WETLANDS, Vol. 27, No. 1, March 2007, pp. 12–23

LANDSCAPE VARIATION OF SEASONAL POOL PLANT COMMUNITIES IN FORESTS OF NORTHERN MINNESOTA, USA

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Abstract: Seasonal forest pools are abundant in the northern Great Lakes forest landscape, but the range of variation in their plant communities and the relationship of this variation to multi-scale landscape features remains poorly quantified. We examined seasonal pools in forests of northern Minnesota USA with the objective of quantifying the range of variation in plant communities within and among different geomorphic and forest settings. Abundances of plant functional groups were highly variable among pools, ranging from those having abundant upland trees, sedges, and perennial forbs to those having abundant wetland sedges, grasses, and forbs. Glacial landform and ecological landtype (local forest and soil type) explained little of this variation, while physical characteristics of the pools (primarily duration of flooding) explained 36% of the variation. Understanding landscape variation in seasonal pool plant communities is important for their conservation and management. If range of variation is understood, representative examples of all variants of pool systems can be identified for conservation, and management prescriptions can be tailored to different landscape settings.

Key Words: seasonal ponds, vernal pools, wetland plants

INTRODUCTION

Ecologists and natural resource managers are paying increased attention to seasonal forest pools (Tiner 2003, Zedler 2003). Their interest stems in part from a growing recognition of the abundance of seasonal pools in many North American forests (Gibbs 1993, Brooks et al. 1998, Palik et al. 2003, Tiner 2003) and from the importance of seasonal pools as amphibian and invertebrate breeding habitat (Brooks 2000, DeGraaf and Yamasaki 2001, Batzer et al. 2004).

Less attention has been given to characterizing plant communities of seasonal forest pools. One reason is that there probably are few, if any, obligate seasonal forest pool plant species (Cutko 1997). Moreover, the value of pools as invertebrate and amphibian breeding habitat may not depend on the specific characteristics of plant communities (Calhoun et al. 2003, Batzer et al. 2004).

While this may be true, there is still value in understanding and characterizing seasonal forest pools from an ecosystem perspective (*sensu* Barnes et al. 1982), that is, as discrete assemblages of plant species that develop in response to an underlying physical template. Whether they support obligate plant species or not, seasonal forest pools make unique contributions to ecosystem diversity at landscape and regional scales. Understanding the range of variation in plant communities of seasonal forest pools, as related to the underlying physical template, is needed if the range of seasonal pool ecosystems is to be identified and conserved. We are aware of few attempts to develop such a characterization of seasonal forest pool plant communities (Calhoun et al. 2003; Vermont Department of Environmental Conservation 2003), and no such studies in the northern Lake States region.

In this study, we quantify the range of variation in plant communities of seasonal pools in a north temperate forest landscape in Minnesota, and we relate this variation to multi-scale, pool-to-landscape factors, including surficial geology, surrounding forest and soil characteristics, and pool hydrology and water chemistry. Specifically, we hypothesized that these factors would explain significant amounts of variation in seasonal pool plant communities.

We addressed our objectives and hypothesis by examining seasonal pools located in the forests of northern Minnesota. We selected the pools using a stratified approach based on differences in the identity of multi-scale upland forest ecosystems in which they occurred. Over the last several years, these pools have been the focus of ongoing research on landscape distribution (Palik et al. 2003), forest management impacts (Palik et al. 2001), invertebrate communities (Batzer et al. 2004), and organic matter flux from upland forests (Palik et al. 2006).

Table 1. Hierarchical structure of matrix ecosystems for two study areas in northern Minnesota.

Study Area	Glacial Landform	Landtype	Pools Sampled
Sucker Lakes	Outwash Plain	**LT 1**: jack and red pine on excessively drained sandy soils	5
		LT 2: mixed pine/deciduous trees on well to moderately well drained, loamy till and fine textured soils	4
		LT 3: boreal hardwood-conifers on moderately well to somewhat poorly drained loamy to fine textured soils	3
	Ground Moraine	**LT 2**: as above	6
		LT 3: as above	5
		LT 4: northern hardwoods on well to moderately well drained loamy to fine textured soils	11
		LT 5: northern hardwood-conifers on moderately well to somewhat poorly drained loamy to fine textured soils	5
Rice River	End Moraine	**LT 1**: as above	5
		LT 2: as above	10
		LT 4: as above	5
		LT 5: as above	5

METHODS

Seasonal Forest Pool Definition

Our use of the term seasonal forest pool is inclusive of vernal pools, defined by Zedler (2003) as small ephemeral wetlands that form reliably, and dry reliably, during the growing season throughout a large portion of their basin. However, we had no *a priori* expectations regarding duration of flooding of the sample pools. In fact, our sampled pools had wide variation in hydroperiod including autumnal and semipermanent; thus, we prefer the modifier seasonal as opposed to vernal. The study pools also largely conform to the definition of a seasonal wetland *sensu* Cowardin et al. (1979), as palustrine, forested, shrub-scrub, or emergent wetlands having a semipermanent or seasonally flooded water regime and a mineral soil substrate. Under this definition, the water regime does not necessarily include a dry period, but water levels experience considerable seasonal fluctuation. Finally, all of our sampled pools occurred in upland forest. We did not include open-water pools occurring within larger wetlands or on floodplains, as some other studies have done (Calhoun et al. 2003).

Study Area

We conducted our study in the Chippewa National Forest in northern Minnesota within the Sucker Lakes and Rice River watersheds. The USDA Forest Service has mapped ecological units at various spatial scales within the study area (Chippewa National Forest 1996), using the hierarchical framework suggested by ECOMAP (1993). The study area falls within the Northern Minnesota Drift and Lake Plains Section (Keys et al. 1995) and includes different landtype associations and landtypes (Table 1). In the classification, landtype association (LTA) corresponds to the predominant glacial landform, while landtype (LT) corresponds to a combination of soil characteristics and dominant vegetation, for example, xeric pine or mesic northern hardwoods (Almendinger et al. 2000).

Seasonal Pool Identification

We used 1:12,000 color infrared aerial photographs to identify seasonal pools in the study area. The photos were taken in the spring of 1994 after snowmelt, but before leaf-flush. In these photos, the bodies of water are black and an experienced interpreter can easily identify small wetlands, although this is more difficult in conifer-dominated or mixed conifer-deciduous forest (Burne 2001, Calhoun et al. 2003). As part of a related study (Palik et al. 2003), we field-checked 10% of the pools, selecting samples for verification from across the two study areas. From this sample, we estimated our error of commission (classifying something as a pool when it was not one) at 20%. Misidentified samples were largely anthropogenic openings, such as old log landings or trail intersections, where water pooled on compacted soil in the spring. Through the course of searching for sample pools during the field check, we encountered very few additional pools (within our size range of interest, see following section) that we had not identified with aerial photography. We estimate our error of omission at less than 10%. In total, we identified 2,064 seasonal pools in 24,622 ha of upland forest in the combined study areas.

Seasonal Pool Selection

We selected pools from the population in the study area based on the following criteria: 1) the surrounding forest was at least 50 years old (ranged up to 108 years); 2) pools and the surrounding forest showed no evidence of recent disturbance; 3) pool basin area was at least 0.02 ha, but less than 0.5 ha; and 4) pools had mineral soil substrates, as opposed to peat.

Our interest was in characterizing relatively undisturbed pools, hence the lower age limit for the surrounding forest. We have examined forest age-related trends in pool characteristics in related work (Palik et al. 2001). Our lower limit on basin size reflected accuracy of photo interpretation. Few field-checked pools that were identified from aerial photography were smaller than 0.02 ha. Smaller pools do exist, but our upper limit on basin size (0.5 ha) reflects the efficacy of the National Wetlands Inventory to consistently detect small wetlands. The photo interpretation was done to detect wetlands that were largely overlooked in the inventory for the study area; that is, very few of the interpreted pools were included in the NWI. When they were included, they tended to be approximately 0.5 ha in size.

Within each glacial landform-landtype combination (Table 1), we randomly selected three to 11 pools from the population of all pools in the class. We assessed each pool relative to the selection criteria, rejected those that did not meet all the criteria, and then randomly selected another pool. In total, we chose 64 pools for study.

Field and Laboratory Procedures

Hydrologic Variables. Water depth was measured using a metal staff gauge placed in the deepest part of each pool's basin. Staff gauges were installed in spring 1997, immediately after pool selection. Gauges were read weekly to biweekly, within a single day for each cycle, during the ice-free season (April 1 through October 31) in 1997–1999. Only 1998 and 1999 data are used in this study because many pools were selected late in spring 1997, hence, early water depth data were missed for many pools that year.

Water samples were collected from each pool in late May 1998 and 1999 for alkalinity determination. We chose alkalinity for characterization because its value indicates water origin in depressional wetlands, i.e., ground water or precipitation, which, in turn, may be related to plant community composition (Brinson 1993, Vitt et al. 1995). Samples were stored in 0.5-liter polyethylene bottles under refrigeration at 4°C for a maximum of 30 days before analysis. Unfiltered samples were analyzed for alkalinity by auto-titration to pH 4.5 (Metler DL20 titrator) followed by Gran plot analysis.

Plant Communities. In each pool, we established a line transect in 1998 or 1999 that spanned the long axis of the basin, beginning and ending at the high water mark for that year. The length of the vegetation transect, along with a second measurement of basin width perpendicular to this transect, was used to estimate pool area, based on the formula for an ellipse.

In each pool, one to four 100 m^2 (5.6 m radius) circular plots (the number of plots depended on pool size) were placed along a transect. Plots were arrayed equidistantly (in pools with two to four plots) to span the length of the transect such that the upland boundaries of the first and last plots were located approximately 3 m inside of the high water marks at the edge of the basins. In small pools, a single plot was placed in the center of the basin. In each plot, species and stem diameter (at 1.4 m height) of all woody species greater than 2.5-cm diameter were recorded. A 1-m wide belt transect was centered on the vegetation transect. The number and species of shrub-sized woody stems ($>$ 1 m tall and $<$ 2.5 cm diameter at 1.4 m height) rooted in the belt were recorded.

Herbaceous plants were sampled in a series of 1-m^2 quadrats arrayed on the center transect. Six or eight quadrats were used, depending on pool size. The first and last quadrats were located just inside of the high water marks in the basin, with the remaining four or six quadrats spaced equidistantly along the transect. In each quadrat, cover of herbaceous species was visually estimated using the following classes: 1 = 5%–15%, 2 = 15%–30%, 3 = 30%–60%, 4 = 60%–100%. We wanted to sample as many pools as possible during mid-summer peak biomass for most herbaceous plants. To facilitate this, a rapid sampling protocol was used that only included species having at least 5% cover in a quadrat. Despite using this approach, we were only able to sample about one-third of the pools in 1998, with the remainder being sampled in 1999. Quadrats were sampled once between late June and mid-August, generally after water levels had fallen significantly and pools were drying.

Canopy openness measured in mid-summer was estimated in the center of each tree plot using a spherical densiometer. At each point, a reading was taken in each of four cardinal directions above the shrub layer ($\sim$1.5 m) if one was present. Because

of the small size of many pools, densiometer readings not only reflected canopy cover over the basins, but also integrated canopy openness of the upland forest adjacent to pools.

Our plant sampling approach had limitations. First, it is likely the timing of sampling in mid-summer missed some obligate wetland herbaceous species, particularly submerged and emergent aquatic plants. However, many of these were still sampled by our approach (e.g., Lemna spp. were sampled in 21 pools), which often included samples from small, deep areas within pool basins. Second, omission of species with less than 5% cover likely reduced the total number of herbaceous species in our analyses; however, by summarizing and analyzing plant data using functional groups (see next section), we believe this omission had little to no influence on the results. Finally, year-to-year variation in climatic and hydrologic variables can influence seasonal development of herbaceous plants such that comparison of plant communities among pools sampled in two different years might be problematic. Again, because we summarize our data into plant functional groups, such that individual species identity is not important, we think this influence was minimal and that broad trends in plant community structure were still evident.

Data Summary and Analyses

Flooding data were summarized in several ways, including consecutive number of days with standing water from April 1 to October 31 (the longest period of consecutive flooding), cumulative number of days with standing water (from April 1 to October 31), maximum depth, and mean depth of water (periods when the pools were dry when measured were excluded from mean depth analysis). Reported values for these flooding measures were averaged between the two sample years (1998 and 1999). Likewise, alkalinity values are the mean of two sample years. Densiometer readings were summarized as mean canopy openness (%) over each pool.

A total of 110 plant species were identified in the study pools (Appendix 1). These species were summarized into several functional groups based on growth form (trees, shrubs, perennial forbs, annual forbs, sedges, grasses) and wetland status (obligate upland, facultative upland, facultative, facultative wetland, obligate wetland) (Reed 1988). For these summarizations, facultative, facultative upland, and obligate upland species were combined into a single upland class and facultative wetland and obligate wetland species were combined into a single wetland class. Resultant classes (and abundance measures) for the functional groups included upland trees and wetland trees (cross-sectional area; m^2/ha), upland shrubs and wetland shrubs (stems/ha), and upland perennial forbs, wetland perennial forbs, upland sedges, wetland sedges, wetland grasses, and wetland annual forbs (percent cover). There were too few pools (< 8) containing other potential classes (upland annual forbs, upland grasses, woody vines) to warrant their analysis.

Pool physical data and plant functional group abundances were summarized in box and whisker plots to display central tendencies and variation among pools. Principal component analysis (PCA; Tabachnik and Fidell 1989), using CANOCO (ter Braak 1987), was used to graphically display variation in plant functional group data. Plant abundance data (i.e., percent cover, basal area, density) were square root–transformed prior to PCA analysis to improve normality and variance structure. PCA was run using sample scaling on a correlation matrix with centering and standardizing on functional group variables. PCA scores were standardized through division by their standard deviation. Upland and wetland shrub densities were down-weighted prior to analysis to prevent undue influence of high abundances on PCA results.

Redundancy analysis (RDA; Davies and Tso 1982) was used to relate variation in plant community data to the hierarchical set of explanatory variables, including glacial landform, landtype, and pool physical data. RDA is a form of constrained ordination that relates variation in a dependent multivariate data set to a second, independent multivariate data set. It is appropriate for data sets containing variables that are measured in dissimilar units, such as the vegetation data in this study. In the RDAs, glacial landform and landtype were included as binary variables, while pool hydrologic data were included as continuous variables. The analyses consisted of a series of three partial RDAs (following ter Braak 1988) in which the independent data sets are included hierarchically and sequentially (glacial landform, followed by landtype, followed by pool physical data), such that the influence of the previous data set is removed from subsequent analysis by inclusion of the former as a covariable. Using this approach, we were able to determine the importance of sequentially smaller-scale factors (glacial landform, landtype, pool environment) for predicting plant community characteristics, independent of the influence of larger scale features. Monte Carlo permutation tests were used to assess the statistical significance of RDA axes. RDAs were run in CANOCO (ter Braak 1987) on correlation

matrices, by centering and standardization on column variables (plant functional groups), with sample scaling. Plant abundance data (i.e., percent cover, basal area, density) were square root–transformed prior to analysis to improve normality and variance structure. Upland and wetland shrub densities were down-weighted to prevent undue influence of high abundances on the analyses. Plant functional group scores were standardized through divisions by their standard deviation.

We used indicator species analysis (Dufrene and Legendre 1997) to test for differences in plant functional groups among glacial landforms and landtypes. Indicator species analysis combined information on the abundance of species (functional groups in our study) and the frequency of occurrence of a species in that group. It produced indicator values for each species in each group, which were tested for statistical significance using a Monte Carlo permutation technique. Indicator values ranged from 0 (no indication or association with a group) to 100 (perfect indication). Indicator analysis was run using PC-ORD (MjM Software).

RESULTS

Plant Functional Groups

Abundances of many plant functional groups varied widely among pools (Figure 1), with the exception of upland shrubs, perennial forbs, and sedges, which had consistently low abundances (Figure 1). The PCA ordination explained 70% of the total variation among plant functional groups, with the first two axes explaining nearly 47% of total variation (Figure 2). PCA axis 1 was related largely to variation in abundance of upland trees, sedges, and perennial forbs, as well as wetland sedges and grasses. Pools on this axis ranged from those having abundant upland trees, sedges, and perennial forbs, with limited wetland sedges and grasses, to those having abundant wetland sedges and grasses and limited upland plants. PCA axis 2 was related largely to variation in abundance of annual and perennial wetland forbs. On this axis, pools ranged from those having high abundance of wetland forbs to those with low abundance of these groups.

Relationships Between Plant Functional Groups and Physical Parameters

Redundancy analysis explained 51.2% of total variation in abundance of plant functional groups among pools; 36.3% of variation was explained on the first two RDA axes (Table 2). Glacial landforms accounted for a small but significant portion of variation (5.9%; $p = 0.050$). The 95% confidence ellipses (around the centroids) for the outwash plain, ground moraine, and end moraine considerably overlapped on the first two axes (data not shown). Ninety percent confidence ellipses were marginally separated, supporting the RDA results of a significant, but low level of predictability in plant functional group distributions based on glacial landform (data not shown). Landtype also accounted for a small but statistically significant portion of total variation (9.7%, $p = 0.050$). In the RDA joint plot based on the landtype-scale analysis, confidence ellipses (both 95% and 90%) were strongly overlapping (data not shown), again indicating minimal discriminating power at this spatial scale.

Indicator species responses for most functional groups confirmed that glacial landform and landtype did not account for significant variation in pool plant communities. Only wetland sedges and grasses varied significantly among glacial landforms (Table 3). Both groups had significantly higher scores ($p = 0.002$ and 0.012, respectively) in pools on outwash, compared to those on the ground and end moraines. At the landtype scale, only wetland grasses had a significant indicator response ($p = 0.048$), with grass cover being higher in landtype 1 (jack and red pine on excessively drained soil) and landtype 2 (mixed pine/deciduous trees on well to moderately well drained, loamy till and fine textured soils) pools compared to those in other landtypes (Table 3).

Pool-scale physical variables were generally highly variable among pools (Figure 3) and collectively explained a larger (compared to glacial landform and landtype) and statistically significant portion of total variation in plant functional groups (35.6%, $p = 0.005$; Table 2). The RDA joint plot of plant functional groups constrained by pool physical variables indicated a predictable relationship between duration of flooding, canopy openness, and occurrence of different plant functional groups (Figure 4). Pools on axis 1 ranged from those having a high abundance of upland trees, along with relatively long and frequent dry periods, to pools having a greater abundance of annual and perennial wetland forbs and longer cumulative and consecutive days with water. RDA axis 2 was largely related to canopy openness. On this axis, pools ranged from those having more open canopies and a higher abundance of wetland sedges, shrubs, and grasses, to those having closed canopies and a greater abundance of upland sedges, shrubs, and perennial forbs, as well as wetland trees.

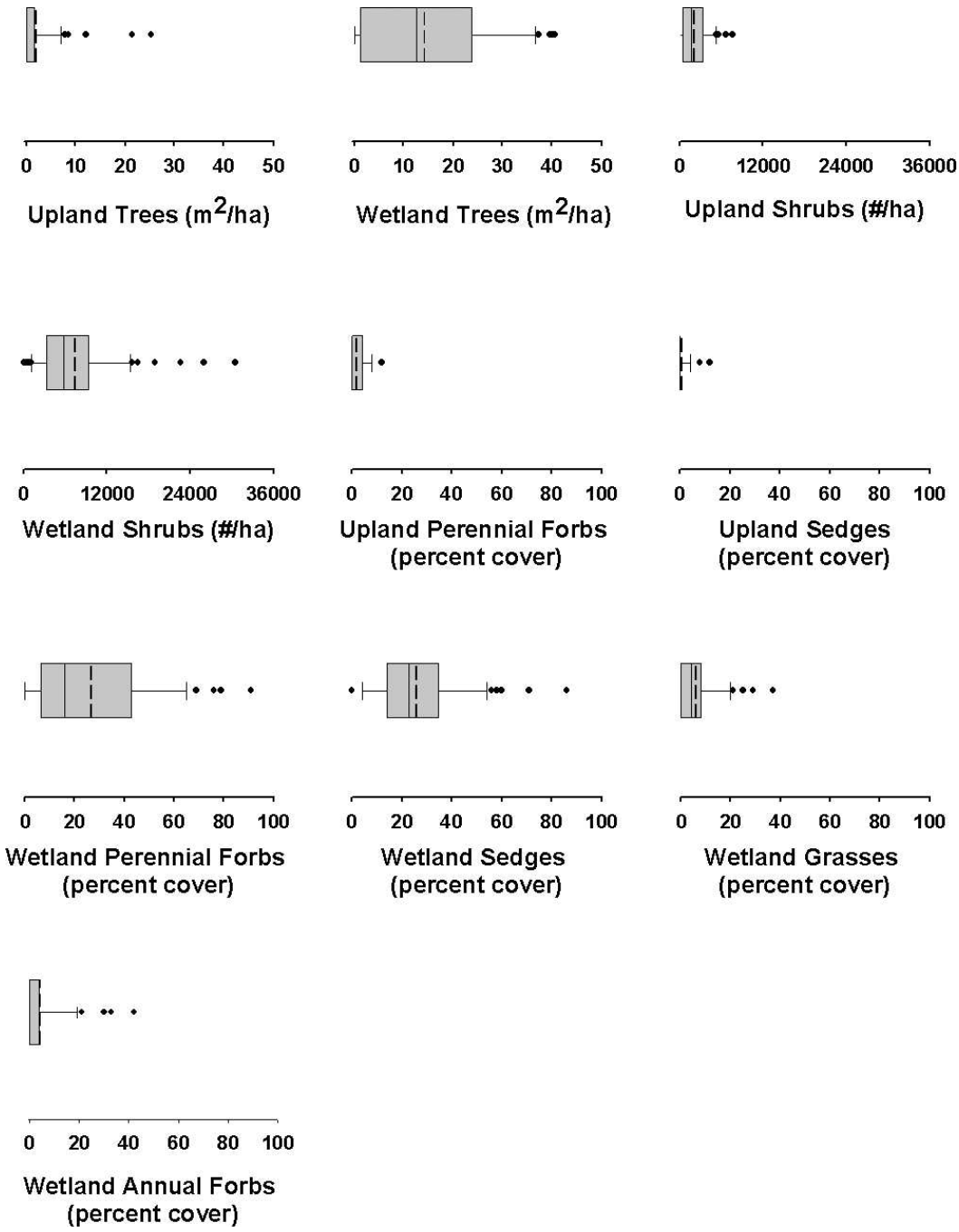

Figure 1. Box plots of plant functional groups for 64 seasonal forest pools. Each box plot shows the mean (dotted vertical line), the median (solid vertical line), the 10^{th}, 25^{th}, 75^{th}, and 90^{th} percentiles, and outliers beyond the 10^{th} and 90^{th} percentiles.

DISCUSSION

Our first objective was to quantify the range of variation in plant communities of small seasonal pools in a northern temperate forest landscape. We found that plant communities, as measured by variation in abundance of functional groups, were highly variable among pools. Some pools supported only a minimal tree component and were dominated by wetland grasses, sedges, and shrubs. Others were dominated by wetland trees and thus were largely canopy covered. Some pools supported upland plant functional groups, along with some wetlands plants.

To our knowledge, ours is the only characterization of seasonal forest pool plant communities in the Great Lakes region and one of only a few studies in

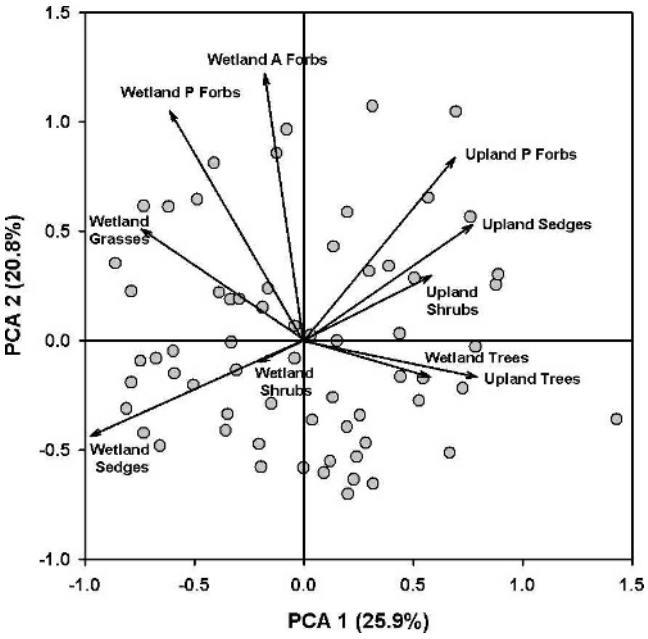

Figure 2. PCA biplot of seasonal pool plant functional groups (upland and wetland trees, upland and wetland shrubs, upland perennial forbs, wetland perennial forbs, upland sedges, wetland sedges, wetland grasses, and wetland annual forbs).

eastern North America that have examined pool vegetation in some fashion (e.g., Calhoun et al. 2003; Vermont Department of Environmental Conservation 2003). The latter studies also documented high variability among small pool vegetation. For example, vegetation of forest pools in Maine showed considerable geographic variation (Calhoun et al. 2003). In a similar study focused on larger wetlands in the Upper Coastal Plain of South Carolina, De Steven and Toner (2004) found wide variation in plant species assemblages among six different wetland types.

Our second objective was to partition variation in pool plant communities using a set of hierarchical predictors ranging from glacial landforms, to landtype (i.e., local forest/soil type), to physical characteristics of the pools themselves. Specifically, we hypothesized that differences in these hierarchically arrayed predictor variables would explain significant amounts of variation in pool plant communities.

Table 2. Partitioned variance from redundancy analysis of seasonal pool plant functional groups constrained by glacial landform, landtype, and pool physical variables.

	Percent of Total Variance		
Source	Axes 1 and 2	All Axes	Probability[3]
Glacial landform	5.9	5.9	0.050
Landtype[1]	7.8	9.7	0.050
Pool[2]	22.6	35.6	0.005
Total	36.3	51.2	

[1] Variance component of landtype after removal of glacial landform component as a covariable.
[2] Variance component of pool physical variables after removal of glacial landform and landtype components as covariables.
[3] Significance of all axes from Monte Carlo Permutation analysis.

A hierarchical approach to understanding and predicting plant communities is the basis of many multifactor ecosystem classifications (e.g., Barnes et al. 1982), which in turn are grounded in hierarchy theory. A key prediction of this theory is that asymmetric relationships occur between levels of a hierarchy, such that upper hierarchical levels constrain the development of lower levels (Allen and Starr 1982, O'Neill et al. 1986). In application, this suggests that the development of plant communities is constrained by physical characteristics of the larger-scale matrix ecosystem in which they occur. This approach is used extensively in terrestrial and wetland ecosystem classifications (e.g., Baker and Barnes 1998, Jorgenson 2000, Palik et al. 2000, Kashian et al. 2003), but has not been applied specifically to understanding plant communities of seasonal forest pools.

Using such an approach, we found that the composition of plant functional group was only marginally predictable from identity of glacial landform. Wetland sedges and grasses were more abundant in pools occurring in the outwash plain compared to ground moraine or end moraine. Similarly, landtype, a hierarchical scale defined by local forest type and soil texture, had only minimal power for predicting occurrence of plant functional groups in seasonal pools. The abundance of wetland grasses was higher in pools occurring on landtypes dominated by pines, with and without deciduous trees, growing on dryer soils. Our results contrast with those of De Steven and Toner (2004), who found strong correlations between Coastal Plain landforms and plant species composition, as well as pool vegetation types. The difference between studies may be related to the range of pool sizes examined, which was considerably smaller in our study, or the types of landforms included in each study.

Plant functional group composition was significantly related to physical characteristics of the pools themselves. As in other studies of wetland plant-environmental relationships (e.g., Wilcox et al. 1986, Galatowitsch and van der Valk 1995, De Steven and Toner 2004), duration of flooding was a significant determinant of vegetation characteristics. Specifically, pools with shorter hydroperiods had a greater abundance of upland trees, while those with longer hydroperiods had a greater abundance of annual and perennial wetland forbs. Moreover, pools having open canopies had a higher abundance of wetland sedges, grasses, and shrubs compared to

Table 3. Seasonal pool plant functional group indicator values by glacial landform and landtype. Asterisks note plants that significantly indicate ($p < 0.05$) a landform or landtype.

	Glacial Landform				Landtype					
Characteristic	Outwash	Ground Moraine	End Moraine	*P*	1	2	3	4	5	*P*
Upland trees	4[1]	27	33	0.440	4	11	12	18	23	0.629
Wetland trees	9	40	40	0.147	3	17	24	26	22	0.418
Upland shrubs	21	38	30	0.278	11	12	17	26	26	0.340
Wetland shrubs	35	33	28	0.845	24	26	18	17	13	0.466
Upland perennial forbs	8	11	15	0.839	13	4	13	1	13	0.700
Upland sedge	4	11	6	0.702	1	1	5	12	7	0.418
Wetland perennial forbs	31	29	26	0.860	20	18	27	14	10	0.268
Wetland annual forbs	14	14	5	0.776	0	5	27	5	10	0.060
Wetland sedge	46	30	22	0.002*	23	22	16	19	16	0.666
Wetland grass	42	7	17	0.012*	22	30	1	6	6	0.048*

[1] Indicator values range from zero (no indication) to 100 (perfect indication meaning that a given characteristic indicates a particular group without error).

those having closed canopies, with the latter containing a greater abundance of upland plants. Pools with closed canopies also contained more wetland trees, a primary reason that their canopies were less open. Unlike the wetlands examined by De Steven and Toner (2004), seasonal pool basin size was not correlated with variation in plant composition, perhaps because the former study covered a larger size range of wetlands than our study.

Our results help identify the range of variation in plant communities of small seasonal pools in northern Minnesota. Understanding landscape variation in seasonal pool plant communities is important for effective conservation of the resource. If range of variation is understood, representative examples of all variants of the ecosystem can be better identified for conservation. Also, understanding the variation in seasonal pool characteristics can help inform management and restoration prescriptions, allowing them to be tailored to different conditions. For instance, concerns over maintaining tree cover within seasonal pools basins are irrelevant in pools that are naturally treeless. In addition, goals

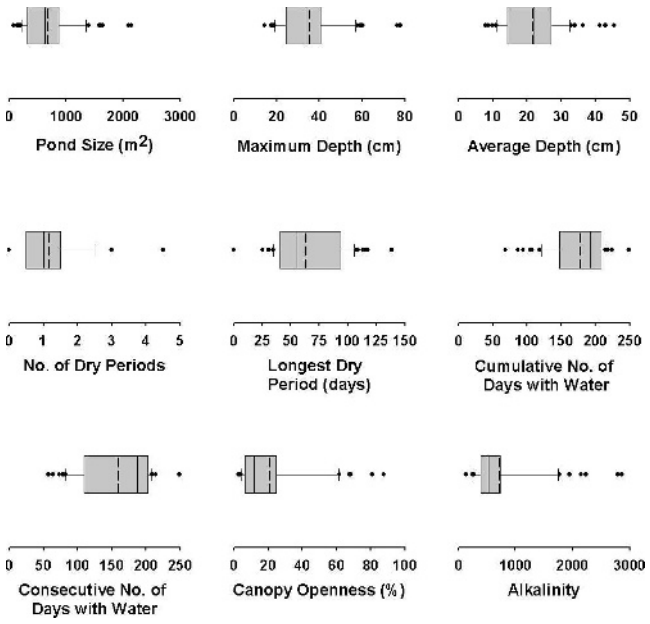

Figure 3. Box plots of physical characteristics for 64 seasonal forest pools. Each box plot shows the mean (dotted vertical line), the median (solid vertical line), the 10th, 25th, 75th, and 90th percentiles, and outliers beyond the 10th and 90th percentiles.

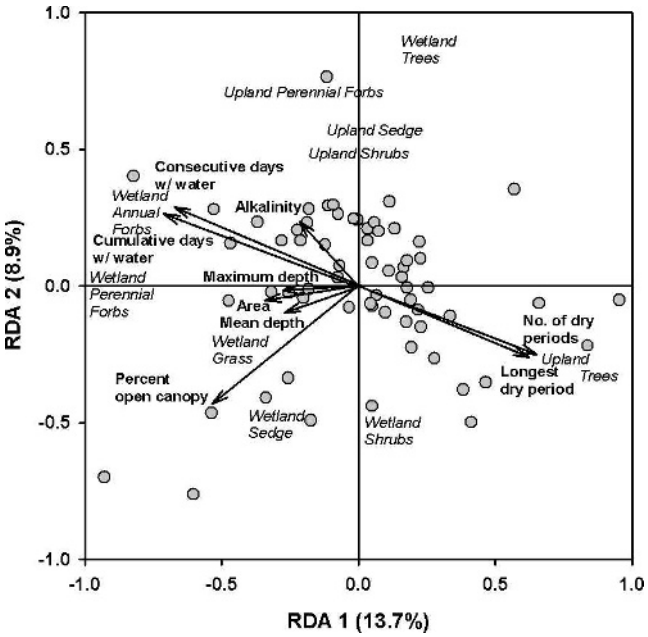

Figure 4. Redundancy analysis joint plot of seasonal forest wetland plant functional groups constrained by pool physical characteristics.

for restoring plant communities in degraded seasonal pools should identify where the target pool occurs along the gradient of vegetation conditions.

ACKNOWLEDGMENTS

This study was supported financially by the USDA Forest Service, North Central Research Station and logistically by the Chippewa National Forest. The comments of several reviewers greatly improved the manuscript.

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Manuscript received 19 December 2005; revisions received 21 July 2006; accepted 10 October 2006.

Appendix 1. Species composition of plant functional groups.

Functional Group	Species	Wetland Status	% of Pools
Upland trees	*Acer rubrum* L.	FAC	23
	Acer saccharum Marsh.	FACU	14
	Acer spicatum Lam.	FACU	11
	Betula alleghaniensis Britton	FAC	36
	Betula papyrifera Marsh.	FACU	3
	Ostrya virginiana (Mill,) K. Koch	FACU	2
	Picea glauca (Moench) Voss	FACU	8
	Populus tremuloides L.	FAC	9
	Quercus macrocarpa Michx.	FAC	11
	Quercus rubra L.	FACU	2
	Tilia americana L.	FACU	9
Wetland trees	*Abies balsamea* (L.) Mill.	FACW	22
	Alnus rugosa (Du Roi) Spreng.	OBL	25
	Fraxinus nigra Marsh.	FACW	69
	Fraxinus pennsylvanica Marsh.	FACW	44
	Larex laricina (Du Roi) K. Koch	FACW	2
	Populus balsamifera L.	FACW	5
	Salix sp.	FACW	3
	Thuja occidentalis L.	FACW	8
	Ulmus americana L.	FACW	38
Upland shrubs	*Acer rubrum* L.	FAC	55
	Acer saccharum Marsh.	FACU	41
	Acer spicatum Lam.	FACU	45
	Amelanchier sp.	FACU	9
	Betula alleghaniensis Britton	FAC	33
	Betula papyrifera Marsh.	FACU	19
	Cornus alternifolia L. F.	FAC	5
	Cornus rugosa Lam.	FAC	3
	Corylus americana Walter	FACU	23
	Corylus cornuta Marsh.	UPL	5
	Lonicera canadensis Marsh.	FACU	6
	Ostrya virginiana (Mill,) K. Koch	FACU	3
	Picea glauca (Moench) Voss	FACU	14
	Populus tremuloides L.	FAC	30
	Prunus virginiana L.	FAC	5
	Prunus pennsylvanica L. F.	FACU	2
	Quercus macrocarpa Michx.	FAC	19
	Quercus rubra L.	FACU	11
	Rubus sp.	FAC	2
	Sambucus racemosa L.	FACU	2
	Tilia americana L.	FACU	6
	Vaccinium augustifolium Ait.	FACU	2
	Viburnum rafinesquianum Schult.	FACU	8
Wetland shrubs	*Abies balsamea* (L.) Mill.	FACW	20
	Alnus rugosa (Du Roi) Spreng.	OBL	41
	Chamaedaphne calyculata L. Moench	OBL	3
	Cornus stolonifera Michx.	FACW	22
	Fraxinus nigra Marsh.	FACW	81
	Fraxinus pennsylvanica Marsh.	FACW	56
	Populus balsamifera L.	FACW	9
	Ribes triste Pallas	OBL	20
	Rubus strigosus Michx.	FACW	11
	Salix sp.	FACW	19
	Spirea alba Du Roi	FACW	8
	Ulmus americana L.	FACW	64
	Viburnum trilobum Marsh.	FACW	3

Appendix 1. Continued.

Functional Group	Species	Wetland Status	% of Pools
Upland perennial forbs	*Amphicarpaea bracteata* (L.) Fernald	FAC	2
	Aralia nudicaulis L.	FACU	5
	Clintonia borealis (Ait.) Raf.	FAC	5
	Epilobium ciliatum Raf.	FACU	2
	Fragaria virginiana Duchesne	FAC	9
	Galium triflorum Michx.	FACU	6
	Maiamthinum canadense Desf.	FAC	9
	Polygala paucifolia Willd.	FACU	2
	Trientalis borealis Raf.	FAC	5
	Uvularia sessilifolia L.	FAC	3
Wetland perennial forbs	*Alisma triviale* Pursh.	OBL	2
	Arisaema tryphyllum (L.) Schott	FACW	3
	Aster lateriflorus (L.) Britton	FACW	5
	Calla palustris L.	OBL	17
	Caltha palustris L.	OBL	9
	Cicuta maculata L.	OBL	11
	Dryopterus carthusiana (Vill.) H. P. Fuchs	FACW	11
	Epilobium strictum Muhl. Ex. Spreng.	OBL	2
	Galium trifidum L.	FACW	6
	Iris versicolor L.	OBL	11
	Laportea canadenseis (L.) Wedd.	FACW	3
	Lemna sp.	OBL	27
	Lycopus uniflorus Michx.	OBL	42
	Lysimachia thyrsiflora L.	OBL	8
	Mentha arvensis L.	FACW	6
	Mitella nuda L.	OBL	3
	Myosotis laxa Lehm.	OBL	2
	Petasites frigidus (L.) Fr.	FACW	2
	Polygonum amphibium L.	OBL	3
	Polygonum punctatum Elliott	OBL	2
	Potentilla palustris (L.) Scop.	OBL	9
	Ranunculus gmelinii D.C.	FACW	2
	Ranunculus pennsylvanicus L.F.	OBL	3
	Rubus pubescens Raf.	FACW	36
	Scutellaria galericulata L.	OBL	6
	Scutellaria lateriflora L.	OBL	25
	Sium suava Walter	OBL	19
	Smilacina trifolia (L.) Desf.	OBL	3
	Triadenum virginicum (L.) Raf.	OBL	2
	Typha latifolia L.	OBL	2
	Utricularia minor L.	OBL	3
Upland sedge	*Carex deweyana* Schweinitz	FACU	2
	Carex gracillima Schweinitz	FACU	11
	Carex tenera Dewey	FAC	5
Wetland sedge	*Carex aquatilis* Wahlenb.	OBL	2
	Carex bebbii (Bailey) Olney Ex. Fernald	OBL	5
	Carex disperma Dewey	OBL	39
	Carex hystericina Muhl. Ex. Willd.	OBL	3
	Carex intumescens Rudge	FACW	47
	Carex lacustris Willd.	OBL	25
	Carex lupulina Muhl. Ex. Willd.	OBL	9
	Carex normalis Mackenz.	FACW	2
	Carex pseudo-cyperus L.	OBL	2
	Carex retrorsa Schweinitz.	OBL	14
	Carex rostrata J. Stokes	OBL	5

Appendix 1. Continued.

Functional Group	Species	Wetland Status	% of Pools
	Carex schweinitzii Dewey	OBL	2
	Carex stricta Lam.	OBL	2
	Carex trisperma Dewey	OBL	3
	Carex tuckermanii Boott	OBL	52
	Carex vesicaria L.	OBL	6
	Scirpus cyperinus (L.) Kunth	OBL	3
Wetland grass	*Alopecurus aequalis* Sobol.	OBL	5
	Calamagrostis canadensis (Michx.) Beauv.	OBL	20
	Cinna latifolia (Trevir.) Griseb.	FACW	20
	Glyceria borealis (Nash) Batch.	OBL	3
	Glyceria canadensis (Michx.) Trin.	OBL	3
	Glyceria striata (Lam.) A. Hitchc.	OBL	28
Wetland annual forbs	*Bidens connata* Muhl. Ex. Willd.	OBL	17
	Bidens frondosa L.	FACW	5
	Cardamine pennsylvanica Muhl. Ex. Willd.	FACW	2
	Impatiens capensis Meerb.	FACW	14
	Polygonum latpathifolium L.	FACW	2