

## COMPARISONS OF UNDEVELOPED AND DEVELOPED SHORELANDS, NORTHERN WISCONSIN, AND RECOMMENDATIONS FOR RESTORATION

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**Abstract:** Development of lakeshores has occurred at unprecedented levels in recent decades. Changes in the shoreland ecosystem concomitant with this development have been little studied. In this study, we compared the structural and floristic characteristics of vegetation at 97 developed and 85 undeveloped (reference) shoreland sites in northern Wisconsin, USA. Quantitative comparisons of vegetation structural characteristics (percent cover of canopy, subcanopy, and understory vegetation layers; percent of shoreline overhung by trees and shrubs; and amount of coarse woody debris) showed significantly greater complexity and cover at undeveloped versus developed sites. We classified plant communities and described plant species composition along three belt transects parallel to shore (upland, shoreline, and shallow water) using ordination techniques to describe the differences between developed and undeveloped sites, as well as among undeveloped sites. The mean number of plant species and the percent of native species were both greater at undeveloped than at developed sites along all three transects. Undeveloped upland sites could be grouped by plant species composition into three types: Northern Wet Forest (bog species), Northern Mesic Forest, and Northern Xeric Forest. Undeveloped shoreline vegetation was also clustered into three categories: bog species, upland species with an abrupt transition to aquatic species, and wet meadow species. Soil characteristics further distinguished the upland and shoreline categories. No distinct vegetation categories emerged in the shallow water ordination. We recommend that appropriate species for shoreland restoration efforts be selected based on the native plant communities present at the undeveloped sites, their relative location along an upland to shallow water gradient, and, in some cases, soil characteristics.

**Key Words:** shoreland, restoration, lakeshore, vegetation structure, reference site, vegetation classification, detrended correspondence analysis

### INTRODUCTION

The Northern Highland Lake District in northern Wisconsin, USA contains the third largest density of freshwater glacial lakes in the world (Thwaites 1929). Vacationers have been attracted to this forested lake district for many years, and now increasing numbers of people are building homes along the lakeshores. Since 1965, two-thirds of previously undeveloped lakes have become developed in this manner, and relatively few undeveloped lakes remain (WDNR 1996).

Simultaneous with increasing shoreland development has been an increasing awareness of the ecological importance of these areas. Riparian and littoral areas of inland lakes are critical habitat for wildlife (Landin 1979, Odum 1979, Racey and Euler 1982,

Fowler and Howe 1987, Chandler et al. 1995, Engel and Pederson 1998, Radomski and Goeman 2001, Woodford and Meyer 2002, Lindsay et al. 2002) and protect water quality (Bannerman et al. 1993, Engel and Pederson 1998, Kent 1998). Additionally, naturally vegetated shorelines have a strong aesthetic appeal (Korth 1994, Shifferd 1998). Because shorelands are transition zones between upland and aquatic ecosystems, they host exceptionally high biodiversity (Odum 1979, Mitsch and Gosselink 1993). Shoreland is a legal term, defined as the extent of land beginning at the ordinary high water mark extending landward (UWEX Website 2003). The width of the shoreland varies according to State Statutes and local zoning ordinances.

Shorelands are affected by terrestrial activities (e.g., sedimentation, erosion, alteration of native vegetation, and non-point pollution runoff), as well as lake-wide factors (e.g., changes in water levels and water chemistry, introduction of exotic species). Shorelands are therefore subject to greater and more rapid changes than either terrestrial or aquatic ecosystems (Crowder et al. 1996).

The potential ecological implications of such alterations are profound and include erosion of shorelines (Dai et al. 1977, Dean 1979, Davidson et al. 1989), inadequate protection of water quality (Sorrano et al. 1996, Henderson et al. 1999), loss of fish and wildlife habitat (Christensen et al. 1996, Engle and Pederson 1998, Jennings et al. 1999), and loss of diversity (Rachel 2002). Recent studies of shoreland fauna show that the species composition of breeding songbirds differs between developed and undeveloped (reference) shorelands (Lindsay et al. 2002), and numbers of breeding green frogs are profoundly fewer at developed shoreland sites than at undeveloped sites (Woodford and Meyer 2002). Greater vegetation structural complexity has been shown to increase bird species richness and density (Niemi and Hanowski 1984, Free-mark and Merriam 1986, Probst et al. 1992). Similarly, natural cover afforded by a diverse and dense ground flora and abundant coarse woody debris benefits many herpetile species (Vogt 1981).

A suite of studies conducted in the 1970s in Ontario, Canada examined the effects of lakeshore development on small mammals (Racey and Euler 1982), breeding birds (Robertson and Flood 1980, Clark et al. 1984), and vegetation (Racey and Euler 1983). These studies were conducted in an area where development was extensive, but not intensive, and where extreme habitat alteration was uncommon (Robertson and Flood 1980). The style of shoreland development has changed dramatically over the years from small seasonal cabins surrounded by forest, as described in the Ontario studies, to large year-round homes with extensive impervious surfaces and reduction of tree cover (WDNR 1999). In this study, we sought to demonstrate the differences in vegetation structure and diversity that occur with continuing lakeside development.

The State of Wisconsin has attempted to protect wildlife habitat, water quality, and aesthetic values by adopting shoreland development ordinances. The Wisconsin Shoreland Management Program (WDNR Chapter NR 115) mandates vegetation cutting standards in a buffer zone along lakeshores. Within this state-mandated buffer zone, which extends approximately 10.8 m landward from the ordinary high water mark (OHWM), 9.4 m of every 31.4 m of shoreland vegetation may be cleared of vegetation. The remain-

der must remain in a naturally vegetated state. In practice, however, these standards have often been ignored, and zoning enforcement has been weak. The result is an abundance of developed lakeshore sites where the native vegetation has been altered dramatically. Such altered lakeshores are candidates for restoration efforts.

The science of lakeshore restoration is in its infancy. We can draw upon the literature for preliminary information on seed banks (Smith and Kadlec 1983, Keddy and Reznicek 1986), effects of disturbance such as wave action and water-level fluctuations (Wilson and Keddy 1986, Day et al. 1988, Wilcox and Meeker 1991), and plant zonation (Spence 1982), but most of the published studies focus on isolated wetlands or on the Great Lakes and may not apply directly to inland lakes. Little has been published on restoration that integrates across the shoreland ecotone, encompassing the terrestrial buffer zone, shoreline, and shallow water (Engle and Pederson 1998).

Private landowners and agency personnel are in dire need of lakeshore restoration guidelines, especially as county zoning offices begin to require mitigation or restoration of the shoreland buffer zone as a condition for granting building or remodeling permits. Identification of site type based on plant communities, plant species appropriate for the land type and specific site, and quantification of natural vegetation structural components (e.g., amount of canopy cover, understory cover, coarse woody debris), are examples of information lacking throughout most of northern Wisconsin's lake district. In order to select plant species appropriate for restoration efforts at each type of site within a physiographic land type, descriptions of native plant communities at undeveloped (reference) sites are also needed.

The popularity of restoration, in general, has increased in recent years, beginning with prairie restorations in southern Wisconsin (Blewett and Cottam 1984) and expanding to other ecosystems (e.g., savanna: Packard 1988, Leach and Givnish 1998; wetlands: Landin 1993, Thompson and Luthin 2000; lakes: Cooke et al. 1993; forests: Troxell et al. 2000). Because private landowners have embraced prairie restoration and prairie plants are widely available commercially, many northern Wisconsin lakeshore owners within this forested ecosystem are misguidedly attempting to "restore" their lakeshores using prairie species (personal observation).

Existing habitat classification systems for the region (e.g., Curtis 1959, Eggers and Reed 1987, Kotar et al. 1988) do not describe lakeshore habitats adequately. The habitat classification systems developed by Curtis (1959) and Kotar et al. (1988) work well at state and regional levels, but these habitat types are too broad

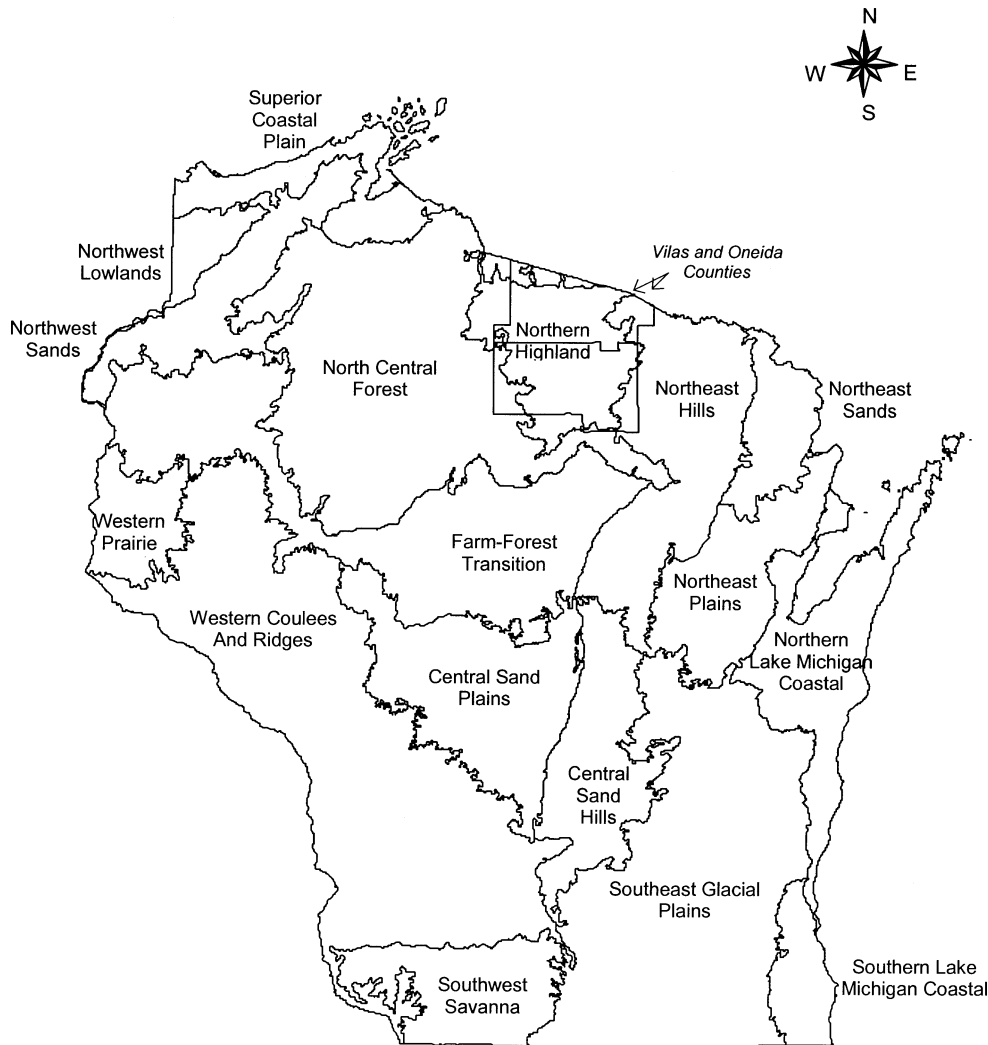


Figure 1. Ecological Landscapes of Wisconsin (National Hierarchical Framework of Ecological Units 1999), showing the study area, Vilas and Oneida Counties, outlined in the center-north and labeled in italics.

for lakeshore classification. The Kotar et al. (1988) system does not address aquatic and other non-forested habitat types. The U.S. Army Corps' Wetland Plant Communities (Eggers and Reed 1987) and other wetland classification systems (e.g., Cowardin 1979) do not address terrestrial habitats. Because shoreland areas generally cross elevational zones, they also cross typical habitat classifications, making existing classification systems inadequate. Therefore, it is important to begin the development of a classification system that takes into account the unique transitional characteristics of lakeshores.

In this study, we gathered information to expand the existing knowledge of northern Wisconsin lakeshores for the purpose of restoration efforts, using methods applicable in other regions and ecosystems. Specifically, our objectives were to 1) identify features most impacted by lakeshore development by quantifying

vegetation structural differences between undeveloped (reference) and developed lakeshores in the study area, 2) classify the plant communities of undeveloped lakeshores (reference sites) to determine types of lakeshore sites in the study area, and 3) determine appropriate species for restoration of developed lakeshores within the study area by describing plant species composition at reference sites.

## METHODS

### Study Area

The study area, Vilas and Oneida Counties in northern Wisconsin, lies almost entirely within the Northern Highland Ecological Landscape of Wisconsin (National Hierarchical Framework of Ecological Units 1999; Figure 1). We chose 12 pairs of lakes for this study,

ranging in size from approximately 11 ha to 162 ha, with one of each pair being mostly developed along the shoreland, and the other mostly undeveloped (Lindsay et al. 2002). Pairs were matched according to surface area, shoreline length, depth, water chemistry, and water source (Wisconsin Department of Natural Resources, Wisconsin Surface Waters Database, unpublished). In addition to the pairs of lakes, we chose four large (>200 ha) developed lakes that had no undeveloped counterpart because none exist within the study area.

We considered undeveloped sites as representative of reference conditions. While these undeveloped lakeshore sites are not pristine (nearly the entire northern third of Wisconsin was clearcut in the late 1800s to early 1900s), they are the best available reference sites.

### Field Methods

*Site Selection.* During the summer of 1997, we surveyed vegetation at 182 sites on 28 lakes. Sites were chosen on each lake by following a compass bearing generated from a random numbers table. From the lake center, the first site was selected using the randomly-generated compass bearing, along with five more sites at 60 degree intervals, for a total of six sites on most lakes (two lakes had seven sites). On three of the four largest lakes we surveyed 10 sites at 36 degree intervals; the fourth lake had six sites, as described above. Each site was characterized as either developed (with the presence of a house or other structure, campground, or with a well-established lawn or beach area) or undeveloped (no sign of human habitation or use), for a total of 97 developed and 85 undeveloped sites. Most undeveloped sites are owned by the State of Wisconsin (Northern Highlands and American Legion State Forests) and are allowed to remain in a natural condition, as opposed to being managed for timber production, because these study areas lie within the State-mandated buffer zone.

*Vegetation Sampling.* Three belt transects (30 m long and 1 m wide) were established parallel to the shoreline at each site, centered around the compass bearing: 1) an upland transect, 3 m inland from the shoreline, within the terrestrial buffer zone, 2) a shoreline transect, directly along the water/land interface, and 3) a shallow water transect, 2.5 m offshore. We listed all plant species in each transect and ranked the estimated percent cover of each species using a modified Daubenmire system (Barbour et al. 1980) from 0 to 6, with 0 = none, 1 = 1–5%, 2 = 6–25%, 3 = 26–50%, 4 = 51–75%, 5 = 76–95%, 6 = 96–100%.

We also estimated structural characteristics in 30-m-long, variable-width transects as follows. 1) In the

terrestrial buffer or upland zone (10.8 m wide, corresponding to the state-mandated buffer width), we estimated the percent cover of the canopy, subcanopy (sublayer, as in Ralph et al. 1993), understory (1 m – 3 m in height), and ground (<1 m tall) vegetation; percent coniferous cover within the canopy, subcanopy, and understory layers; relative amount of coarse woody debris (CWD), where 0 = none, 1 = sparse (fewer than 10 pieces, >5 cm diameter and >0.5 m in length), 2 = abundant (more than 10 pieces of previously noted size); and soil type (excessively well-drained sandy soil, moderately well-drained sandy-loam or loamy-sand, or organic peat or muck). 2) Along the shoreline (1-m-wide transect), we estimated the percent of shoreline overhung by trees (>3 m in height); percent of shoreline overhung by shrubs (<3 m in height); relative amount of CWD (as above); and bank height (measured to the nearest 0.05 m). 3) In the shallow water zone (approximately 10-m-wide transect), we estimated the percent cover of aquatic macrophyte types (floating, submerged, narrow-leaved and broad-leaved emergents, isoetids); percent of lake bottom unvegetated; relative amount of CWD (as above); substrate type (organic or inorganic); and water depth at 2.5 m from shore.

We chose to estimate these particular structural characteristics because 1) they may contribute to our understanding of differences among types of sites (e.g., soil and substrate types, water depth, bank height), or 2) they may affect the presence and abundance of fish and other wildlife (feeding, nesting, resting habitat in the forest layers; overhanging trees and shrubs along the shoreline providing shade and regulating shallow water temperatures; food, refuge, and egg-laying sites in the shallow water).

### Data Analyses

In all analyses described below, we considered each transect as a separate sample, rather than treating whole lakes as samples. Shoreland vegetation often differs greatly from one part of a lake to another (Keddy 1983, and personal observation). For example, a *Sphagnum* bog may exist along a portion of the shoreland, while across the lake may be a steep slope with dry, sandy soils, supporting dry forest species. Aquatic vegetation also varies within a given lake due to wave action and other disturbance effects (Hutchinson 1975). Additionally, both developed and undeveloped portions of shoreland may occur on a given lake.

*Comparisons of Developed and Undeveloped Sites.* We conducted Mann-Whitney *U* tests to compare undeveloped sites with developed sites for the following characteristics: mean % cover in the canopy,

subcanopy, understory, and ground layers; mean % conifer cover within the canopy, subcanopy, and understory layers; mean % of shoreline with overhanging trees and shrubs; mean % of shallow water area covered by floating, submerged, narrow-leaved emergent, broad-leaved emergent, and isoetid vegetation types; and mean % of shallow water area unvegetated. We also used Mann-Whitney  $U$  tests to compare the mean species richness and % native species at undeveloped vs. developed sites. We used Chi-square tests to examine differences between development types in the relative amount of CWD in the terrestrial buffer zone, along the shoreline, and in the shallow water area. In all cases, we considered  $p \leq 0.05$  as statistically significant.

In addition to the above comparisons, we also used Detrended Correspondence Analysis (DCA), which is appropriate for ecological data (Gauch 1982, Pielou 1984, McCune and Mefford 1995), to compare developed vs. undeveloped sites based on species composition, and tested significance among groups using Multiple Response Permutation Procedure (MRPP). MRPP is a non-parametric procedure for testing no difference between two or more groups (Zimmerman et al. 1985). The test statistic, based on the within-group average of pair-wise distance measures, describes the separation between groups (Biondini et al. 1985, McCune and Mefford 1995). Sites located near each other in ordination space have similar species composition. We conducted separate ordinations for each elevational zone (upland, shoreline, shallow water). The species cover class data (0–6) was used to ordinate sites in species space with PC-ORD version 3.0 (McCune and Mefford 1997). All species were used in the ordinations, although species encountered infrequently were downweighted, so as to avoid distortion of DCA results (McCune and Mefford 1995).

*Ordination of Undeveloped (Reference) Sites.* In order to describe differences in plant communities among undeveloped sites, we used DCA. As explained above, we conducted separate ordinations for each elevational zone, we used species cover class data to ordinate sites in species space, and we used all species in the ordinations. When a tree species  $\geq 2.5$  cm diameter at breast height (DBH) and  $< 2.5$  cm DBH occurred in a transect, we included both in the data matrix (e.g., *Acer* and *Acer* sapling/seedling). We used environmental data (terrestrial soil type, % cover in various vegetation strata, aquatic substrate type, aspect, bank height, and water depth) to help explain the axes.

*Classification of Vegetation at Undeveloped (Reference) Sites.* We used two-way indicator species analysis (TWINSPAN; Gauch and Whittaker 1981) to de-

scribe plant communities. We interpret TWINSPAN-generated lists of species' preferentials as species associated with, or affiliated with, a group of sites. TWINSPAN non-preferential species are generally widespread among site groups.

## RESULTS AND DISCUSSION

### Comparisons of Undeveloped (Reference) vs. Developed Sites

*Structural Differences.* Structural characteristics of vegetation differed significantly between undeveloped (reference) and developed lakeshore sites along all three elevational transects (Mann-Whitney  $U$  tests). Within the terrestrial buffer zone, the percent cover of the canopy, subcanopy, and understory levels of vegetation was greater at undeveloped sites than at developed sites (Table 1a). No differences were observed in the percent ground cover or in the percent coniferous component within the canopy, subcanopy, and understory layers (Table 1a).

Along shoreline transects, overhanging trees and shrubs covered greater percentages of undeveloped (reference) shorelines than developed shorelines (Table 1b).

In the shallow water areas, percent cover of floating vegetation was greater at undeveloped (reference) than at developed transects (Table 1c). Percent cover of other aquatic vegetation types did not differ between undeveloped and developed transects. Developed transects showed a greater percentage of unvegetated shallow water areas than undeveloped transects (Table 1c).

The relative amount of coarse woody debris (CWD) in all three variable-width transects was dependent on development. The majority of undeveloped sites contained an abundant amount of CWD, while the majority of developed sites contained no CWD (Table 2). These results are consistent with those of Christensen et al. (1996), who showed strong relationships among CWD abundance, riparian vegetation characteristics, and cabin density. With increasing cabin density, they observed a dramatic decrease in the number of riparian trees and the amount of CWD.

The above differences in percent cover of various forest layers and percent of shoreline overhung with trees and shrubs at developed compared to undeveloped (reference) sites detail the simplification of vegetation structure at developed sites. Our results are generally consistent with those of previous studies, although because these previous studies measured vegetation differently than we did, we could not compare the degree of difference. Racey and Euler (1982) found a decrease in tree, shrub, and ground cover with increasing development. The area cleared in the shrub

Table 1. Mean percent cover of vegetation and percent coniferous component and 2 standard errors (2SE) in structural layers in the upland (a), mean percent and 2 standard errors (2SE) of shoreline covered by overhanging trees and shrubs (b), and mean percent cover and 2 standard errors (2SE) of aquatic vegetation types (c) at undeveloped (reference) and developed sites, Vilas and Oneida Counties, Wisconsin, 1997. '\*\*' and '\*\*\*' indicate significance at  $p < 0.01$  and  $p < 0.001$ , respectively, Mann-Whitney  $U$  tests.

|                        | Mean % Cover (2SE)                |             |
|------------------------|-----------------------------------|-------------|
|                        | (N = 84)                          | (N = 97)    |
| <b>a) UPLAND</b>       | Undeveloped                       | Developed   |
| Canopy***              | 55.4 (5.30)                       | 40.1 (4.94) |
| Subcanopy***           | 22.0 (3.93)                       | 12.1 (2.60) |
| Understory***          | 34.5 (5.41)                       | 17.4 (4.13) |
| Ground                 | 66.4 (6.28)                       | 63.0 (5.96) |
|                        | Mean % Coniferous Component (2SE) |             |
|                        | Undeveloped                       | Developed   |
| Canopy                 | 56.9 (8.75)                       | 51.5 (8.10) |
| Subcanopy              | 46.9 (8.99)                       | 56.5 (9.67) |
| Understory             | 60.0 (8.14)                       | 62.8 (9.15) |
|                        | Mean % Shoreline (2SE)            |             |
| <b>b) SHORELINE</b>    | Undeveloped                       | Developed   |
| Trees**                | 38.8 (6.77)                       | 29.5 (6.15) |
| Shrubs***              | 66.7 (6.98)                       | 28.0 (6.62) |
|                        | Mean % Cover (2SE)                |             |
| <b>c) AQUATIC</b>      | Undeveloped                       | Developed   |
| Floating**             | 15.7 (5.50)                       | 5.8 (2.54)  |
| Shrub                  | 1.8 (2.34)                        | 0.4 (0.50)  |
| Narrow-leaved emergent | 1.2 (1.17)                        | 1.4 (1.14)  |
| Broad-leaved emergent  | 0.9 (0.71)                        | 1.6 (1.21)  |
| Submergent             | 14.0 (5.85)                       | 3.9 (2.21)  |
| Isoetid                | 1.7 (1.16)                        | 0.8 (0.81)  |
| Unvegetated***         | 65.0 (7.48)                       | 85.5 (3.73) |

layer was greater than that in both the tree and ground layers (Racey and Euler 1983). Robertson and Flood (1980) reported a reduction of vertical structural diversity at developed sites, even though the ground flora was largely intact. Clark et al. (1984) found tree density, canopy volume, and shrub coverage negatively correlated with development.

In addition to the differences in vegetation structural characteristics, the mean number of plant species was greater at undeveloped (reference) sites than at developed sites (31.7 vs. 26.5,  $p < 0.001$ ; Mann-Whitney  $U$  test), as was the mean percent of native species (99.2 vs. 88.3,  $p < 0.001$ ). Clark et al. (1984) did not observe a difference in the number of ground flora species due to development and attributed this lack of

Table 2. Percent of undeveloped and developed sites showing relative amount of coarse woody debris in upland, shoreline, and shallow water transects, Vilas and Oneida Counties, Wisconsin, 1997. '\*\*\*' indicates  $p < 0.001$  for the chi-square test of independence.

|                         | % Transects With Coarse Woody Debris |        |          |
|-------------------------|--------------------------------------|--------|----------|
|                         | None                                 | Sparse | Abundant |
| <b>Upland***</b>        |                                      |        |          |
| Undeveloped             | 1.2                                  | 24.1   | 74.7     |
| Developed               | 60.0                                 | 29.5   | 10.5     |
| <b>Shoreline***</b>     |                                      |        |          |
| Undeveloped             | 1.2                                  | 32.1   | 66.7     |
| Developed               | 54.2                                 | 31.2   | 14.6     |
| <b>Shallow water***</b> |                                      |        |          |
| Undeveloped             | 7.6                                  | 26.6   | 65.8     |
| Developed               | 58.3                                 | 24.0   | 17.7     |

difference to the introduction of exotic species. It is possible that the owners of developed lakeshores in the 1970s–1980s were not as vigilant at controlling weeds in their lawns as are the lakeshore owners today.

Although Mann-Whitney  $U$  tests showed significant differences in the percent of native species between developed and undeveloped (reference) sites, because some native ground flora may occur at developed sites (beneath the shrubs along the property boundaries, for example), the magnitude of this difference is minimized. In addition, the lack of differences in percent total ground cover between developed and undeveloped transects is misleading (Table 1a). An analysis of the percent of each site covered by native ground flora (which was not possible in great detail due to the cover class system we used) would undoubtedly reveal much greater differences between the two types of sites. A few examples illustrate these points.

The frequency of occurrence of *Carex pensylvanica*, a small sedge with a growth form similar to lawn grass, was similar at developed and undeveloped upland transects (26% and 30% of transects, respectively). When this species occurred, however, its percent cover differed greatly between development types. *Carex pensylvanica* occurred at >5% cover at 35% of the undeveloped transects compared to only 8% of the developed transects that hosted the species. We recorded exotic lawn grasses, our second example, at both developed and undeveloped upland transects. However, the frequency of occurrence and the percent cover differed vastly between development types. Forty-three percent of upland developed transects contained lawn grasses, with a mean cover of 50–75%, compared to only one undeveloped transect with a

cover of 25–50%. The final example is that of the widespread shoreline shrub, *Chamaedaphne calyculata*. Similar percentages of developed and undeveloped shoreline transects (15% and 20%, respectively) supported a sparse cover ( $\leq 5\%$ ) of this species. However,  $>5\%$  cover occurred at many more undeveloped shoreline transects (48%) than at developed shoreline transects (12%). Such details aid in describing differences between developed and undeveloped sites. While the percent ground cover differs little, the species composition often differs substantially, with native species often replaced by exotic lawn grasses at developed sites. When native species occur at developed sites, their percent cover is often much less than at undeveloped sites.

The aesthetic appeal of conifer trees, such as *Pinus resinosa* and *Pinus strobus* may explain the lack of significant differences in the percent coniferous component in the various vegetation layers. Pines are often allowed to stand when a lakeshore is developed, and young pines are often nurtured or planted when lake lots are landscaped (personal observation). *Pinus strobus*, for example, grew at similar numbers of developed and undeveloped (reference) upland transects (33% and 35%, respectively).

Because lakes with inorganic substrates are preferentially developed over those with peat or muck substrates (chi-square test for independence,  $p < 0.005$  for our sample sites), it is possible that the difference we found between undeveloped and developed (reference) sites in the amount of unvegetated shallow-water area (Table 1c) is influenced by substrate type. However, substrate alone does not explain this difference. We observed that people remove aquatic vegetation from their littoral areas in some cases, and approximately 30% of undeveloped aquatic transects (both organic and inorganic substrates) were largely ( $\geq 97\%$ ) unvegetated. Unmeasured confounding factors, such as degree of disturbance (e.g., fetch, wave action, amount of motorized traffic), likely contribute to the relationship between substrate type and percent unvegetated shallow water area (Hutchinson 1975, Keddy 1983, Asplund and Cook 1997). A study of these interacting factors would provide valuable information for the restoration of vegetation in shallow water areas.

**Ordination Differences.** Besides differences in structure, the developed and undeveloped (reference) sites also differ in species composition, as demonstrated by Detrended Correspondence Analysis (DCA). Upland and shoreline graphs show some overlap of developed and undeveloped transects, although developed transects tend to have higher axis 1 scores than undeveloped transects (Figures 2a and 2b). MRPP results in-

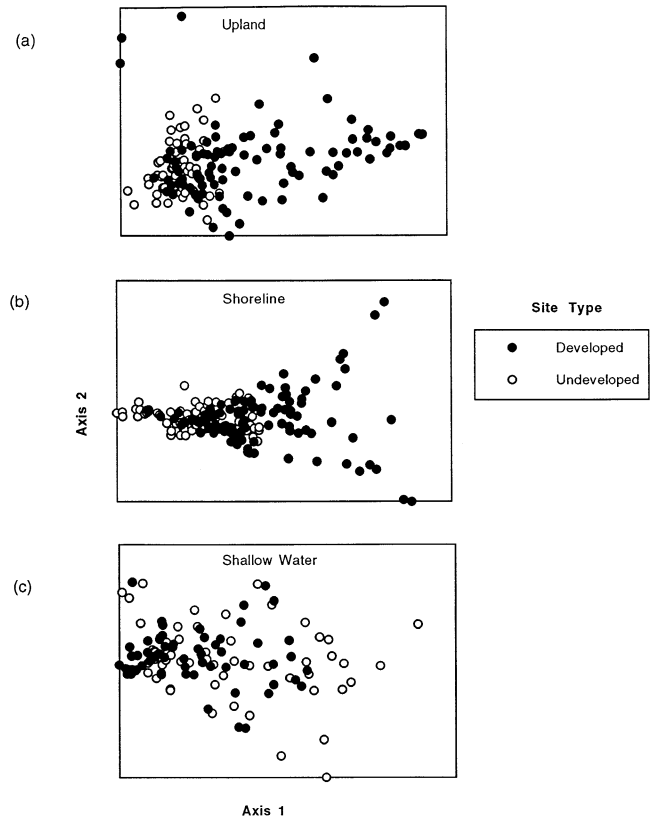


Figure 2. Detrended correspondence analysis, based on species composition at developed and undeveloped (reference) transects in the upland (a), along the shoreline (b), and in the shallow water (c), Vilas and Oneida Counties, Wisconsin, 1997.

dicate significant differences between the two types of transects at both upland and shoreline transects ( $p < 0.001$ ). These differences are due in large part to species diversity and presence or absence of exotic species. For example, *Hieracium* spp., *Oxalis stricta*, *Plantago major*, *Taraxacum officinalis*, and lawn grasses (all non-native species) dominate the undeveloped sites with high axis 1 scores. Developed sites with low axis 1 scores, overlapping with undeveloped sites, generally support some native ground flora, such as *Maianthemum canadense*, *Clintonia borealis*, *Cornus Canadensis*, *Trientalis borealis*, and additionally along the shoreline, *Iris versicolor* and *Carex* spp.

In the upland ordination (Figure 2a), axis 2 represents a moisture gradient. Moist sites hosting species such as *Coptis trifolium*, *Tsuga canadensis*, and *Dryopteris intermedia* have higher axis 2 scores; dry sites with species such as *Quercus rubra*, *Pinus resinosa*, and *Melampyrum lineare* have lower axis 2 scores.

Most of the sites in the shoreline ordination (Figure 2b) show little variation in axis 2 scores. The exceptions are sites dominated by a sandy beach (high axis

2 scores), with only a few small annual taxa such as *Polygonum* spp., and sites dominated by a retaining wall or rip-rap (low axis 2 scores), with a few taxa such as *Carex* spp., *Cicuta bulbifera*, and *Scutellaria galericulata* sprouting in the cracks of the wall and rip-rap.

An ordination of the shallow water transects shows more overlap of developed and undeveloped transects (Figure 2c) than the other two elevational zones, although the MRPP again distinguishes a significant difference ( $p < 0.001$ ). Sites with low axis 1 scores have sparse vegetation, while those with higher axis 1 scores are more heavily vegetated, especially with submerged (e.g., *Ceratophyllum demersum*, *Potamogeton* spp., and *Myriophyllum* spp.) and floating-leaved taxa (e.g., *Nuphar variegata*, *Nymphaea odorata*, and *Brasenia schreberi*). A large percent of the shallow water areas of both developed and undeveloped sites was unvegetated, contributing to the overlap of sites in Figure 2c.

Variety in the complexity of vegetation and number of native species exists among developed sites, resulting in the overlap observed in the Figure 2 ordinations. Developed sites vary from park-like, with a perfect lawn and only a few scattered trees (usually a flat site), to something approaching an undeveloped (reference) site (usually on a steep slope), with native trees, native and/or exotic shrubs, patches of native ground flora, and a small lawn area. Typically, however, developed sites consist of an extensive manicured lawn area with no coarse woody debris, scattered native trees, small patches of native and exotic shrubs near the property boundaries, and some native ground flora beneath the shrubs. The shoreline of a typical developed site is devoid of overhanging shrubs, except perhaps near the lot lines in order to afford an expansive view of the lake (Shifferd 1998), and contains a dock. The shallow water area surrounding the dock is usually denuded of vegetation and coarse woody debris. Aquatic vegetation may occur in the shallow water away from the swimming and boat launch areas. Undisturbed areas along the borders between lots existed in the study by Racey and Euler (1983) and persist today. The presence of native species at developed sites, even if only a few species in limited areas, contributed to the overlap of developed and undeveloped sites seen in Figure 2 ordinations.

#### Classification of Plant Communities at Undeveloped (Reference) Sites

In this descriptive portion of the study, we used Detrended Correspondence Analysis and two-way indicator species analysis to classify and describe plant communities. Results of these ordination techniques

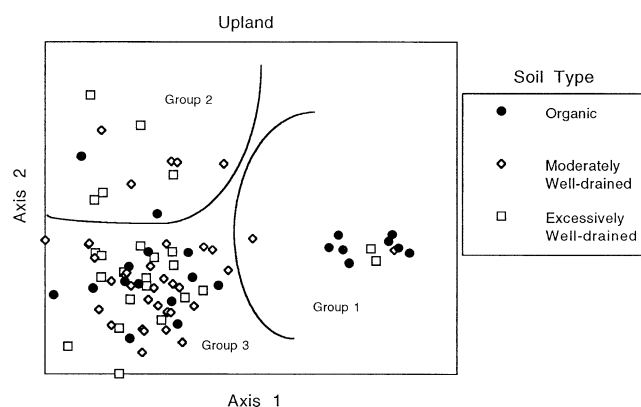


Figure 3. Detrended correspondence analysis of undeveloped (reference) upland transects with soils overlay, Vilas and Oneida Counties, Wisconsin, 1997. Groups are based on species composition; all species (158) are included in the analysis.

allow us to offer typical species for restoration of developed shorelands.

**Upland Ordination and Classification.** DCA ordination results of upland transects show three distinct clusters (Figure 3). TWINSPLAN classification shows that typical bog taxa, such as *Sphagnum* spp., *Picea mariana*, and several ericaceous shrubs, are associated with group 1 (Table 3). Group 2 transects are dominated by *Tsuga Canadensis*, *Abies balsamea*, and a rather sparse ground cover that includes *Lycopodium annotinum* and *Lycopodium clavatum* (Table 3). *Quercus rubra*, *Amelanchier* sp., *Aster macrophyllus*, and *Comptonia peregrina* are among the taxa dominating group 3 transects (Table 3).

Of the structural characteristics we estimated, percent cover and deciduous component in the canopy show the strongest correlations to axis 1 ( $r = -0.430$ ,  $r = -0.627$ , respectively). The deciduous component in the canopy is also weakly correlated with axis 2 ( $r = 0.269$ ). Percent deciduous component in the subcanopy is correlated negatively with axis 1 ( $r = -0.414$ ). Remaining structural characteristics showed weaker correlations to the axes. An overlay of soils information helps to explain the axes, with muck and peat soils largely to the right on axis 1 (overlying most of group 1 transects), and better-drained soils to the left on axis 1 (Figure 3). Excessively well-drained sand and loamy sand transects generally have lower axis 2 scores (overlying group 3 transects). Sites with moderately well-drained loam and sandy loam soils have scores spread across axis 2. Site aspect did not aid in axes explanations.

Different soil types generally support distinct plant communities (Curtis 1959, Donahue et al. 1977) largely explaining the three upland groups in Figure 3. These upland groupings are consistent with the North-



Table 3. Number of upland transects at which plant species were observed, Vilas and Oneida Counties, Wisconsin, 1997. Species in bold are affiliated with a site type (associated frequency also in bold) as identified through TWINSpan species preferentials. Species occurring less than 3 times, total, are excluded.

| Genus and Species                                | Number of Transects           |  |   | Total # Transects<br>N = 83 |
|--|-------------------------------|--|---|-----------------------------|
|  | Group 1:<br>Organic<br>N = 12 | Group 2:<br>Moderately<br>Well-Drained<br>N = 12 | Group 3:<br>Excessively<br>Well-Drained<br>N = 59 |                             |
| <i>Abies balsamea</i> (L.) Miller                | 1                             | <b>11</b>  | 20  | 32                          |
| <i>Acer rubrum</i> L.                            | 6                             | 5  | 44  | 55                          |
| <i>Alnus crispa</i> (Aiton) Pursh                | 0                             | 0  | 6   | 6                           |
| <i>Alnus rugosa</i> (DuRoi) Sprengel             | 1                             | 2  | 11  | 14                          |
| <b>Amelanchier species</b>                       | 0                             | 1  | <b>37</b>   | 38                          |
| <b>Andromeda glaucophylla</b> Link               | <b>4</b>                      | 0  | 0   | 4                           |
| <i>Apocynum androsaemifolium</i> L.              | 0                             | 0  | 7   | 7                           |
| <i>Aralia nudicaulis</i> L.                      | 0                             | 4  | 36  | 40                          |
| <b>Aster macrophyllus</b> L.                     | 0                             | 0  | <b>12</b>   | 12                          |
| <i>Betula papyrifera</i> Marsh.                  | 1                             | 7  | 24  | 32                          |
| <i>Calamagrostis canadensis</i> (Michaux) Beauv. | 0                             | 0  | 5   | 5                           |
| <b>Calla palustris</b> L.                        | <b>5</b>                      | 0  | 0   | 5                           |
| <b>Carex disperma</b> Dewey                      | <b>5</b>                      | 1  | 0   | 6                           |
| <b>Carex oligosperma</b> Michaux                 | <b>6</b>                      | 0  | 0   | 6                           |
| <i>Carex pedunculata</i> Willd.                  | 0                             | 2  | 6   | 8                           |
| <b>Carex pensylvanica</b> Lam.                   | 0                             | 1  | <b>24</b>   | 25                          |
| <i>Carex stricta</i> Lam.                        | 0                             | 0  | 4   | 4                           |
| <b>Carex trisperma</b> Dewey                     | <b>4</b>                      | 0  | 1   | 5                           |
| <b>Chamaedaphne calyculata</b> (L.) Moench       | <b>11</b>                     | 0  | 3   | 14                          |
| <i>Chimaphila umbellata</i> (L.) W.P.C. Barton   | 0                             | 0  | 6   | 6                           |
| <b>Clintonia borealis</b> (Aiton) Raf.           | 0                             | 1  | <b>14</b>   | 15                          |
| <b>Comptonia peregrina</b> (L.) Coulter          | 0                             | 0  | <b>13</b>   | 13                          |
| <b>Coptis trifolia</b> (L.) Salisb.              | 0                             | <b>3</b>   | 3   | 6                           |
| <i>Cornus canadensis</i> L.                      | 1                             | 3  | 23  | 27                          |
| <b>Corylus species</b>                           | 0                             | 0  | <b>37</b>   | 37                          |
| <i>Diervilla lonicera</i> Miller                 | 0                             | 0  | 7   | 7                           |
| <i>Dryopteris intermedia</i> (Muhl.) A. Gray     | 2                             | 1  | 2   | 5                           |
| <b>Dulichium arundinaceum</b> (L.) Britton       | <b>4</b>                      | 0  | 0   | 4                           |
| <i>Epigaea repens</i> L.                         | 0                             | 2  | 8   | 10                          |
| <b>Eriophorum angustifolium</b> Honck.           | <b>4</b>                      | 0  | 0   | 4                           |
| <i>Galium asprellum</i> Michaux                  | 0                             | 1  | 3   | 4                           |
| <b>Gaultheria hispidula</b> (L.) Bigelow         | <b>5</b>                      | 0  | 0   | 5                           |
| <i>Gaultheria procumbens</i> L.                  | 4                             | 4  | 35  | 43                          |
| <b>Glyceria canadensis</b> (Michaux) Trin.       | 3                             | 0  | 1   | 4                           |
| <i>Hieracium species</i>                         | 0                             | 2  | 5   | 7                           |
| <i>Ilex verticillata</i> (L.) A. Gray            | 1                             | 1  | 3   | 5                           |
| <b>Kalmia polifolia</b> Wangenh.                 | <b>6</b>                      | 0  | 0   | 6                           |
| <b>Larix laricina</b> (DuRoi) K. Koch            | <b>10</b>                     | 0  | 1   | 11                          |
| <b>Ledum groenlandicum</b> Oeder                 | <b>11</b>                     | 1  | 6   | 18                          |
| <i>Lonicera canadensis</i> Marshall              | 0                             | <b>3</b>   | 5   | 8                           |
| <b>Lycopodium annotinum</b> L.                   | 0                             | <b>4</b>   | 2   | 6                           |
| <b>Lycopodium clavatum</b> L.                    | 0                             | <b>4</b>   | 5   | 9                           |
| <i>Lycopodium obscurum</i> L.                    | 0                             | 2  | 11  | 13                          |
| <b>Lysimachia terrestris</b> (L.) BSP.           | <b>3</b>                      | 0  | 1   | 4                           |
| <i>Maianthemum canadense</i> Desf.               | 1                             | 11   | 47  | 59                          |
| <b>Melampyrum lineare</b> Desr.                  | 0                             | 0  | <b>18</b>   | 18                          |
| <i>Moneses uniflora</i> L.                       | 2                             | 1  | 1   | 4                           |
| <b>Moss species</b>                              | 0                             | <b>10</b>  | 15  | 25                          |
| <i>Myrica gale</i> L.                            | 2                             | 0  | 2   | 4                           |
| <b>Nemopanthus mucronatus</b> (L.) Loes.         | <b>4</b>                      | 0  | 3   | 7                           |

Table 3. Continued.

| Genus and Species                           | Number of Transects           |  |   | Total # Transects<br>N = 83 |
|---|-------------------------------|--|---|-----------------------------|
|   | Group 1:<br>Organic<br>N = 12 | Group 2:<br>Moderately<br>Well-Drained<br>N = 12 | Group 3:<br>Excessively<br>Well-Drained<br>N = 59 |                             |
| <i>Oryzopsis asperifolia</i> Michaux        | 0                             | 1  | 23  | 24                          |
| <i>Osmunda cinnamomea</i> L.                | 2                             | 0  | 4   | 6                           |
| <i>Picea mariana</i> (Miller) BSP.          | 11                            | 2  | 5   | 18                          |
| <i>Pinus resinosa</i> Aiton                 | 1                             | 5  | 28  | 34                          |
| <i>Pinus strobus</i> L.                     | 3                             | 10   | 40  | 53                          |
| Poaceae species                             | 0                             | 2  | 15  | 17                          |
| <i>Polygonatum pubescens</i> (Willd.) Pursh | 0                             | 0  | 5   | 5                           |
| <i>Pteridium aquilinum</i> (L.) Kuhn        | 0                             | 5  | 52  | 57                          |
| <i>Quercus rubra</i> L.                     | 2                             | 6  | 46  | 54                          |
| <i>Rubus</i> species                        | 0                             | 0  | 7   | 7                           |
| <i>Smilacina trifolia</i> (L.) Desf.        | 6                             | 0  | 0   | 6                           |
| <i>Sphagnum</i> species                     | 12                            | 0  | 1   | 13                          |
| <i>Trientalis borealis</i> Raf.             | 3                             | 6  | 45  | 54                          |
| <i>Tsuga canadensis</i> (L.) Carr.          | 0                             | 10   | 1   | 11                          |
| <i>Vaccinium angustifolium</i> Aiton        | 6                             | 0  | 40  | 46                          |
| <i>Vaccinium macrocarpon</i> Aiton          | 4                             | 0  | 0   | 4                           |
| <i>Vaccinium myrtilloides</i> Michaux       | 1                             | 4  | 15  | 20                          |
| <i>Vaccinium oxycoccos</i> L.               | 5                             | 0  | 0   | 5                           |
| <i>Viola</i> species                        | 0                             | 0  | 7   | 7                           |

ern Wet Forest (organic soil, Group 1), Northern Mesic Forest (moderately well-drained, Group 2) and Northern Xeric or Dry Mesic Forest (excessively well-drained, Group 3) of Curtis (1959).

*Shoreline Ordination and Classification.* Ordination results of shoreline transects are similar to those of the upland transects, although the groups are not as dis-

tinct (Figure 4). TWINSpan classification shows that typical bog taxa (e.g., *Sphagnum* spp., *Larix laricina*, *Picea mariana*, *Sarracenia purpurea* and ericaceous shrubs) again dominate shoreline group 1 transects (Table 4). These transects correspond to moss wetlands and/or forested wetlands, needle-leaved deciduous and needle-leaved evergreen, as classified by Cowardin et al. (1979). Taxa associated with shoreline group 2 transects include *Acer rubrum*, *Amelanchier* sp., *Maianthemum canadense*, and *Cornus canadensis* (Table 4). These transects generally supported upland vegetation to a bank above the water's edge, with only a narrow band of obligate wetland species and an abrupt transition to the aquatic habitat. Group 3 transects are typified by *Juncus effuses*, *Carex stricta*, and *Calamagrostis canadensis* (Table 4). This type of transect had a gradual transition to the aquatic zone, with characteristics of one or more wetland type (e.g., palustrine emergent wetland, nonpersistent; scrub-shrub wetland, broad-leaved deciduous; Cowardin et al. 1979).

TWINSpan lists of non-preferentials at shoreline transects reveal much species overlap among groups (Table 4). Along the water/land interface, the vegetation is often similar across soil types, probably due to the over-riding influence of water-table proximity and the increased light availability from the open canopy

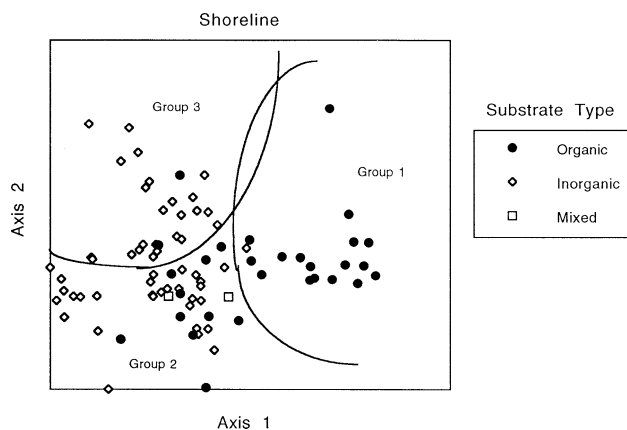


Figure 4. Detrended correspondence analysis of undeveloped (reference) shoreline transects with shallow water substrate overlay, Vilas and Oneida Counties, Wisconsin, 1997. Groups are based on species composition; all species (183) are included in the analysis.

Table 4. Number of shoreline transects at which plant species were observed, Vilas and Oneida Counties, Wisconsin, 1997. Species in bold are affiliated with a site type (associated frequency also bold) as identified through TWINSPAN species preferentials. Species occurring less than 3 times, total, are excluded.

| Genus and Species                                       | Number of Transects                |   |  | Total # Transects<br>N = 85 |
|---|------------------------------------|---|--|-----------------------------|
|   | Group 1:<br>Sphagnum Bog<br>N = 17 | Group 2:<br>Abrupt Transition<br>N = 43 | Group 3:<br>Gradual Transition<br>N = 25 |                             |
| <i>Abies balsamea</i> (L.) Miller                       | 0                                  | 5                                       | 0  | 5                           |
| <b><i>Acer rubrum</i> L.</b>                            | 11                                 | <b>33</b>                               | 13                                       | 57                          |
| <i>Agrostis hyemalis</i> (Walter) BSP.                  | 0                                  | 4                                       | 1  | 5                           |
| <i>Agrostis</i> species                                 | 0                                  | 3                                       | 1  | 4                           |
| <i>Alnus rugosa</i> (DuRoi) Sprengel                    | 1                                  | 30                                      | 18                                       | 49                          |
| <b><i>Amelanchier</i> species</b>                       | 3                                  | <b>19</b>                               | 3  | 25                          |
| <b><i>Andromeda glaucophylla</i> Link</b>               | <b>8</b>                           | 0                                       | 1  | 9                           |
| <i>Aralia nudicaulis</i> L.                             | 1                                  | 9                                       | 3  | 13                          |
| <b><i>Aronia prunifolia</i> (Marsh.) Rehder</b>         | <b>6</b>                           | 3                                       | 2  | 11                          |
| <i>Betula alleghaniensis</i> Britton                    | <b>5</b>                           | 3                                       | 4  | 12                          |
| <b><i>Betula papyrifera</i> Marsh.</b>                  | 1                                  | <b>23</b>                               | 4  | 28                          |
| <i>Bidens comosus</i> (A. Gray) Wiegand                 | 1                                  | 6                                       | 2  | 9                           |
| <i>Brasenia schreberi</i> J.F. Gmelin                   | 3                                  | 1                                       | 0  | 4                           |
| <b><i>Calamagrostis canadensis</i> (Michaux) Beauv.</b> | 1                                  | 14                                      | <b>15</b>                                | 30                          |
| <i>Calla palustris</i> L.                               | 7                                  | 14                                      | 7  | 28                          |
| <i>Callitriche</i> species                              | 0                                  | 1                                       | 3  | 4                           |
| <i>Carex brunnescens</i> (Pers.) Poiret                 | 2                                  | 5                                       | 2  | 9                           |
| <i>Carex comosa</i> Boott                               | 0                                  | 2                                       | 2  | 4                           |
| <b><i>Carex crinita</i> Lam.</b>                        | 1                                  | <b>16</b>                               | 2  | 19                          |
| <b><i>Carex disperma</i> Dewey</b>                      | 2                                  | <b>11</b>                               | 1  | 14                          |
| <i>Carex interior</i> Bailey                            | 3                                  | 7                                       | 5  | 15                          |
| <i>Carex lasiocarpa</i> Ehrh.                           | 1                                  | 0                                       | 4  | 5                           |
| <b><i>Carex limosa</i> L.</b>                           | <b>4</b>                           | 0                                       | 0  | 4                           |
| <b><i>Carex ovales</i> group</b>                        | 0                                  | 3                                       | <b>5</b>                                 | 8                           |
| <b><i>Carex stricta</i> Lam.</b>                        | 3                                  | 10                                      | <b>19</b>                                | 32                          |
| <b><i>Carex trisperma</i> Dewey</b>                     | <b>4</b>                           | 0                                       | 0  | 4                           |
| <b><i>Chamaedaphne calyculata</i> (L.) Moench</b>       | <b>16</b>                          | 24                                      | 18                                       | 58                          |
| <i>Cicuta bulbifera</i> L.                              | 5                                  | 25                                      | 16                                       | 46                          |
| <i>Clintonia borealis</i> (Aiton) Raf.                  | 0                                  | 8                                       | 0  | 8                           |
| <i>Comptonia peregrina</i> (L.) Coulter                 | 0                                  | 3                                       | 2  | 5                           |
| <i>Coptis trifolia</i> (L.) Salisb.                     | 1                                  | 3                                       | 0  | 4                           |
| <b><i>Cornus canadensis</i> L.</b>                      | 0                                  | <b>9</b>                                | 1  | 10                          |
| <i>Corylus</i> species                                  | 0                                  | 4                                       | 1  | 5                           |
| <i>Diervilla lonicera</i> Miller                        | 0                                  | 3                                       | 1  | 4                           |
| <b><i>Drosera rotundifolia</i> L.</b>                   | <b>7</b>                           | 2                                       | 1  | 10                          |
| <b><i>Dryopteris intermedia</i> (Muhl.) A. Gray</b>     | 0                                  | 5                                       | <b>6</b>                                 | 11                          |
| <i>Dulichium arundinaceum</i> (L.) Britton              | 9                                  | 12                                      | 10                                       | 31                          |
| <i>Epigaea repens</i> L.                                | 0                                  | 4                                       | 0  | 4                           |
| <b><i>Eriocaulon septangulare</i> With.</b>             | <b>5</b>                           | 0                                       | 0  | 5                           |
| <b><i>Eriphorum angustifolium</i> Honck.</b>            | <b>6</b>                           | 0                                       | 0  | 6                           |
| <b><i>Galium</i> species</b>                            | 2                                  | 2                                       | <b>5</b>                                 | 9                           |
| <i>Galium trifidum</i> L.                               | 1                                  | 4                                       | 2  | 7                           |
| <i>Gaultheria procumbens</i> L.                         | 1                                  | 7                                       | 4  | 12                          |
| <b><i>Glyceria canadensis</i> (Michaux) Trin.</b>       | <b>7</b>                           | 10                                      | 4  | 21                          |
| <i>Glyceria striata</i> (Lam.) Hitchc.                  | 0                                  | 3                                       | 1  | 4                           |
| <i>Ilex verticillata</i> (L.) A. Gray                   | 4                                  | 14                                      | 5  | 23                          |
| <i>Impatiens capensis</i> Meerb.                        | 1                                  | 19                                      | 11                                       | 31                          |
| <i>Iris versicolor</i> L.                               | 3                                  | 17                                      | 9  | 29                          |
| <b><i>Juncus effusus</i> L.</b>                         | 3                                  | 10                                      | <b>13</b>                                | 26                          |
| <b><i>Kalmia polifolia</i> Wangenh.</b>                 | <b>6</b>                           | 0                                       | 0  | 6                           |
| <b><i>Larix laricina</i> (DuRoi) K. Koch</b>            | <b>8</b>                           | 1                                       | 2  | 11                          |

Table 4. Continued.

| Genus and Species                        | Number of Transects                |   |  | Total # Transects<br>N = 85 |
|--|------------------------------------|---|--|-----------------------------|
|  | Group 1:<br>Sphagnum Bog<br>N = 17 | Group 2:<br>Abrupt Transition<br>N = 43 | Group 3:<br>Gradual Transition<br>N = 25 |                             |
| <i>Ledum groenlandicum</i> Oeder         | <b>12</b>                          | <b>13</b>                               | 1  | 26                          |
| <i>Lycopodium clavatum</i> L.            | 1                                  | 2                                       | 1  | 4                           |
| <i>Lycopus uniflorus</i> Michaux         | 14                                 | 32                                      | 18                                       | 64                          |
| <i>Lysimachia terrestris</i> (L.) BSP.   | 8                                  | 15                                      | 7  | 30                          |
| <i>Lysimachia thyrsiflora</i> L.         | 0                                  | 9                                       | <b>11</b>                                | 20                          |
| <i>Maianthemum canadense</i> Desf.       | 1                                  | <b>17</b>                               | 4  | 22                          |
| Moss species                             | 0                                  | 19                                      | 6  | 25                          |
| <i>Myrica gale</i> L.                    | <b>9</b>                           | 9                                       | 3  | 21                          |
| <i>Nemopanthus mucronatus</i> (L.) Loes. | 8                                  | <b>23</b>                               | 6  | 37                          |
| <i>Nuphar variegata</i> Durand           | <b>4</b>                           | 0                                       | 1  | 5                           |
| <i>Nymphaea odorata</i> Aiton            | <b>4</b>                           | 1                                       | 0  | 5                           |
| <i>Onoclea sensibilis</i> L.             | 0                                  | 2                                       | 4  | 6                           |
| <i>Osmunda cinnamomea</i> L.             | 1                                  | <b>11</b>                               | 2  | 14                          |
| <i>Phalaris arundinacea</i> L.           | 0                                  | 4                                       | 1  | 5                           |
| <i>Picea mariana</i> (Miller) BSP.       | <b>12</b>                          | 7                                       | 1  | 20                          |
| <i>Pinus resinosa</i> Aiton              | 0                                  | <b>20</b>                               | 1  | 21                          |
| <i>Pinus strobus</i> L.                  | 2                                  | <b>21</b>                               | 5  | 28                          |
| <i>Poa</i> species                       | 0                                  | 4                                       | 1  | 5                           |
| Poaceae species                          | 0                                  | 1                                       | 3  | 4                           |
| <i>Potentilla norvegica</i> L.           | 0                                  | 4                                       | 3  | 7                           |
| <i>Potentilla palustris</i> (L.) Scop.   | 1                                  | 0                                       | <b>6</b>                                 | 7                           |
| <i>Pteridium aquilinum</i> (L.) Kuhn     | 0                                  | 9                                       | 4  | 13                          |
| <i>Quercus rubra</i> L.                  | 1                                  | <b>27</b>                               | 6  | 34                          |
| <i>Rubus strigosus</i> Michaux           | 0                                  | 3                                       | 1  | 4                           |
| <i>Rubus</i> species                     | 4                                  | 4                                       | <b>6</b>                                 | 14                          |
| <i>Sarracenia purpurea</i> L.            | <b>4</b>                           | 0                                       | 0  | 4                           |
| <i>Scirpus cyperinus</i> (L.) Junth      | 1                                  | <b>12</b>                               | 2  | 15                          |
| <i>Scutellaria galericulata</i> L.       | 0                                  | 11                                      | 5  | 16                          |
| <i>Scutellaria lateriflora</i> L.        | 0                                  | 4                                       | 1  | 5                           |
| <i>Sphagnum</i> species                  | <b>16</b>                          | <b>12</b>                               | 0  | 28                          |
| <i>Spiraea</i> species                   | 6                                  | 15                                      | 16                                       | 37                          |
| <i>Triadenum fraseri</i> (Spach) GI.     | <b>9</b>                           | 5                                       | <b>9</b>                                 | 23                          |
| <i>Trientalis borealis</i> Raf.          | 3                                  | 9                                       | 5  | 17                          |
| <i>Tsuga canadensis</i> (L.) Carr.       | 1                                  | 7                                       | 0  | 8                           |
| <i>Utricularia vulgaris</i> L.           | 0                                  | 4                                       | 2  | 6                           |
| <i>Vaccinium angustifolium</i> Aiton     | 2                                  | <b>18</b>                               | 3  | 23                          |
| <i>Vaccinium macrocarpon</i> Aiton       | <b>6</b>                           | 0                                       | 0  | 6                           |
| <i>Vaccinium myrtilloides</i> Michaux    | 1                                  | 10                                      | 4  | 15                          |
| <i>Vaccinium oxycoccus</i> L.            | <b>4</b>                           | 0                                       | 0  | 4                           |
| <i>Viola</i> species                     | 1                                  | 2                                       | <b>9</b>                                 | 12                          |

over the lake. A complicated interaction among soil type, bank height, depth to saturated conditions, prevailing winds, and aspect probably exists along the shoreline.

Overlays of soil (terrestrial, not shown) and substrate (aquatic) types help to explain the axes (Figure 4). Transects with an organic shallow water substrate and organic terrestrial soils dominate group 1, with high axis 1 scores. Transects in groups 2 and 3, with low axis 1 scores, contain a mix of substrates and soils.

The percent of shoreline overhung by trees is negatively correlated with both axes ( $r = -0.311$  and  $r = -0.387$ ; axes 1 and 2, respectively); percent of shoreline overhung by shrubs is weakly correlated with axis 1 ( $r = 0.283$ ). Bank height and aspect do not add to our understanding.

*Shallow Water Ordination and Classification.* Ordination results of shallow water transects show a cluster in the middle, with three endpoints (Figure 5). TWIN-

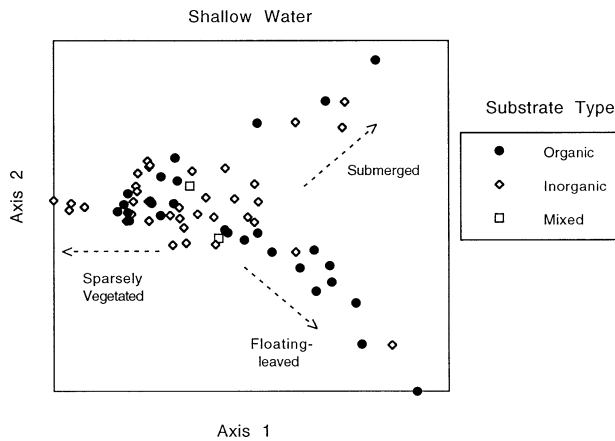


Figure 5. Detrended correspondence analysis of undeveloped (reference) shallow water transects with substrate overlay, Vilas and Oneida Counties, Wisconsin, 1997, based on species composition. All (55) species are included in the analysis.

SPAN classification reveals a great degree of overlap among groups. However, correlations of plant growth form with axes were strong in the cases of floating-leaved and submerged species. Floating-leaved species such as *Brasenia schreberi*, *Nuphar variegata*, and *Nymphaea odorata* dominate transects with high axis 1 scores and low axis 2 scores ( $r = 0.692$  and  $r = -0.657$ , respectively). Submerged taxa (e.g., *Elodea Canadensis*, *Najas flexilis*, *Ceratophyllum demersum*, *Potamogeton* spp., *Myriophyllum* spp.) dominate transects with high scores for both axes 1 and 2 ( $r = 0.371$ ,  $r = 0.441$ ; respectively). These transects contained large logs anchored to the bottom in protected bays, forming a microhabitat. Additional taxa growing on these logs or in the surrounding protected water include *Andromeda glaucophylla*, *Calla palustris*, *Chamaedaphne calyculata*, *Eriocaulon septangulare*, *Isoetes* sp., and *Myrica gale*. Transects with low axis 1 scores are largely unvegetated, hosting only a sparse cover of *Lobelia dortmanna*, *Ceratophyllum demersum*, *Potamogeton zosteriformis*, or *Vallisneria spiralis*. We do not provide a table of affiliated plant species for the shallow water ordinations because of the high degree of overlap among groups, but we list all shallow water species, by substrate type, in Table 5.

Substrate type does not contribute to an understanding of the axes, as sites with organic and inorganic substrates are dispersed throughout the ordination (Figure 5). Plant communities in shallow water areas may be less dependent on substrate characteristics than either upland or shoreline transects. Mean water depth is also not correlated with either axis. Disturbance factors contribute to our understanding of the shallow water ordination, with transects dominated by floating-

leaved species occurring in calm bays, transects behind anchored logs supporting submerged species, and transects along higher energy shorelines hosting only sparse vegetation. It is likely that disturbance factors override other environmental variables regarding establishment and persistence of macrophytes (Sculthorpe 1967).

The environmental factors we measured do not explain the differences in species composition among shallow water transects. Aquatic species composition is often related to interactions among water depth, substrate type, water chemistry, and availability of light and nutrients (Sculthorpe 1967, Spence 1982, Chambers 1987, Neill 1990). Degree of disturbance is undoubtedly a factor, affecting not only the presence or absence of aquatic vegetation, but also the species composition (Sculthorpe 1967, Wilcox and Meeker 1991, Wilcox et al. 1992). Well-established, well-anchored species are more likely to withstand disturbances than young or shallow-rooted species. Additionally, those plants able to withstand disturbances provide protection in the form of wave attenuation to other nearby plants. Future studies that analyze the interacting effects of environmental conditions, degree of disturbance, and community composition will benefit littoral restoration efforts.

#### Recommendations for Restoration of Shorelands

Our results enable us to make recommendations for restoration of lakeshores within our study area. In general, we recommend 1) increasing the amount of cover in the canopy, subcanopy, and especially the understory, or shrub, layers; 2) increasing the amount the shoreline frontage overhung by trees and (especially) shrubs; 3) increasing the amount of coarse woody debris in the terrestrial buffer zone, along the shoreline, and in the shallow water area; and 4) converting portions of mowed lawn to native plant species. It is important to use native species appropriate for the site conditions in all restoration attempts.

The amount of coarse woody debris (CWD) is directly related to the riparian vegetation Christensen et al. (1996). While planting trees and shrubs in the terrestrial buffer zone will increase the amount of cover in the various forest layers and eventually provide CWD (through maturity, decline, and fall of trees), without active input of CWD restoration of this important component of lakeshore ecosystems could take centuries (Christensen et al. 1996). Therefore, we advocate the active input of CWD. We advise consulting local zoning ordinances prior to adding CWD to the shallow water area, as in some regions it is necessary to acquire a permit. Addition of CWD to terrestrial habitats is at the discretion of the landowner.

Table 5. Number of shallow water transects at which plant species were observed, by substrate type, Vilas and Oneida Counties, Wisconsin, 1997. All species are included.

| Genus and Species                                | Number of Transects           |                            |                                 | Total # Transects<br>N = 84 |
|--|-------------------------------|----------------------------|---------------------------------|-----------------------------|
|  | Group 1:<br>Organic<br>N = 29 | Group 2:<br>Mixed<br>N = 2 | Group 3:<br>Inorganic<br>N = 53 |                             |
| <i>Andromeda glaucophylla</i> Link               | 1                             | 0                          | 1                               | 2                           |
| <i>Brasenia schreberi</i> J.F. Gmelin            | 11                            | 0                          | 13                              | 24                          |
| <i>Calamagrostis canadensis</i> (Michaux) Beauv. | 0                             | 0                          | 1                               | 1                           |
| <i>Calla palustris</i> L.                        | 0                             | 0                          | 2                               | 2                           |
| <i>Carex comosa</i> Boott                        | 0                             | 0                          | 1                               | 1                           |
| <i>Ceratophyllum demersum</i> L.                 | 1                             | 0                          | 2                               | 3                           |
| <i>Chamaedaphne calyculata</i> (L.) Moench       | 3                             | 0                          | 4                               | 7                           |
| <i>Chara</i> species                             | 0                             | 0                          | 1                               | 1                           |
| <i>Decodon verticillatus</i> (L.) Ell.           | 0                             | 0                          | 1                               | 1                           |
| <i>Dulichium arundinaceum</i> (L.) Britton       | 4                             | 1                          | 7                               | 12                          |
| <i>Eleocharis smallii</i> Britton                | 1                             | 0                          | 1                               | 2                           |
| <i>Eleocharis</i> species                        | 0                             | 0                          | 4                               | 4                           |
| <i>Elodea canadensis</i> Michaux                 | 2                             | 0                          | 7                               | 9                           |
| <i>Eriocaulon septangulare</i> With.             | 8                             | 0                          | 7                               | 15                          |
| <i>Isoetes</i> species                           | 3                             | 1                          | 13                              | 17                          |
| <i>Juncus effusus</i> L.                         | 0                             | 0                          | 1                               | 1                           |
| <i>Larix laricina</i> (DuRoi) K. Koch            | 1                             | 0                          | 0                               | 1                           |
| <i>Ledum groenlandicum</i> Oeder                 | 2                             | 0                          | 0                               | 2                           |
| <i>Lemna minor</i> L.                            | 1                             | 0                          | 0                               | 1                           |
| <i>Lemna trisulca</i> L.                         | 0                             | 0                          | 1                               | 1                           |
| Liverwort species                                | 0                             | 0                          | 1                               | 1                           |
| <i>Lobelia dortmanna</i> L.                      | 2                             | 0                          | 8                               | 10                          |
| <i>Megalodonta beckii</i> (Sprengel) Greene      | 0                             | 0                          | 1                               | 1                           |
| <i>Myrica gale</i> L.                            | 3                             | 0                          | 3                               | 6                           |
| <i>Myriophyllum</i> species                      | 1                             | 0                          | 6                               | 7                           |
| <i>Najas flexilis</i> (Willd.) Rostk. & Schmidt  | 1                             | 0                          | 7                               | 8                           |
| <i>Nuphar variegata</i> Durand                   | 16                            | 1                          | 12                              | 29                          |
| <i>Nymphaea odorata</i> Aiton                    | 14                            | 1                          | 12                              | 27                          |
| <i>Pontederia cordata</i> L.                     | 9                             | 0                          | 8                               | 17                          |
| <i>Potamogeton amplifolius</i> Tuckerman         | 1                             | 0                          | 2                               | 3                           |
| <i>Potamogeton confervoides</i> Reichenb.        | 1                             | 1                          | 0                               | 2                           |
| <i>Potamogeton epihydrus</i> Raf.                | 3                             | 0                          | 0                               | 3                           |
| <i>Potamogeton foliosus</i> Raf.                 | 0                             | 0                          | 4                               | 4                           |
| <i>Potamogeton natans</i> L.                     | 2                             | 0                          | 1                               | 3                           |
| <i>Potamogeton oakesianus</i> Robbins            | 1                             | 0                          | 0                               | 1                           |
| <i>Potamogeton richardsonii</i> (Benn.) Rydb.    | 1                             | 0                          | 3                               | 4                           |
| <i>Potamogeton robbinsii</i> Oakes               | 0                             | 0                          | 3                               | 3                           |
| <i>Potamogeton</i> species                       | 1                             | 0                          | 0                               | 1                           |
| <i>Potamogeton zosteriformis</i> Fern.           | 0                             | 0                          | 5                               | 5                           |
| <i>Potentilla palustris</i> (L.) Scop.           | 0                             | 0                          | 2                               | 2                           |
| <i>Sagittaria graminea</i> Michaux               | 3                             | 0                          | 3                               | 6                           |
| <i>Sagittaria latifolia</i> Willd.               | 0                             | 0                          | 1                               | 1                           |
| <i>Sagittaria rigida</i> Michaux                 | 1                             | 0                          | 1                               | 2                           |
| <i>Scirpus americanus</i> Pers.                  | 0                             | 0                          | 1                               | 1                           |
| <i>Scirpus subterminalis</i> Torrey              | 6                             | 2                          | 5                               | 13                          |
| <i>Scirpus validus</i> Vahl                      | 0                             | 0                          | 2                               | 2                           |
| <i>Sparganium eurycarpum</i> Engelm.             | 0                             | 0                          | 2                               | 2                           |
| <i>Sparganium fluctuans</i> (Morong) Robinson    | 4                             | 0                          | 2                               | 6                           |
| <i>Sparganium minimum</i> (Hartman) Fries        | 1                             | 0                          | 4                               | 5                           |
| <i>Spiraea</i> species                           | 1                             | 0                          | 0                               | 1                           |
| <i>Utricularia purpurea</i> Walter               | 3                             | 1                          | 3                               | 7                           |
| <i>Utricularia vulgaris</i> L.                   | 2                             | 0                          | 6                               | 8                           |
| <i>Vaccinium oxycoccus</i> L.                    | 0                             | 0                          | 1                               | 1                           |
| <i>Vallisneria americana</i> Michaux             | 0                             | 0                          | 5                               | 5                           |

Our main purpose in providing Tables 3 and 4 is to list plant species appropriate for use in restoration efforts of upland and shoreline areas within our study area. We list species affiliated with the different site types (defining upland types largely by soil characteristics and shoreline types by the descriptors Sphagnum bog, abrupt transition, and gradual transition, as detailed above), as well as species common across site types. Using Table 3 as an example, restoration of the upland area of a site with moderately well-drained soil could include planting *Abies balsamea*, *Tsuga Canadensis*, *Lonicera Canadensis*, *Lycopodium annotinum*, *Lycopodium clavatum*, affiliated with site type; *Betula papyrifera*, *Maianthemum canadense*, *Pinus strobus*, and *Trientalis borealis*, common at both moderately and excessively well-drained site types; and *Quercus rubra*, affiliated with excessively well-drained sites, but common at moderately well-drained sites. (For this example we considered a species common if it occurred at 50% or more of the moderately well-drained sites. Expansion of the 'common' category would, of course, allow inclusion of additional species.) To encourage a rich assemblage of native species in restoration efforts, we recommend planting species that are common across site types along with species affiliated with a particular site type.

When restoring shallow water areas, we concur with the suggestions of Henderson et al. (1999) to choose species found in other parts of the same lake or in nearby lakes. In many situations, aquatic plants may require protection from disturbance in order to become established. Consult zoning ordinances prior to planting aquatic species, as well as prior to placing wave barriers, as in some regions, any modifications occurring below the ordinary high water mark require a permit.

Specific guidelines on how to restore shorelands, such as passive vs. active techniques, safe removal of non-native species, and spacing of plantings, are becoming increasingly available (e.g., UWEX website, Henderson et al. 1999). While we support the currently available guidelines, we recognize that rigorous testing of different techniques under various conditions has not yet occurred. As the science of shoreland restoration matures, undoubtedly guidelines will change and become more specific.

### SUMMARY

Our study shows that the structural characteristics of vegetation are greatly altered when shorelands are developed. The understory, or shrub layer, and coarse woody debris are the features most impacted, being virtually eliminated. Species composition is also altered, although the modified Daubenmire method of

estimating cover classes minimized the differences between developed and undeveloped (reference) sites. Our data not only facilitate comparisons between developed and reference conditions, but also suggest goals towards which to strive in a restoration effort.

We explained variation in plant communities using ordination techniques in order to determine the types of sites in the study area and the plant species appropriate for restoration efforts. We identified three main types of upland and shoreline sites. While common species occurred across these site types, fairly distinct plant communities existed. In the shallow water area, much greater overlap of species occurred across sites. Unmeasured and complex interacting factors probably exist in this area. Future studies that focus on some of these interacting factors (bank height, wave action, substrate type, prevailing winds, etc.) will benefit our understanding of shoreland restoration needs, successes, and failures.

Surveys of lakeshore reference sites in adjacent physiographic land types demonstrate that even within relatively small geographic regions (i.e., several counties within a state), the type of sites and their associated plant communities may vary by land type (Elias, unpublished). Therefore, it is important to repeat a process similar to ours across land types prior to restoration efforts, rather than to extrapolate results from a limited area across a large region.

Tables 3 and 4 are useful not only because they indicate species affiliated with each type of site within our study area, but also because they list those species that are common across site types. We recommend using both affiliated and common species for restoration efforts.

With the current level of interest in shoreland restoration, it is important to provide agency personnel and lakeshore property owners with the information they need. Documenting the degree of change in structural characteristics demonstrates the need for restoration, while describing plant communities at reference locations provides data on native species appropriate for restoration efforts.

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