GROUND-FLORA COMMUNTIES OF HEADWATER RIPARIAN AREAS IN AN OLD-GROWTH CENTRAL HARDWOOD FOREST

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ABSTRACT.—The composition and structure of ground-flora vegetation was examined across headwater riparian areas of Johnson Woods, an old-growth forest located in north-central Ohio. While the distribution patterns of these species groups is variable, classification and gradient analyses indicate that ground-flora vegetation is related strongly to landform and distance from the bankfull channel, suggesting that species are ordered along a complex environment from the stream edge, across the floodplains, and into the adjacent uplands. No significant differences in species richness were observed between the floodplain and upland landforms. However, there are differences in functional lifeform guilds between landforms. Specifically, graminoids, annual forbs, and perennial forbs dominate the floodplains, while woody seedling and vines dominate the adjacent uplands.

Our understanding of riparian areas has evolved considerably over the past 20 years from viewing riparian areas as individual units of the landscape to viewing them as ecotones located between aquatic and terrestrial systems (Gregory and others 1991, Illhardt and others 2000). Through a variety of empirical studies, we have discovered that riparian areas are complex ecotones characterized by gradients of structural and functional change from the water's edge to the uplands, and it is the juxtaposition of these dynamic ecotones with water which leads ultimately to many of the important ecological services provided by riparian areas (Gregory and others 1991, Illhardt and others 2000, Naiman and others 2000). For example, surface and subsurface connections with water typically result in a diverse array of different habitat that supports numerous plant and animal species (Pollack and others 1998, Brinson and Verhoeven 1999). Furthermore, these ecotones are known to regulate inputs of organic matter to the aquatic systems (Vannote and others 1980), and consequently, control the structure of the aquatic foodweb, as well as the cycling of nutrients at the watershed level (Peterson and others 2001).

Based on the important ecological contributions riparian areas provide, understanding the natural variability and patterns in riparian vegetation, as well as the factors that mediate the structure and function of riparian vegetation, is critical for predicting vegetation change in these complex systems. In most riparian settings, landscape features resulting from the interaction of hydrologic and geomorphic processes are believed to be important constraints on the composition and structure of riparian areas (Gregory and others 1991, Auble and others 1994, Hupp and Osterkamp 1996). While the distribution of woody vegetation across riparian areas is closely tied to hydrogeomorphic processes, the composition and spatial distribution of ground flora species can also be influenced strongly by a variety of additional factors, including the composition and structure of other vegetation layers (McCune and Antos 1981, Goebel and Hix 1997), microtopography (Titus 1990), and seasonal change (Goebel and others 1999).

In order to understand which of these factors are the most important variables controlling the distribution of ground-flora vegetation, it is

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important that we determine the factors that influence vegetation patterns across riparian areas. One common approach is to examine how individual species or groups of species are arranged on different fluvial landforms, as fluvial landforms are surrogates of the prevalent hydrogeomorphic processes of the stream valley (Fetherston and others 1995). It is important to understand that this approach is based on the premise that species with similar distributions along environmental gradients (i.e., a riparian ecotone) can be grouped together to help elucidate the relationships between vegetation and the environment (Pregitzer and Barnes 1982). Additionally, in areas where the factors influencing the composition, structure, and diversity of ground-flora vegetation are dynamic and spatially heterogeneous (such as an individual landform or riparian ecotone), the use of species groups or functional plant guilds, may be more useful for elucidating the ecological patterns and underlying ecosystem processes than individual species alone (Pabst and Spies 1998).

Because vegetative descriptions of headwater Central Hardwood riparian areas are lacking, and characterization of the composition and structure of riparian vegetation provides the foundation for subsequent ecological and management studies, we examined the relationships among ground-flora vegetation and environmental factors across riparian ecotones located in a small old-growth headwater basin located in north-central Ohio. Specifically, we addressed the following questions:

1) How does ground flora vegetation change across riparian areas in this old-growth headwater basin?
2) Are there individual or groups of ground-flora species that can be used to help identify the extent of headwater riparian area?

STUDY AREA

We conducted our study at the Johnson Woods State Nature Preserve (JWSNP), a virgin 83 ha old-growth forest located in Wayne County, Ohio (fig. 1). Johnson Woods is located in the Western Glaciated Allegheny Plateau, a maturely dissected plateau modified by glaciation and characterized by rounded hills, ridges, broad valleys, and a variety of glacial landforms (Keys and others 1994). The study area has a humid-continental climatic regime with mean annual temperatures of 10ºC. Mean annual precipitation ranges from 900 to 1,020 mm, and is fairly evenly distributed throughout the year (Keys and others 1994).

The uplands of Johnson Woods are dominated by gentle slopes (< 5 percent), well-drained soils, and old-growth plant communities of mixed oaks (*Quercus* spp.), hickories (*Carya* spp.), and an increasing component of shade-tolerant species, including sugar maple (*Acer saccharum* Marsh.) and American beech (*Fagus grandifolia* Ehrh.). In addition to these well-drained uplands, there are many depressional areas or vernal pools that feed a first-order, intermittent stream characterized predominately by narrow floodplains and a gentle slope into the uplands (fig. 1). The poorly drained soils associated with these vernal pools are often deep and underlain by glacial outwash and are dominated by a mixture of woody species, including swamp white oak (*Quercus bicolor* Willd.), white ash (*Fraxinus americana* L.), and buttonbush (*Cephalanthus occidentalis* L.).

METHODS

During the summer of 2001, we collected ground-flora data from 24 transects that bisected the stream valley along the entire 0.75 km length of the intermittent channel located in JWSNP. Each transect extended from the stream edge (i.e., bankfull channel edge) into the uplands, with transects arrayed perpendicular to streamflow. The location of the first transect was determined randomly beginning 40 m from the preserve boundary; successive transects were then located randomly at least 20 m but no more than 40 m apart in the upstream direction. Sample plots were located along each transect systematically at 5 m intervals (e.g., 0, 5, 10, 15, and so on), with at least two sample plots located in the adjacent upland forest on each transect. Individual transects had between 6 to 10 plots, depending on the valley width, for a total of 193 sample plots.

In each sample plot, we recorded the landform (floodplain, upland), distance from the stream bankfull channel, and percent cover of all species < 1 m tall in a 1 m^2 quadrant. Cover classes included: < 1 percent, 1-5 percent, 6-10 percent, 11-20 percent, 21-40 percent, 41-70 percent, and 71-100 percent. We also sorted the species into functional lifeform groups (annual forbs, perennial forbs, graminoids, pteridophytes, epiphytes, woody vines, woody shrubs, and woody seedlings) and estimated the percent cover of each group. Nomenclature and life form categories follow Voss (1996), except for pteridophytes (Gleason and Cronquist 1991).

Finally, we classified each species in terms of its wetland indicator status—obligate wetland

(OBL), facultative wetland (FACW), facultative (FAC), facultative upland (FACU), and obligate upland (UPL) (Reed 1988). By definition: obligate wetland species (OBL) are plants that almost always occur (99 percent) in wetlands; facultative wetland species (FACW) are plants that usually occur (67-99 percent) in wetlands; facultative species (FAC) are plants that occur (33-67 percent) in both wetlands and uplands; facultative upland species (FACU) are plants that occasionally occur (1-33 percent) in wetlands; and, obligate upland species (UPL) are plants that almost always occur (99 percent) in the uplands.

We used several different methods to quantify and compare patterns of change in ground-flora vegetation and physiographic factors. Because rare species can mask patterns in vegetation, we dropped species occurring on less than 5 percent of all sample plots (9 out of 193 plots) for all classification and ordination analyses. An initial classification based on the floristic dissimilarity of species on all plots was made using Two Way Indicator Species Analysis (TWINSPAN) (Hill 1979) using default settings and seven pseudospecies cut levels corresponding to the lower limit of each percent cover class, e.g., 0, 1, 6, 11, 21, 41, and 71. The results of this initial classification provided the basis for eight ecological species groups, each named for the species with the greatest ecological amplitude and importance. Mean cover of each ecological species group was calculated by landform and distribution patterns examined.

Distributions of individual species were examined with detrended correspondence analysis (DCA) using PC-ORD software (McCune and Mefford 1995). We used Spearman rank correlations of the sample unit scores and environmental factors to help interpret the relationships between the first two DCA axes. We also used a one-way analysis of variance (ANOVA) to compare the species richness (total species per m^2), percent cover of lifeform categories between the floodplain and upland landforms, and the total cover of wetland (OBL and FACW) and upland (FAC, FACU, and UPL) species between the floodplain and upland landforms. Data were transformed (arcsin transformation for percentage data) prior to analyses to stabilize variances (Zar 1996) and all analyses were conducted using SAS version 8.1 (SAS Institute, Cary, NC).

Finally, we supplemented the traditional gradient analyses with Dufrene and Legendre's (1997) indicator analysis using PC-ORD (McCune and Mefford 1995). These analyses

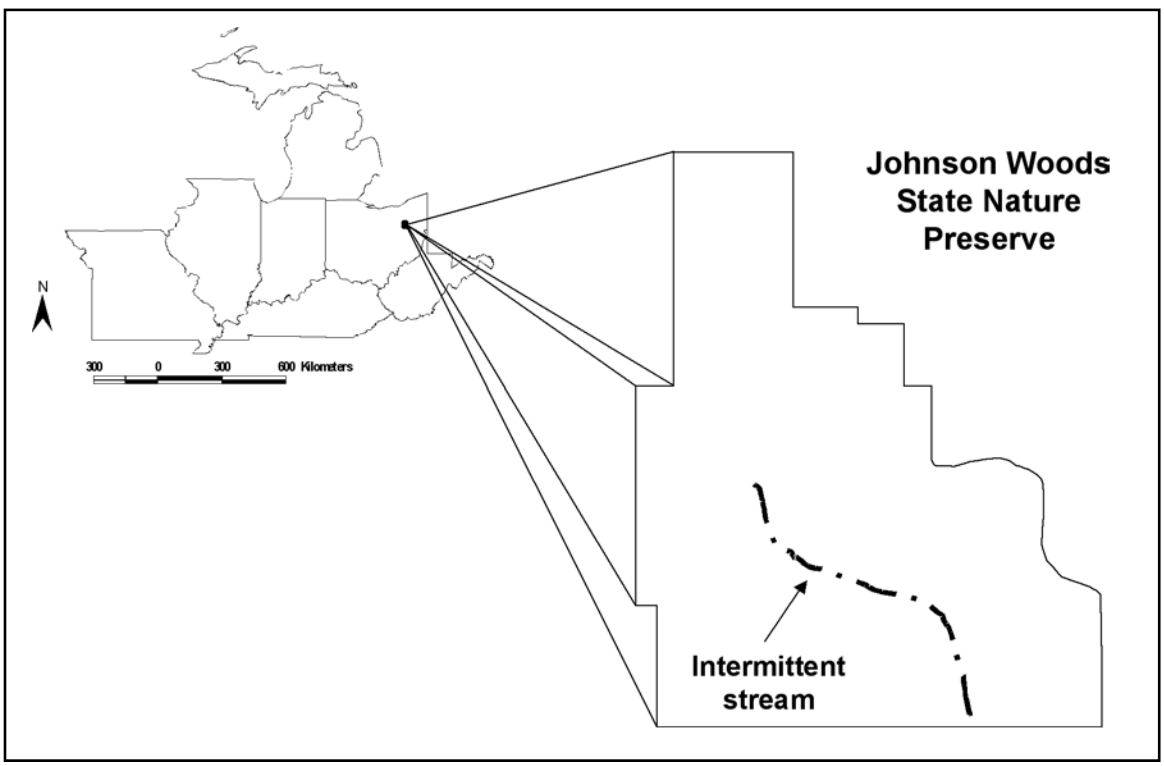

Figure 1.—*Location of Johnson Woods State Nature Preserve, an old-growth forest located in north-central Ohio.*

use Monte Carlo permutation procedures to test the association of each species with each valley landform, and generate a *p*-value that is the proportion of randomized trials in the permutation procedure with an indicator value equal to or exceeding the observed indicator value (Dufrene and Legendre 1997).

RESULTS

Ground-flora Classification and Ordination

We sampled a total of 75 species, of which almost half of these species are perennial forbs (45 percent), while the remaining species are classified as woody seedlings (20 percent), woody shrubs (8 percent), pteridophytes (8 percent), woody vines (7 percent), graminoids (5 percent), annual forbs (5 percent), or epiphytes (1 percent). Approximately a third of all species sampled are considered wetland species (classified as either facultative wetland (28 percent) or obligate wetland (3 percent) species), while the remaining are classified as upland species (facultative (20 percent), facultative upland (32 percent), or upland obligate (4 percent) species). According to the National Wetland Indicator List, 10 of the 75 species sampled (13 percent) are not classified (Reed 1988), but most are typically found in moist or wet forest sites (and therefore were classified as facultative species for the remaining analyses).

Using TWINSPAN, we classified the 28 most common species (those occurring on at least 5 percent of the sample plots) into eight groups within which the component ground-flora species have similar patterns of occurrence. These include the following species groups: *Viburnum*, *Acer*, *Parthenocissus*, *Fraxinus*, *Quercus*, *Circea*, *Impatiens*, and *Leersia* (table 1). The occurrence of eight different species groups reflects the variability in species composition and dominance within and among the different landforms. Three of the species groups are common on the floodplains (*Impatiens*, *Leersia*, and *Fraxinus*); all of which are dominated primarily by either facultative wetland or obligate wetland species (e.g., *Leersia virginica* Willd.) (see Appendix).

The upland landforms were dominated by four groups of ground-flora species, including members of the *Acer, Fraxinus, Parthenocissus*, and *Impatiens* groups (table 1). Only the *Acer* group is dominated entirely by facultative or facultative upland species (sugar maple, American beech, partridge-berry (*Mitchella repens* L.), Solomon-seal (*Polygonatum pubescens* (Willd.) Pursh), and black cherry (*Prunus serotina* Ehrh.). Members of the other species groups (e.g., V*iburnum, Circea, Quercus*) are less dominant across individual riparian ecotones.

The ordination analysis of the ground-flora data demonstrates the complex compositional gradient that occurs along riparian ecotones of Johnson Woods (fig. 2). The first DCA axis (eigenvalue = 0.49) represents a compositional and topographical gradient from the uplands to the streamside, with the extremes dominated by members of the *Acer* group in the uplands, and the *Leersia* and *Impatiens* species groups strongly associated with the floodplains. Although there is some overlap among sample points, the distribution of plots is arranged by landform. Correspondingly, the moderate Spearman rank correlation between DCA first axis scores and distance from the stream channel (m) supports this interpretation ($r = -0.39$; $P < 0.05$).

The distribution of sample points and species along the second DCA axis (eigenvalue = 0.25) is less clear. The gradient is determined largely by the difference between the *Viburnum* species group, with high axis 2 scores, and the *Parthenocissus* and *Fraxinus* groups, both with low axis 2 scores (fig. 2). This axis may represent a gradient of soil moisture, as several of the species that comprise both the *Parthenocissus* and *Fraxinus* groups are either facultative wetland or obligate wetland species. However, further research related to the soils of each plot is needed to determine whether, in fact, this ordination axis does represent a gradient of soil moisture nested within the gradient of

Table 1.—*Mean cover of ground-flora ecological species groups by landform for riparian areas of Johnson Woods, north-central Ohio. See Appendix for list of species in each group.*

	LANDFORM CATEGORY	
Species group	**Floodplain (*n*=56)**	**Upland (*n*=137)**
Viburnum	0.72 (0.45)[a]	2.88 (0.88)
Acer	2.11 (0.98)	10.95 (1.29)
Parthenocissus	3.04 (0.96)	8.71 (1.13)
Fraxinus	5.24 (1.42)	10.35 (1.28)
Quercus	1.02 (0.20)	0.62 (0.11)
Circea	1.74 (0.68)	2.34 (0.43)
Impatiens	23.27 (4.00)	6.61 (1.30)
Leersia	6.79 (1.54)	0.31 (0.23)

[a]Values are mean ± 1 standard error.

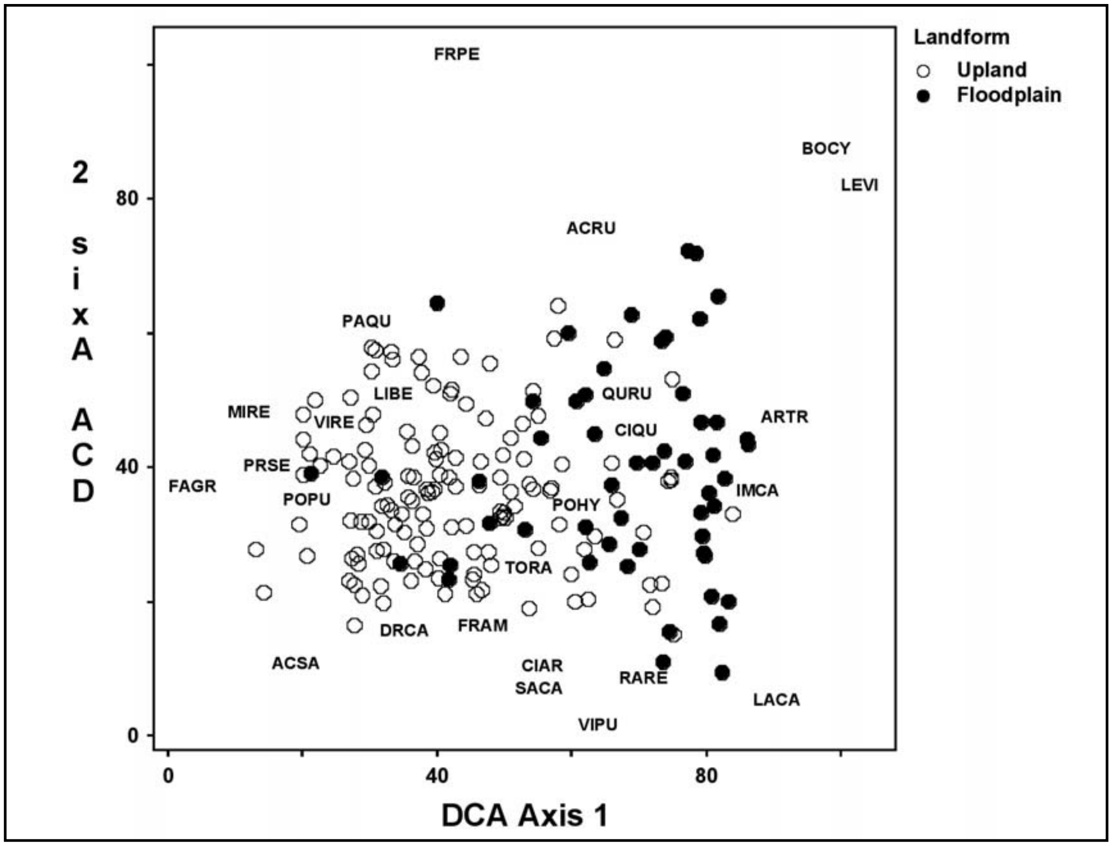

Figure 2.—*DCA ordination of the ground-flora of Johnson Woods, showing the distribution of sample plots by landform and common (those occurring on > 5 percent of the sample plots) ground-flora species. See Appendix for species codes.*

increasing distance from the stream channel as represented by the first DCA axis.

Species Richness and Ground-Flora Cover Analyses

No significant difference in species richness (per m^2) was observed between the floodplain and upland landforms (table 2). Similar results are observed when total cover is examined, with a total cover of 53.18 percent ± 5.74 percent (mean + 1 SE) for the floodplain and 49.50 percent ± 3.18 percent for the upland landforms, respectively. However, when the ground-flora was separated into different lifeform categories there are significant differences between the floodplain and upland landforms. For instance, the floodplains have significantly higher cover of annual forbs, perennial forbs, and graminoids than the adjacent upland landforms. Conversely, the uplands have higher cover of woody seedlings and vines. Finally, the upland landforms are dominated by species classified as upland indicator species (FAC, FACU, UPL), while the floodplains are dominated by both upland and wetland indicator species (FACW, OBL).

Ground-Flora Indicator Analyses

Using Dufrene and Legendre's (1997) indicator analysis, we identified 11 common species that are strong indicators of either the upland or floodplain landforms, and by extension can be used to help identify the extent of the riparian area. Seven of the species are upland indicator species, and include a variety of perennial forbs, woody seedlings, and woody vines: sugar maple, jack-in-the-pulpit, (*Arisaema triphyllum* (L.) Schott), American beech, white ash (*Fraxinus americana* L.), Virginia creeper (*Parthenocissus quinquefolia* (L.) Planchon), Solomon-seal, and black cherry (table 3). The remaining four species are significant floodplain indicators and include: false nettle (*Boehmeria cylindrica* (L.) Sw.), touch-me-not (*Impatiens capensis* Meerb.), wood-nettle (*Laportea canadensis* (L.) Wedd.), and white grass (*Leersia virginica* Willd.).

DISCUSSION

Unlike other regions of North America, little research has focused on understanding compositional and structural changes across riparian areas of Ohio, or the Central Hardwood region. Those studies that have examined riparian

Table 2.—*Comparison of species richness, percent cover by lifeform, and percent cover by wetland indicator status (upland vs. wetland) between floodplain and upland landforms for riparian areas of Johnson Woods, north-central Ohio*

	LANDFORM CATEGORY		ONE-WAY ANOVA	
Parameter	**Floodplain (*n*=56)**	**Upland (*n*=137)**	**F-statistic**	***P*-value**
Richness (species per m^2)	5.02 (0.35)[a]	5.27 (0.20)	0.42	0.517
Total cover (%)	53.18 (5.74)	49.50 (3.18)	0.36	0.552
Lifeforms				
Cover of annual forbs (%)	12.16 (2.67)	4.97 (0.96)	9.96	0.002
Cover of perennial forbs (%)	22.77 (0.96)	10.55 (1.40)	17.94	<0.001
Cover of graminoids (%)	8.13 (1.66)	2.14 (0.60)	15.88	<0.001
Cover of pteridophytes (%)	0.14 (0.14)	1.16 (0.45)	2.09	0.150
Cover of woody shrubs (%)	0.43 (0.24)	2.30 (0.61)	3.75	0.054
Cover of woody seedlings (%)	4.16 (1.00)	14.68 (1.49)	18.78	<0.001
Cover of woody vines (%)	5.38 (1.27)	13.60 (1.49)	11.05	0.001
Wetland Indicators				
Cover of upland species (%)	26.70 (3.33)	36.12 (2.43)	4.68	0.032
Cover of wetland species (%)	24.98 (3.88)	10.70 (1.54)	17.08	<0.001

[a]Values are mean ± 1 standard error.

areas in the region have usually focused on either a single landform, such as floodplains (e.g., Williams and others 1999), or individual streamside forests (McCarthy and others 1987, Hix and Pearcy 1997). None of these studies have treated riparian areas as ecotones in an attempt to understand how vegetation patterns may change across these small-scale gradients, especially in headwater stream systems. Consequently, our research is one of the first quantitative studies to

1) focus on riparian areas as ecotones in the region, and
2) to quantify vegetation change across these riparian ecotones.

Our results show that, as in many other riparian landscapes, ground-flora vegetation patterns across riparian areas of Johnson Woods are variable yet ordered along a complex compositional gradient related to distance from the bankfull channel (Franz and Bazzaz 1977, Pabst and Spies 1998, Goebel 2001). Such relationships support the assertion that riparian areas are ecotones rather than discrete units of the landscape, as the gradient is influenced by a host of interacting factors, including physiography, soils, disturbances, and climatic conditions (Gosz 1993). Specifically, the factors believed to have the greatest influence on riparian vegetation are:

1) hillslope processes,
2) hydrologic disturbances,
3) tolerance of saturated soils, and
4) mineral soil disturbances (Gregory and others 1991, Pabst and Spies 1998, Naiman and others 2000).

Although more research related to the specific mechanisms controlling the changes in vegetation across these riparian areas is needed, it is likely that a tolerance for saturated soils and seasonal hydrologic disturbances (as reflected by the dominance of wetland species on the floodplain landforms) are the most important factors regulating the distribution of ground flora species in the gently sloping headwater systems of Johnson Woods.

Contrasted to other riparian areas of the Upper Midwest, the headwater systems of Johnson Woods are similar in terms of species richness to old-growth headwater systems located in Upper Michigan. In these first-order stream valleys dominated by northern hardwood forests, Goebel (2001) found no significant differences in species richness between floodplains and upland landforms (mean richness = 5.4 and 4.0, respectively). The similarities in species richness between the two landforms may be the result of a variety of microsites that support a diverse array of species in both the uplands as well as the riparian areas. These similarities,

Table 3.—*Indicator analysis of common ground-flora species of riparian ecotones in Johnson Woods. Comparison is between floodplain and upland landform classes*

Species name	Code	Observed indicator value	Indicator value from randomized permutation procedure[a]	P[b]
Acer rubrum	ACRU	19.5	17.6 (2.6)	0.197
Acer saccharum	ACSA	32.3	20.4 (3.0)	.003†
Arisema triphyllum	ARTR	14.5	6.8 (1.9)	.007†
Boehmeria cylindrica	BOCY	18.9	5.1 (1.7)	.001*
Cinna arundinacea	CIAR	9.0	9.5 (2.2)	.503
Circea quadrisulcata	CIQU	9.5	9.5 (2.2)	.396
Dryopteris carthusiana	DRCA	5.1	4.3 (1.5)	.273
Fagus grandifolia	FAGR	24.0	12.9 (2.4)	.001†
Fraxinus americana	FRAM	30.4	23.7 (3.1)	.037†
F. pennsylvanica	FRPE	6.6	6.2 (1.7)	.352
Impatiens capensis	IMCA	36.2	18.0 (2.6)	.001*
Laportea canadensis	LACA	37.4	15.6 (2.6)	.001*
Leersia virginica	LEVI	49.6	11.1 (2.2)	.001*
Lindera benzoin	LIBE	6.2	5.7 (1.8)	.311
Mitchells repens	MIRE	3.8	4.3 (1.6)	.623
Parthenocissuss quinquefolia	PAQU	33.2	21.1 (2.8)	.003†
Polygonum hydropiper	POHY	10.0	9.7 (2.2)	.364
Polygonatum pubescens	POPU	23.6	12.7 (2.5)	.002†
Prunus serotina	PRSE	16.4	9.8 (2.2)	.015†
Quercus rubra	QURU	6.7	4.0 (1.4)	.080
Ranunculus recurvatus	RARE	2.7	4.3 (1.5)	.999
Sambucus canadensis	SACA	4.7	5.2 (1.7)	.537
Toxicodendron radicans	TORA	24.7	22.2 (2.8)	.169
Viola pubescens	VIPU	15.2	12.9 (2.4)	.150
Viburnum recognitum	VIRE	5.3	4.3 (1.5)	.264

[a] Mean (± 1 standard deviation).
[b] Proportion of randomized trials with indicator value equal to or exceeding the observed indicator value;
* indicates a floodplain indicator species,
† indicates an upland indicator species.

however, are not observed when second-growth sites are examined. For example, in headwater systems located in both unglaciated western Pennsylvania and north-central Minnesota, the ground-flora of the floodplains have higher ground-flora species richness than the adjacent uplands (Williams and others 1999, Goebel 2001).

While species richness of headwater systems in north-central Ohio and Upper Michigan are similar, the structure of the ground-flora vegetation is markedly different. In Johnson Woods we observed riparian areas dominated by forbs and graminoids, while riparian areas in Upper Michigan are dominated almost exclusively by graminoids (Goebel 2001). These differences are most likely attributed to the different types of hydrogeomorphic processes operating in each system. For example, the influence of flooding on the riparian forest canopy of Johnson Woods may be relatively benign, as the forest canopy is relatively continuous across the riparian area into the uplands. Conversely, the forest canopy of headwater riparian areas in Upper Michigan is more heterogeneous, grading from a closed canopy of sugar maple and eastern hemlock (*Tsuga canadensis* L.) to open sedge (*Carex* spp.) meadows influenced strongly by seasonal flows and active beaver dams (Goebel 2001).

The fact that distance from the bankfull channel was only moderately correlated with the DCA axes suggests that distance from the bankfull channel by itself is not a reliable indicator of riparian status. However, an approach based on landform classification and indicator species has promise to help identify the extent of the riparian area. Our results suggest that a mixture of different species assemblages may be a good indicator of the extent of riparian areas in headwater systems of north-central Ohio. Specifically, the presence of several graminoid and forb species can be used to help determine the extent of the floodplain in these headwater systems, a process that can be problematic considering the gentle slopes and little stream valley development associated with these headwater systems. Additionally, the presence of white grass, touch-me-nots, wood-nettle, and false nettle likely indicate a floodplain surface and a riparian environment. Such information may be useful as riparian area management moves from a "one-size-fits-all" approach to a more functional approach that takes into consideration a variety of ecological services provided by riparian areas, many of which are mediated by specific hydrogeomorphic processes (Illhardt and others 2000).

Finally, while descriptive, the information reported here provides a basis for future research directives focused on understanding the functional processes associated with these critical headwater systems. By conducting these analyses in the few remaining intact old-growth forests located in the Central Hardwood region such as Johnson Woods, these areas provide an excellent opportunity to examine the influences of different hydrogeomorphic processes on riparian vegetation in an undisturbed setting. While restoring all the functional properties associated with these riparian areas in disturbed headwater systems of north-central Ohio may be unrealistic, it is only through understanding the dynamics of riparian areas in an undisturbed setting that we can decompose the factors that control the properties of specific riparian areas. Consequently, these old-growth riparian areas of Johnson Woods provide an "endpoint" along a disturbance gradient with which we can compare the composition, structure, and function of manipulated or restored riparian areas in north-central Ohio and beyond.

LITERATURE CITED

Auble, G.T.; Friedman, J.M; Scott, J.L. 1994. Relating riparian vegetation to present and future streamflows. Ecological Applications. 4: 544-554.

Brinson, M.M.; Verhoeven, J. 1999. Riparian forests. In: Hunter, M.L. Jr., ed. Maintaining biodiversity in forest ecosystems. Cambridge, MA: Cambridge University Press: 265-299.

Dufrene, M.; Legendre, P. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecological Monographs. 67: 345-366.

Fetherston, K.L.; Naiman, R.J.; Bilby, R.E. 1995. Large woody debris, physical process, and riparian forest development in montane river networks of the Pacific Northwest. Geomorphology. 13: 133-144.

Franz, E.H.; Bazzaz, F.A. 1977. Simulation of vegetation response to modified hydrologic regimes: a probabilistic model based on niche differentiation in a floodplain forest. Ecology. 58: 176-183.

Gleason, H.A.; Cronquist, A. 1991. Manual of vascular plants of Northeastern United States and adjacent Canada. New York, NY: New York Botanical Garden.

Goebel, P.C. 2001. Hydrogeomorphic controls on riparian areas of the northern Lake States. Houghton, MI: Michigan Technological University. PhD dissertation.

Goebel, P.C.; Hix, D.M. 1997. Correlations among stand ages and forest strata in mixed-oak forests of southeastern Ohio. In: Pallardy, S.G.; Cecich, R.A.; Garrett, H.G.; Johnson, P.S., eds. Proceedings, 11th Central Hardwood Forest conference. Gen. Tech. Rep. NC-188. St. Paul, MN: U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station: 269-282.

Goebel, P.C.; Hix, D.M.; Olivero, A.M. 1999. Seasonal ground-flora patterns and site factor relationships of second-growth and old-growth south-facing ecosystems, southeastern Ohio, USA. Natural Areas Journal. 19: 12-29.

Gosz, J.R. 1993. Ecotone hierarchies. Ecological Applications. 3: 369-376.

Gregory, S.V.; Swanson, F.J.; McKee, W.A. 1991. An ecosystem perspective of riparian zones. BioScience. 40: 540-541.

Hill, M.O. 1979. TWINSPAN - a FORTRAN program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes. Ecology and Systematics. Ithaca, NY: Cornell University.

Hix, D.M.; Pearcy, J.N. 1997. Forest ecosystems of the Marietta Unit, Wayne National Forest, southeastern Ohio: multifactor classification and analysis. Canadian Journal of Forest Research. 27: 1117-1131.

Hupp, C.R.; Osterkamp, W.R. 1996. Riparian vegetation and fluvial geomorphic processes. Geomorphology. 14: 277-295.

Keys, J., Jr.; Carpenter, C.; Hooks, S.; Koenig, F.; McNab, W.H.; Russell, W.; Smith, M.L. 1994. Ecological units of the eastern United States - first approximation (map and booklet of map unit tables). Atlanta, GA: U.S. Department of Agriculture, Forest Service.

Illhardt, B.L., Verry, E.S.; Palik, B.J. 2000. Defining riparian areas. In: Verry, E.S.; Hornbeck, J.W.; Dolloff, C.A., eds. Riparian management in forests of the continental eastern United States. New York, NY: Lewis Publishers: 23-42.

McCarthy, B.C.; Hammer, C.; Kauffman, G.; Cantino, P. 1987. Vegetation patterns and structure of an old-growth forest in southeastern Ohio. Bulletin of the Torrey Botanical Club. 114: 33-45.

McCune, B.; Antos, J. 1981. Correlations between forest layers in the Swan Valley, Montana. Ecology. 62: 1196-1204.

McCune, B.; Mefford, M.J. 1995. PC-ORD. Multivariate analysis of ecological data. Version 2.0. Gleneden Beach, OR: MJM Software Design.

Naiman, R.J.; Bilby, R.E.; Bisson, P.A. 2000. Riparian ecology and management in Pacific Coastal Rain Forest. BioScience. 50: 996-1011.

Pabst, R.J.; Spies, T.A. 1998. Distribution of herbs and shrubs in relation to landform and canopy cover in riparian forests of coastal Oregon. Canadian Journal of Botany. 76: 298-315.

Peterson, B.J.; Wollheim, W.M.; Mulholland, P.J.; Webster, J.R.; Meyer, J.L.; Tank, J.L.; Marti, E.; Bowden, W.B.; Valett, H.M.; Hershey, A.E.; McDowell, W.H.; Dodds, W.K.; Hamilton, S.K.; Gregory, S.; Morrall, D.D. 2001. Control of nitrogen export from watersheds by headwater streams. Science. 292: 86-90.

Pollock, M.M.; Naiman, R.J.; Hanley, T.A. 1998. Plant species richness in riparian wetlands - a test of biodiversity theory. Ecology. 79: 94-105.

Pregitzer, K.S.; Barnes, B.V. 1982. The use of ground-flora to indicate edaphic factors in upland ecosystems of the McCormick Experimental Forest, Upper Michigan. Canadian Journal of Forest Research. 12: 661-672.

Reed, P.B. 1988. National list of plant species that occur in wetlands. National Summary. Biol. Rep. 88. U.S. Department of Interior, Fish and Wildlife Service.

Titus, J.H. 1990. Microtopography and woody plant regeneration in a hardwood floodplain swamp in Florida. Bulletin of the Torrey Botanical Club. 117: 429-437.

Vannote, R.L.; Minshall, G.W.; Cummins, K.W.; Sedell, J.R.; Cushing, C.E. 1980. The river continuum concept. Canadian Journal of Fisheries and Aquatic Sciences. 37: 130-137.

Voss, E.C. 1996. Michigan flora. Vols. I-III. Bloomfield, MI: Cranbrook Institute of Science.

Williams, C.E.; Moriarity, W.J.; Walters, G.L. 1999. Overstory and herbaceous layer of a riparian savanna in northwestern Pennsylvania. Castanea. 64: 90-97.

Zar, J.H. 1996. Biostatistical analysis, 3d ed. Upper Sadle River, NJ: Prentice-Hall, Inc. 662 p.

APPENDIX

List of species in each ground-flora ecological species group, including species code (e.g., FRPE), lifeform class (e.g., annual forb, perennial forb, graminoids, pteridophytes, woody seedling, woody shrub, woody vine), and wetland indicator status (e.g., OBL, obligate wetland; FACW, facultative wetland; FAC, facultative; FACU, facultative upland; UPL, obligate upland).

***Viburnum* species group**
Fraxinus pennsylvanica Marshall – FRPE; woody seedling; FACWa
Lindera benzoin (L.) Blume – LIBE; woody shrub; FACW
Viburnum recognitum Fernald – VIRE; woody shrub; FAC

***Acer* species group**
Acer saccharum Marsh. – ACSA; woody seedling; FACU
Fagus grandifolia Ehrh. – FAGR; woody seedling; FACU
Mitchella repens L. – MIRE; perennial forb; FACU
Polygonatum pubescens (Willd.) Pursh – POPU; perennial forb; FAC
Prunus serotina Ehrh. – PRSE; woody seedling; FACU

***Parthenocissus* species group**
Cinna arundinacea L. – CIAR; graminoid; FACW
Dryopteris carthusiana (Villars) H.P.Fuchs – DRCA; pteridophyte; FAC
Parthenocissuss quinquefolia (L.) Planchon – PAQU; woody vine; FACU

***Fraxinus* species group**
Fraxinus americana L. – FRAM; woody seedling; FACU
*Polygonum hydropipe*r L. – POHY; annual forb; OBL
Sambucus canadensis L. – SACA; woody seedling; FACW
Toxicodendron radicans (L.) Kuntze – TORA; woody vine; FAC

***Quercus* species group**
Acer rubrum L. – ACRU; woody seedling; FAC
Quercus rubra L. – QURU; woody seedling; FACU

***Circea* species group**
Circea quadrisulcata (Maxim.) Franchet & Savat – CIQU; perennial forb; FAC
Ranunculus recurvatus Poiret – RARE; perennial forb; FAC
Viola pubescens Aiton – VIPU; perennial forb; FAC

***Impatiens* species group**
Arisaema triphyllum (L.) Schott – ARTR; perennial forb; FACW
Impatiens capensis Meerb. – IMCA; annual forb; FACW
Laportea canadensis (L.) Wedd. – LACA; perennial forb; FACW

***Leersia* species group**
Leersia virginica Willd. – LEVI; graminoids; OBL
Boehmeria cylindrica (L.) Sw. – BOCY; perennial forb; FACW