.
Carex rostrata Stokes	0.5	.	.	.	1.9	.	.	.
Carex sychnocephala Carey	.	.	.	.	.	.	.	.
Chara spp.	.	.	11.9	16.2	.	.	.	.
Cicuta bulbifera L.	.	.	.	.	.	.	.	.
Cyperus aristatus Rottb.	.	.	.	.	.	.	.	.
Cyperus strigosus L.	.	.	.	.	.	.	.	.
Elatine minima (Nutt.) Fischer & C. Meyer	.	0.5	.	.	.	7.8	.	.
Eleocharis acicularis (L.) K. & S.	.	15.9	.	.	0.4	26.7	.	.
Eleocharis obtusa (Willd.) Schultes	.	.	.	.	.	.	.	.
Eleocharis smallii Britton	2.6	11.9	.	.	.	3.7	.	.
Epilobium coloratum Biehler	.	.	.	.	.	.	.	.
Galium trifidum L.	3.1	.	.	.	4.3	.	.	.
Geranium bicknellii Britton	.	.	.	.	.	.	.	.
Glyceria borealis (Nash) Batch.	.	15.9	.	.	.	10.7	.	.
Hypericum majus (A. Gray) Britton	5.0	.	.	.	5.0	.	.	.
Impatiens capensis Meerb.	.	.	.	.	.	.	.	.
Isoetes echinospora Durieu.	.	.	.	.	.	2.3	.	.
Juncus brevicaudatus (Engelm). Fern.	4.3	5.0	.	.	4.0	.	.	.
Juncus pelocarpus Meyer	0.4	.	.	.	.	.	.	.
Littorella uniflora (L.) Aschers.	.	.	.	.	.	.	.	.
Lycopus americanus Muhl.	.	.	.	.	.	.	.	.
Lysimachia terrestris (L.) BSP.	5.4	.	.	.	5.5	.	.	.
Mentha arvensis L.	1.8	.	.	.	4.8	.	.	.
Myrica gale L.	3.4	.	.	.	1.4	.	.	.
Myriophyllum spp.	.	1.4	7.1	2.6	.	1.1	26.1	25.4
Najas flexilis (Willd.) Rostik. & Schmidt	.	7.1	41.0	29.9	.	4.0	2.2	.
Nitella spp.	.	.	.	.	.	.	4.4	15.6
Nuphar variegata Durand	.	1.1	2.3	.	.	.	.	.
Nymphaea odorata Aiton	.	1.5	14.8	.	.	9.9	24.2	13.2
Panicum sp.	.	.	.	.	.	.	.	.
Polygonum amphibium L.	.	4.2	.	.	1.5	.	.	.
Polygonum lapathifolium L.	.	.	.	.	.	.	.	.
Polygonum punctatum Ell.	.	.	.	.	.	3.2	.	.
Polygonum sagittatum L.	.	.	.	.	.	.	.	.
Potamogeton amplifolius Tuckerman	.	.	.	.	.	.	.	26.0
Potamogeton epihydrus Raf.	.	4.8	0.7	2.5	.	.	.	.
Potamogeton foliosus Raf.	.	.	1.0	7.7	.	.	.	.
Potamogeton gramineus L.	.	3.7	.	.	.	2.8	.	.
Potamogeton richardsonii (Benn.) Rydb.	.	.	2.8	3.1	.	0.5	5.1	2.7
Potamogeton robbinsii Oakes	.	.	1.0	19.4	.	.	.	.
Potamogeton spirillus Tuckerman	.	8.4	7.0	4.9	.	0.5	.	.
Potamogeton vaseyi Robbins	.	.	2.1	.	.	2.2	.	.
Potamogeton zosteriformis Fern.	.	.	2.1	0.7	.	.	3.3	6.3
Potentilla norvegica L.	.	.	.	.	.	.	.	.
Potentilla palustris (L.) Scop.	1.1	.	.	.	3.9	.	.	.
Ranunculus longirostris Godon	.	.	0.5	.	.	2.2	3.2	.
Ranunculus pennsylvanica L. T.	0.4	.	.	.	3.2	.	.	.
Ranunculus reptans L.	0.4	.	.	.	1.4	.	.	.
Rorippa palustris (L.) Besser	.	.	.	.	.	.	.	.
Sagittaria spp.	.	8.3	.	.	.	3.0	.	.
Scirpus cyperinus (L.) Kunth	3.1	.	.	.	0.6	.	.	.
Sium suave Walter	2.9	6.5	.	.	4.5	3.4	.	.
Solidago graminifolia (L.) Salisb.	7.8	.	.	.	2.9	.	.	.
Sparganium fluctuans (Morong) Robinson	.	4.7	.	.	.	6.7	.	.
Thelypteris palustris Schott.	12.7	.	.	.	10.1	.	.	.
Tillaea aquatica L.	.	.	.	.	.	.	.	.
Triadenum fraseri (Spach.) Gl.	4.2	.	.	.	1.9	.	.	.
Utricularia vulgaris L.	.	0.5	0.5	.	.	2.2	2.6	.
Vallisneria americana Michaux	.	.	2.1	11.7	.	.	8.0	10.8
Viola spp.	0.4	.	.	.	1.2	.	.	.

NOTE: Taxa found in less than 1% of the total number of quadrats are not shown.

2 at Lac La Croix (L), Rainy Lake (R), and Namakan Lake (N)

R1				R2				N1				N2			
a	*b*	*c*	*d*	*a*	*b*	*c*	*d*	*a*	*b*	*c*	*d*	*a*	*b*	*c*	*d*
1.6	1.2	.	.	2.6	2.9	.	.	2.0	.	.	.	.	.	.	.
.	.	.	.	.	.	0.8	.	.	.	.	.	.	.	.	.
1.1	.	.	.	1.4	7.2	.	.	.	.	.	.	.	.	.	.
17.4	.	.	.	16.6	.	.	.	19.9	.	.	.	25.1	.	.	.
0.4	.	.	.	.	.	.	.	1.6	.	.	.	2.6	.	.	.
.	.	.	.	0.7	.	.	.	0.4	1.4	0.4	.	.	.	.	.
5.2	4.4	.		.	3.6	.	.	.	.	.	.	.	.	.	.
4.0	3.3	.	.	.	5.3	.	.	.	.	.	.	.	.	.	.
0.4	.	.	.	1.9	0.3	.	.	16.5	6.6	.	.	2.3	.	.	.
6.0	0.8		.	9.1	.	.	.	9.5	16.2	.	.	20.1	10.8		.
0.8	.	.	.	.	5.8	.	.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	0.5	34.4		.	4.2	22.8
.	.	.	.	.	.	.	.	2.9	.	.	.	0.7	.	.	.
0.8	3.5	.	.	.	0.3	.	.	.	.	.	.	.	.	.	.
1.7	4.7	.	.	.	.	.	.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.	3.8	.	0.5	.	9.9	7.0	8.3
0.9	6.4	10.9	.	1.3	4.5	3.5	.	0.4	6.2	33.4	7.9	.	6.9	9.4	6.2
2.4	15.2	.	.	.	1.9	.	.	.	.	.	.	.	.	.	.
1.0	1.0	5.8	.	1.9	0.3	.	.	0.4	.	.	.	0.7	2.8	.	.
0.8	0.9	.	.	1.1	1.2	.	.	.	.	.	.	0.7	.	.	.
1.8	.	.	.	0.8	.	.	.	.	.	.	.	1.4	.	.	.
0.8	3.0	.	.	.	0.6	.	.	.	.	.	.	.	.	.	.
0.4	1.5		.	.	1.5	.	.	.	5.4	13.8	.	2.7	13.1	0.9	.
8.6	12.2	.	.	5.8	13.1	.	.	0.4	3.1		.	.	0.5	.	.
0.4	.	.	.	.	.	.	.	2.2	.	.	.	0.7	.	.	.
.	.	21.1	.	.	.	16.5	.	.	3.1	7.5	5.8	.	5.3	2.5	8.6
0.4	0.6	.	.	.	.	.	.	.	.	.	.	.	.	.	.
2.1	8.1		.	0.4	0.9	.	.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	.	.	.	6.4	.	.
0.4	.	.	.	0.5	.	.	.	5.6	.	.	.	3.1	.		.
2.7	.	.	.	4.8	.	.	.	5.1	.	.	.	12.5	.	.	.
.	.	.	.	0.7	.	.	.	.	.	.	.	2.8	.	.	.
6.2	.	.	.	1.3	.	.	.	3.5	.	.	.	2.2	.	.	.
.	.	.	.	.	.	1.4	.	.	.	.	2.2	.	.	.	1.1
.	.	.	.	.	.	8.0	.	.	1.5	3.3	5.6	.	.	0.9	4.3
.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
.	1.2	.	.	.	.	.	.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	5.4	4.6	.	.	.	1.1
0.4	3.1	.	.	1.7	1.8	.	.	.	.	.	.	.	.	.	.
1.2	0.9	.	.	5.1	.	.	.	1.9	.	.	.	2.7	2.1	.	.
7.3	18.1	.	.	7.1	31.0	.	.	0.4	25.4	6.9	.	.	6.4	3.8	.
2.0	3.5	.	.	8.0	3.9	.	.	1.3	.	.	.	5.0	1.6	.	.
3.6	0.6	.	.	1.1	0.6	.	.	0.5	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
.	.	1.7	.	.	.	7.5	4.6	.	.	.	8.8	.	.	.	.
.	.	5.4	.	.	.	3.1	6.0	.	0.5	2.4	0.5	.	.	2.4	3.0
.	.	1.2	22.4	.	.	6.7	9.6	.	1.0	0.9	7.6	.	.	.	13.7
.	.	.	.	.	.	8.6	.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	1.4	.	.	.	0.5	2.7
.	.	.	.	.	.	.	.	.	.	2.1	9.5	.	.	.	.
.	.	.	.	.	.	.	.	.	.	.	0.5	.	.	.	0.4
4.4	1.2	.	.	7.3	7.2	.	.	0.5	.	.	.	.	.	.	.
.	.	.	.	2.3	.	.	.	1.6	.	.	.	1.2	.	.	.
.	.	.	.	.	.	.	.	.	0.5	0.9	2.6	.	.	.	0.4
0.4	.	.	.	.	.	.	.	1.1	.	.	.	.	.	.	.
2.3	4.2	.	.	1.1	2.5	.	.	1.5	15.7	0.9	.	2.9	24.9	42.0	1.8
.	0.3	.	.	1.3	2.5	.	.	0.4	0.5	1.4	.	.	.	.	.
.	0.3	14.8	.	.	.	4.1	.	.	0.5	2.7	1.0	.	.	8.6	.
4.4	.	.	.	11.1	.	.	.	6.4	.	.	.	4.5	.	.	.
1.2	0.3	.	.	1.9	.	.	.	1.9	0.5	.	.	.	.	.	.
.	.	.	.	0.3	.	.	.	.	.	.	.	.	.	.	.
.	.	15.1	.	.	.	13.0	.	.	.	.	.	.	.	0.6	.
.	.	.	.	.	.	.	.	.	.	.	.	0.8	.	.	.
1.1	0.6	.	.	.	1.0	.	.	0.4	8.5	12.6	8.4	.	9.4	11.9	6.5
0.8	.	.	.	0.7	.	.	.	4.3	.	.	.	1.6	.	.	.
.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
.	.	24.0	77.6	.	.	26.9	79.8	.	.	5.1	.	.	.	5.3	19.0
0.4	.	.	.	.	.	.	.	2.2	.	.	.	0.7	.	.	.

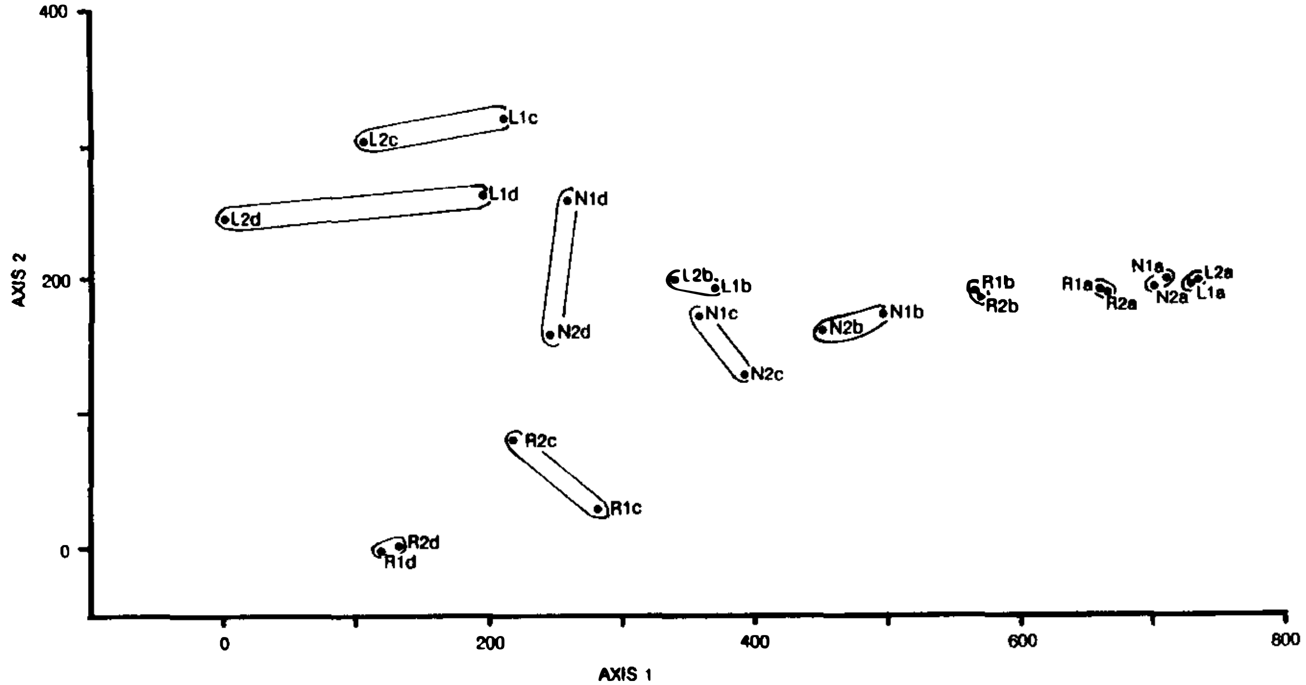

FIG. 3. Two-dimensional plot of DCA ordination of the importance value × transect matrix (eigenvalues: axis 1 = 0.879; axis 2 = 0.403). Points plotted are transects, labelled by lake, site, and transect codes.

these are moist-soil species (Voss 1972, 1985; Swink and Wilhelm 1979; Wilcox et al. 1985), although *C. rostrata* also grows in shallow water. Since all of these species had axis 1 scores greater than 600 (Fig. 4), all *a* transects clustered to the right in Fig. 3. Since we used mean high water as the shoreline of the lakes in this study, transects R1*a*, R2*a*, N1*a*, and N2*a* were not flooded throughout the growing season in all years. In low-water years, these transects were ecologically similar to L1*a* and L2*a*, as reflected by the similarities in vegetation on the shoreline transects of the lakes.

On the 0.5-m transects (*b*), Lac La Croix was dominated by *E. acicularis* and *G. borealis*, which are common in drawdown zones (Nichols 1975; Renman 1989; Rorslett 1989). Rainy Lake was dominated by *Hypericum majus* and *Polygonum lapathifolium* at this depth; the latter species is an annual that is common on mudflats but may tolerate standing water (Swink and Wilhelm 1979; Voss 1985). The *b* transect at Namakan Lake was dominated by *Polygonum lapathifolium*, *C. rostrata*, and mat-forming *R. reptans*. Differences in dominants at this depth caused differences in transect ordination scores. Transects R1*b* and R2*b* more closely resembled the shoreline transects (*a*) than did L1*b*, L2*b*, N1*b*, and N2*b* because Rainy Lake had lower than normal water levels in 1987 and more shoreline species growing along the dewatered 0.5-m transect.

On the 1.25-m transects (*c*), Lac La Croix was dominated by the aquatic taxa *Najas flexilis*, *Nymphaea odorata*, *Myriophyllum* spp., and *B. beckii*; Rainy Lake was dominated by the aquatic *V. americana* and *Sparganium fluctuans*, plus *I. echinospora*; Namakan Lake was dominated by *E. acicularis*, *R. reptans*, and *Tillaea aquatica*. These last three species and *Isoetes* are short, bottom-dwelling plants favored by drawdown (Ashton and Bissell 1987; Renman 1989; Rorslett 1989). The lack of any similar dominants at this depth among lakes resulted in disparate transect ordination scores. Transects R1*c* and R2*c* showed less similarity to their *b* transect counterparts than did the *b* and *c* transects in Namakan Lake and Lac La Croix because there is a true habitat difference between the *b* and *c* transects in Rainy Lake; the *b* transects are amphibious and the *c* transects are always submersed. In Namakan Lake and Lac La Croix, these transects are both emersed during parts of winter and spring.

On the 1.75-m transects (*d*), Lac La Croix had numerous prevalent aquatic taxa, including *V. americana*, *Myriophyllum* spp., *Najas flexilis*, *Potamogeton amplifolius*, *Potamogeton robbinsii*, and *Chara* spp. Only four species were encountered on the *d* transects at Rainy Lake; *V. americana* was the dominant species, and *Potamogeton richardsonii* was also prevalent. Namakan Lake at this depth was dominated by *Chara* spp. and *Potamogeton richardsonii* and included substantial amounts of *V. americana* and bottom-dwelling *I. echinospora*, *Tillaea aquatica*, and *E. acicularis*. Again, the transect ordination scores differed widely between lakes. The paired ordination scores for Lac La Croix and Namakan Lake at this contour depth varied more than for other transect pairs because more species were sharing the dominant role. Transect L2*d* is an outlier from the other transects because of the dominance of *Potamogeton amplifolius* and *Nitella* spp.

The ordination scores for Namakan Lake transects are compressed on both axis 1 and axis 2 (Fig. 3), probably as a result of drawdowns that included the deeper transects in Namakan Lake and limited the number of species that can grow well there. *Potamogeton amplifolius*, *Nitella* spp., *Myriophyllum* spp., *B. beckii*, and *Potamogeton robbinsii* were lacking from the *c* and *d* transects of the lake, whereas they were dominant in Lac La Croix. *Sparganium fluctuans* was found in only small amounts on transect N2*c*; it was a dominant on the *c* transect of Rainy Lake, which was never dewatered. The larger, erect aquatic macrophytes that did occur along the deeper transects in Namakan Lake seemed to have survived by being deeply

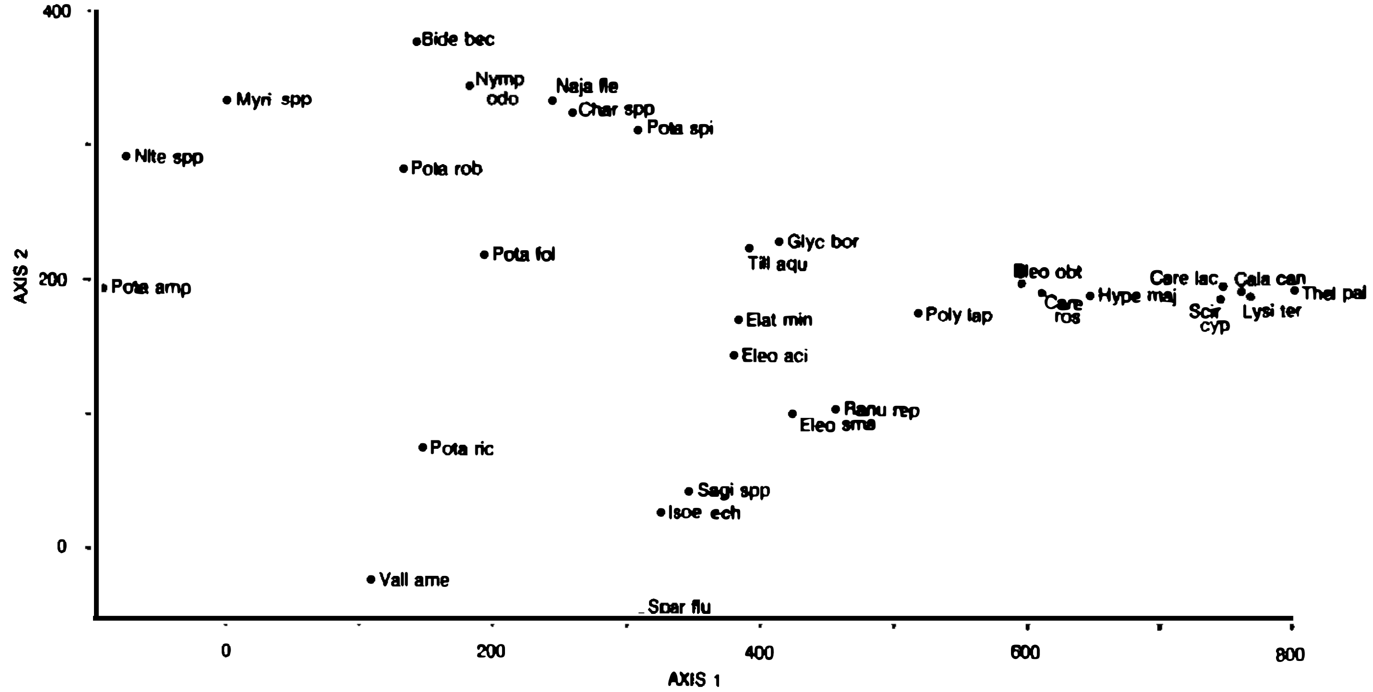

FIG. 4. Two-dimensional plot of DCA ordination of the importance value × transect matrix (eigenvalues: axis 1 = 0.879; axis 2 = 0.403). Points plotted are selected taxa.

TABLE 2. Sums of the mean importance values for 26 of the most prominent plant taxa on transects *b*, *c*, and *d* of Lac La Croix, Rainy Lake, and Namakan Lake

	Lac La Croix			Rainy Lake			Namakan Lake		
	b	*c*	*d*	*b*	*c*	*d*	*b*	*c*	*d*
Thin-stem emergents	21.1	0	0	36.0	2.9	0	43.4	13.3	0
Mat-formers	25.4	0	0	8.9	7.2	0	33.6	46.4	12.4
Low rosettes	6.8	0	0	1.0	28.3	0	13.5	22.8	13.6
Low-growth aquatics	9.9	33.8	43.0	0	8.3	0	0.8	5.4	34.9
Erect aquatics	16.1	52.5	52.1	0	49.1	96.8	0.5	8.7	29.2
Total	79.3	86.3	95.1	45.9	95.8	96.8	91.8	96.6	90.1

NOTE: Taxa were separated into morphologically similar groups. Water depths were 0.5 m for transect *b*, 1.25 m for transect *c*, and 1.75 m for transect *d*.

rooted in the mud cracks that were characteristic of the area. The deeper transects were dominated by mat-forming and low-growth aquatic species, plants whose morphology or physical structure enables them to tolerate the extreme fluctuations in water levels. Although they are generally considered to be stress tolerators (sensu Grime 1979), *E. acicularis* and *R. reptans* form vegetative mats that may competitively exclude other macrophytes through site preemption; the planting of *E. acicularis* is even under consideration as a mechanism for controlling undesirable aquatic plants (Ashton and Bissell 1987). Wilson and Keddy (1986) found that small rosettes and mat formers, which produced little shade and were usually not competitive dominants, were sometimes dominant in environments where they could withstand damage that destroyed tall, leafy plants.

Ice is a damaging factor that may be important in drawdown zones. The *c* transect in Namakan Lake is under water when ice forms but is dewatered in early winter, leaving blocks of ice resting on the bottom substrate. Near the upper part of the shore, the ice freezes solidly to the bottom; in the lower part, frost grows into the water-saturated, silty bottom and causes upheaval through formation of needle ice (Renman 1989). *Ranunculus reptans* has a stoloniferous habit of growth that may make it sensitive to freezing and frost heave, but it aborts stolons and reduces mass prior to winter, thus increasing its ability to withstand frost heave (Renman 1989). The thin rhizomes of *E. acicularis* are broken into pieces by ice disturbance, but each piece of rhizome may grow vegetatively in the spring to become a new plant, helping this species to become dominant in this part of the dewatered zone (Renman 1989).

The *d* transects at Rainy Lake diverge from the other points plotted in Fig. 3. The dense and heavily leaved *V. americana* and *Potamogeton richardsonii* extending through the water column probably shade out smaller, low-growth plant forms. Since dewatering never occurs at this depth to provide disturbance, no openings are created for invasion by other species.

Structure of aquatic vegetation

Since the morphology of a plant must be suited to environmental conditions for the plant to survive, it is possible that the plant communities in these lakes with different water-level regimes would differ in physical structure and provide different types of habitat for fish and wildlife. As a means of assessing this possibility, we included in Table 2 the mean IV of the most important macrophyte taxa, by transect and structural group for each lake.

The amphibious zone of Lac La Croix (0.5 m, transect *b*) supported a structurally diverse plant community. Mat formers and low rosettes provided plant cover at the lake bottom. Low-growth aquatics extended this cover higher into the water column. Thin-stem emergents and erect aquatics extended through all or nearly all of the water column; the erect aquatics provided more underwater surface area and cover than did the thin-stem emergents (which also provided cover for wildlife above the water surface). In the submersed and deep-water zones in Lac La Croix (transects *c* and *d*), only low-growth and erect aquatics were present, but they created a patchy environment with leaf surfaces for colonization and cover at all depths, plus areas of open water.

The shallow waters of Rainy Lake (transect *b*) differed from those of Lac La Croix in 1987 in having no low-growth or erect aquatics. This was expected because the transect was dewatered during that unusually dry season; thin-stem emergents (primarily *Polygonum lapathifolium*) replaced the aquatic species. Along the *c* transect, erect aquatics were present in numbers similar to those at Lac La Croix, but the lake bottom contained fewer low-growth aquatics and instead supported numerous low rosettes and some mat formers. These structure types offer less surface area and cover than do low-growth aquatics. Along the *d* transect in Rainy Lake, erect aquatics were the only structure type. The patchiness, interspersed open-water areas, and dense cover at the lake bottom found in Lac La Croix were missing.

The shallow waters (transect *b*) of Namakan Lake also differed from Lac La Croix in 1987; there were very few low-growth or erect aquatics, and some thin-stem emergents appeared in this low-water year. Along the *c* transect, Namakan Lake was depauperate in both low-growth and erect aquatics; there was virtually no cover in the upper water column. The stress-tolerant mat formers and low rosettes that were dominant represent structure types that offer less surface area for colonization than do the low-growth aquatics of Lac La Croix. Along the *d* transect, Namakan Lake was more similar to Lac La Croix; however, the mat formers and low rosettes favored by drawdowns were also present.

Conclusions and recommendations

In an effort to effect management for natural systems, this study was conducted to test the hypothesis that water-level regulation in Rainy and Namakan lakes has resulted in aquatic macrophyte communities in the littoral zone that differ in composition and structure from those in an unregulated lake. The data supported the hypothesis in each lake; altered hydrology in Rainy and Namakan lakes not only resulted in a difference in species that dominated each transect but also resulted in structural differences in the vegetation. The effects were more pronounced along the deeper transects.

Connell (1978) proposed that highest diversity is maintained at intermediate scales of disturbance. Keddy (1983) confirmed this hypothesis as applied to shoreline vegetation in his study of an Ontario lake. The water levels in Lac La Croix vary naturally from year to year, and this variability spreads out the effects of extreme environmental conditions across a wider area over time. Consequently, the longer intervals between similar disturbances at any specific depth enable more species to invade and increase local diversity (Connell 1978). The hydrologic regime at Lac La Croix represented intermediate disturbance.

There has been too little disturbance from water-level fluctuations in Rainy Lake, and a stable macrophyte community with little diversity has developed at depths that are flooded year-round. There has been too much disturbance from water-level fluctuations in Namakan Lake; only species that are well adapted to pervasive physical disruptions or that can invade and mature quickly have survived at depths that undergo long winter drawdowns.

If the National Park Service is to manage for natural macrophyte communities and the faunal habitats they present, our results suggest that both Rainy and Namakan lakes should be returned to more natural hydrologic regimes. Namakan Reservoir should be regulated to reach its maximum water level in early June. Both Rainy Lake and Namakan Reservoir should be gradually drawn down in summer so that near minimums are reached before ice forms. Finally, the amplitude of the drawdown should be increased at Rainy Lake and decreased at Namakan Reservoir to approximate natural drawdowns of 1.8–1.9 m, and the amount of drawdown should vary between years. As shown for Lac La Croix, these hydrologic conditions could, over time, result in more natural and structurally diverse macrophyte communities in the littoral zone of the regulated lakes and more diverse habitats for aquatic fauna.

Acknowledgments

We thank James Moore for assistance in fieldwork and taxonomy, Greg LeGault for assistance in fieldwork; Larry Kallemeyn for providing valuable information throughout the project and logistical support during the fieldwork; Lucy Tyrrell for suggestions regarding data analysis; Lisa Kensler for preparing some of the figures and tables; and John Gannon, Paul Keddy, Larry Kallemeyn, and Paul Eschmeyer for reviewing a previous draft of the manuscript. We thank former National Park Service Regional Chief Scientist, Mike Ruggiero, and Indiana Dunes National Lakeshore for arranging financial support for the field portion of this study.

ASHTON, F. M., and BISSELL, S. R. 1987. Influence of water regime on growth of dwarf spikerush and slender spikerush. J. Aquat. Plant Manage. **25**: 51–54.

CONNELL, J. H. 1978. Diversity in tropical rain forests and coral reefs. Science (Washington, D.C.), **199**: 1302–1310.

CURTIS, J. T. 1959. The vegetation of Wisconsin. University of Wisconsin Press, Madison.

FLUG, M. 1986. Analysis of lake levels at Voyageurs National Park. U.S. Department of the Interior, National Park Service Water Resources Report No. 86-5.

GLEASON, H. A., and CRONQUIST, A. 1963. Manual of vascular plants of northeastern United States and adjacent Canada. Van Nostrand Reinhold Co., New York.

GRIME, J. P. 1979. Plant strategies and vegetation processes. John Wiley & Sons, Chichester, England.

KALLEMEYN, L. W., REISER, M. H., SMITH, D. W., and THURBER, J. M. 1988. Effects of regulated lake levels on the aquatic ecosystem of Voyageurs National Park. *In* Interdisciplinary approaches to freshwater wetlands research. *Edited by* D. A. Wilcox. Michigan State University Press, East Lansing. pp. 133–146.

KEDDY, P. A. 1983. Shoreline vegetation in Axe Lake, Ontario: effects of exposure on zonation patterns. Ecology, **64**: 331–344.

KEPNER, R., and STOTTLEMYER, R. 1988. Physical and chemical factors affecting primary production in the Voyageurs National Park lake system. Mich. Technol. Univ. Great Lakes Area Res. Stud. Unit Tech. Rep. No. 29.

MCCUNE, B. 1987. Multivariate analysis of the PC-ORD system. A Biotic Resources Project Report. Butler University Holcomb Research Institute Report No. 75.

MUELLER-DOMBOIS, D., and ELLENBERG, H. 1974. Aims and methods of vegetation ecology. John Wiley & Sons, New York.

NICHOLS, S. A. 1975. The impact of overwinter drawdown on the aquatic vegetation of the Chippewa Flowage, Wisconsin. Trans. Wis. Acad. Sci. Arts Lett. **63**: 176–186.

NILSSON, C. 1981. Dynamics of the shore vegetation of a north Swedish hydro-electric reservoir during a 5-year period. Acta Phytogeogr. Suec. **69**: 1–96.

NILSSON, C., and KEDDY, P. A. 1988. Predictability of change in shoreline vegetation along a hydroelectric reservoir, northern Sweden. Can. J. Fish. Aquat. Sci. **45**: 1896–1904.

PIP, E., and STEPANIUK, J. 1988. The effect of flooding on wild rice, *Zizania aquatica* L. Aquat. Bot. **32**: 283–290.

RENMAN, G. 1989. Distribution of littoral macrophytes in a north Swedish riverside lagoon in relation to bottom freezing. Aquat. Bot. **33**: 243–256.

RORSLETT, B. 1989. An integrated approach to hydropower impact assessment: II. Submerged macrophytes in some Norwegian hydro-electric lakes. Hydrobiologia, **175**: 65–82.

SCULTHORPE, C. D. 1967. The biology of aquatic vascular plants. Edward Arnold Ltd., London.

SPENCE, D. H. N. 1982. The zonation of plants in freshwater lakes. Adv. Ecol. Res. **12**: 37–124.

SWINK, F., and WILHELM, G. 1979. Plants of the Chicago region. The Morton Arboretum, Lisle, IL.

THOMAS, A. G., and STEWART, J. M. 1969. The effect of different water depths on the growth of wild rice. Can. J. Bot. **47**: 1525–1531.

TYRRELL, L. E. 1987. A floristic survey of button-bush swamps in Gahanna Woods State Nature Reserve, Franklin County, Ohio. Mich. Bot. **26**: 29–38.

VOSS, E. G. 1972. Michigan flora. Part I. Gymnosperms and monocots. Cranbrook Inst. Sci. Bull. No. 55.

——— 1985. Michigan flora. Part II. Dicots. Cranbrook Inst. Sci. Bull. No. 59.

WILCOX, D. A., PAVLOVIC, N. B., and MUEGGLER, M. E. 1985. Selected ecological characteristics of *Scirpus cyperinus* and its role as an invader of disturbed wetlands. Wetlands, **5**: 87–97.

WILSON, S. D., and KEDDY, P. A. 1986. Species competitive ability and position along a natural stress/disturbance gradient. Ecology, **67**: 1236–1242.