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Landscape hierarchies influence riparian ground-flora communities in Wisconsin, USA

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Abstract

We examined the distribution of ground-flora species (herbaceous and woody species <1 m tall) across riparian areas of northeastern Wisconsin in an effort to understand how hierarchical landscape properties, such as the physiographic system (ground moraine and outwash plain), valley system (constrained and unconstrained), and valley floor landforms influence distribution patterns of ground-flora species and functional plant guilds across riparian areas of small streams and rivers in a glacial landscape. A total of 162 species were recorded on 417 (1 m^2) plots stratified by four different valley types that reflect the dominant physiographic system and valley system (constrained ground moraine, constrained outwash plain, unconstrained ground moraine, unconstrained outwash plain) and transverse geomorphic structure (valley floor landforms including floodplains, terraces, slopes, and adjacent uplands). Although distribution patterns of individual ground-flora species are highly variable among the four valley types, canonical correspondence analyses (CCA) of individual valley types indicate that ground-flora vegetation is related strongly to hierarchical landscape properties, including valley type and the transverse geomorphic structure of the stream valley. Vegetation ultimately reflects the influence of hydrogeomorphic processes that shape valley floor landforms. Constrained valley types tend to be characterized by diverse floodplain ground-flora communities dominated by graminoids and pteridophytes, while the terraces and slope plant communities are comprised of facultative upland and obligate upland perennial forb and woody species whose distribution appears to be a function of topographic features, such as aspect. However, ground-flora communities of unconstrained valley types appear to be responding not only to changes associated with the transverse geomorphic structure of the riparian ecotone, but also to more localized changes in environmental conditions associated with flooding and hydrologic regime. As a result, floodplain, terrace, and slope ground-flora communities tend to be diverse, dominated by a mixture of obligate wetland, facultative wetland, and facultative species. Thus, variation in riparian plant community characteristics can be explained using a nested, hierarchical landscape framework to organize and group different riparian settings based on the underlying geomorphic processes shaping stream valleys. Based on these results, we suggest that riparian management zones (RMZs) designed to maintain riparian function should be variable in width rather than fixed, encompassing variation in valley floor landforms and valley walls, regardless of the physiographic system.

Keywords: Riparian areas; Valley floor landforms; Floodplains; Streamside forests; Diversity; Ordination; Lake States

1. Introduction

Riparian areas are complex ecotones characterized by gradients of structural and functional change from the water's edge to the upland (Gregory et al., 1991; Ilhardt et al., 2000). At local or individual reach scales, riparian plant communities tend to be species rich and highly variable in composition (Salo et al., 1986; Gregory et al., 1991; Pollock et al., 1998; Brinson and Verhoeven, 1999; Goebel et al., 2003), while at the landscape and regional scales, riparian areas often influence the longitudinal distribution of plant species along river corridors (Nilsson et al., 1994), provide refugia for vernal herb species (Bratton et al., 1994), and mediate exotic plant invasions (Stohlgren et al., 1998). Although riparian areas are characterized by a variety of different ecosystem processes at a variety of spatial scales, a suite of hierarchical, hydrogeomorphic processes are believed to be the important factors constraining the composition and structure of plant communities across and among riparian areas (Gregory et al., 1991; Auble et al., 1994;

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Hupp and Osterkamp, 1996; Swanson et al., 1998; Bendix and Hupp, 2000; Verry et al., 2004; Holmes et al., 2005).

Within different physiographic systems at the landscape scale, the geologic setting or position in the stream network often mediates stream flows and stream valley characteristics that in turn mediate disturbance regimes, soil development, and the organization and structure of plant communities (Rowe and Sheard, 1981; Host and Pregitzer, 1992; Fetherston et al., 1995; Pregitzer et al., 2001). In most stream valleys, repeatable longitudinal sequences of stream valley segments (e.g., constrained, unconstrained) and transverse sequences of valley floor landforms (e.g., floodplain, low terrace, high terrace, slopes or valley wall) reflect dominant hydrogeomorphic processes of different physiographic systems (Pabst and Spies, 1998; Bendix and Hupp, 2000; Verry, 2000). Where stream channels and stream valleys are controlled by bedrock, floodwaters will reflect the constraining influence of the bedrock and will regulate the local distribution and organization of valley floor landforms across the stream valley in a different manner than in unconstrained stream valley types.

At local scales, valley floor landforms (e.g., floodplains, terraces) regulate the composition and structure of riparian plant communities (e.g., Hupp and Osterkamp, 1996; Goebel et al., 1996; Bendix and Hupp, 2000; Holmes et al., 2005). When compared to the adjacent upland ecosystems, most riparian areas are often species rich and dominated by species with unique traits not found in many upland species, allowing these species or groups of species with similar morphological and physiological characteristics (e.g., functional lifeform guilds) to persist in a frequently disturbed and heterogeneous environment (Stromberg et al., 1996; Smith et al., 1997; Brinson and Verhoeven, 1999; Goebel et al., 2003). However, there are likely to be differences in plant community structure and composition among fluvial landforms within a stream valley.

As the distribution of stream valley segments and valley floor landforms reflect predominate hydrogeomorphic processes operating across a broad landscape, these geomorphic structures are likely surrogates for the hydrogeomorphic processes occurring in stream valleys (Gregory et al., 1991). When examined together, they also provide a hierarchical structure (*sensu* O'Neill et al., 1986) for characterizing vegetation change across riparian ecotones, as both valley types and valley floor landforms reflect the influence of the terrestrial and aquatic environments. Few studies, however, have used a hierarchical approach to quantify the effects of longitudinal and transverse geomorphic structure on riparian plant communities (Ilhardt et al., 2000). In glacial landscapes, Baker and Barnes (1998) observed that composition and structure of floodplain forests differ among physiographic systems (i.e., areas characterized by similar surficial geology and parent material), specifically those associated with outwash plain and moraine landtype associations. This study focused primarily on the floodplains of large river systems, and it is not clear whether similar hierarchical factors control vegetation patterns associated with other valley floor landforms (e.g., terraces, slopes) or with smaller streams in glacial landscapes. Additionally, Baker and Barnes (1998) focused primarily on overstory species, especially woody floodplain species. Less is known about ground-flora species, which are thought to be more sensitive to the various environmental gradients operating across riparian ecotones than overstory species (Stromberg et al., 1996; Ilhardt et al., 2000).

In this paper, we quantify the hierarchical relationships among different physiographic systems (ground moraine, outwash plain), valley segments (constrained, unconstrained), valley floor landforms (floodplains, terraces, valley wall, and adjacent uplands), and riparian plant communities in a large watershed located in northeastern Wisconsin, USA (Fig. 1). Specifically, we: (1) assess the influence of hierarchical geomorphic controls on the composition of ground-flora communities across and among riparian areas located in different physiographic systems, valley types, and valley floor landforms and (2) examine patterns in plant diversity and assemblages of functional plant guilds within this same hierarchical framework.

2. Study area

Study sites were located in the Popple River watershed on the Nicolet National Forest in northeastern Wisconsin, USA (Fig. 2). The study area has a humid-continental climate with mean annual temperatures ranging from 4 to 7 °C. Mean annual precipitation ranges from 660 to 910 mm, most of which occurs during the summer (Keys et al., 1994). The regional terrain of the Popple River watershed reflects the influence of Pleistocene glaciation. Physiographic systems are distributed in a landscape mosaic that includes gently rolling drumlinized terrain with isolated ice-contact, sand-gravel outwash plains, and sandy to loamy till moraines (Keys et al., 1994). These porous glacial materials allow for rapid percolation and high storage capacity of water in forest soils. Stream and river valleys tend to be wide where not constrained by bedrock or glacial substrate, reflecting the periglacial meltwater channels. This often results

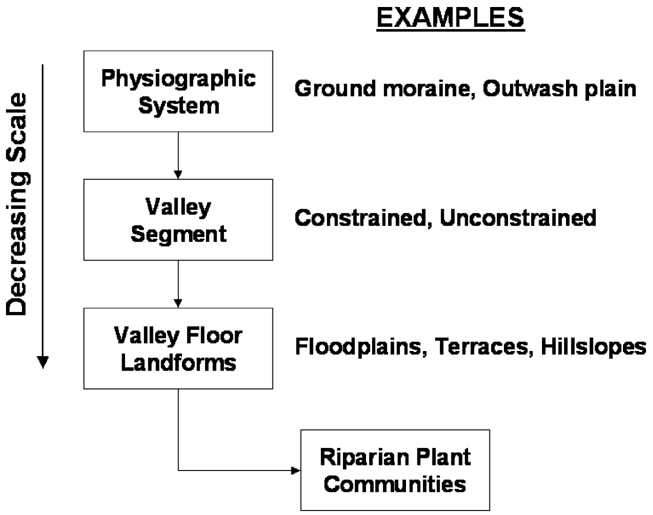

Fig. 1. Generalized diagram of the hierarchical factors regulating the development of plant communities among and across riparian areas, with examples of each hierarchical level.

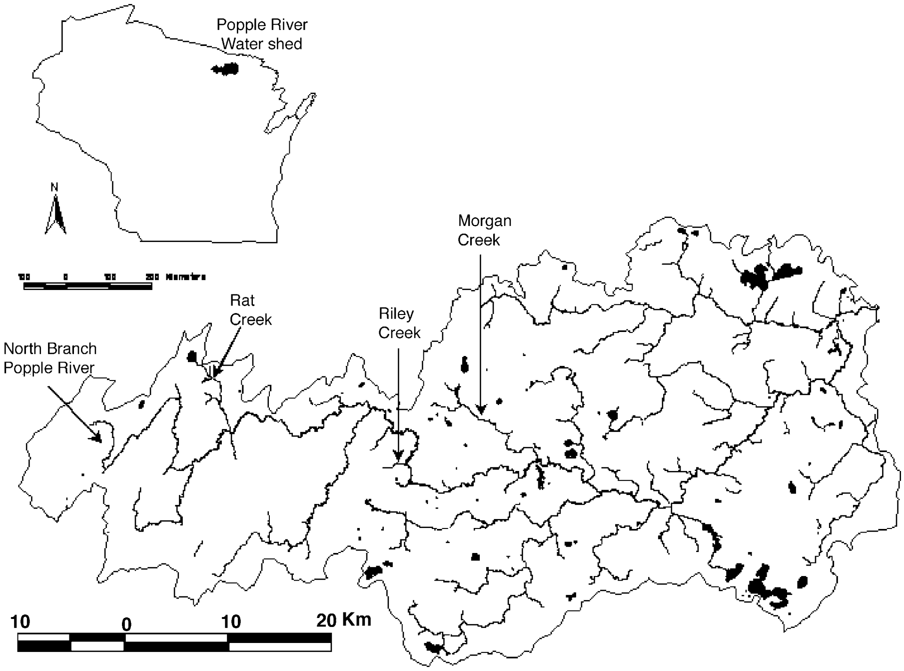

Fig. 2. Location of the Popple River watershed and study sites in northeastern Wisconsin.

in broad, low-lying valleys drained by smaller modern-day stream and river channels, often fed by large groundwater inputs (Keys et al., 1994). These valleys usually contain a floodplain, one or more higher terraces, and a distinct valley wall or slope.

We stratified study sites by physiographic system (ground moraine and outwash plain) and valley system (constrained and unconstrained) to form the following classes: (1) constrained ground moraine (GMC); (2) unconstrained ground moraine (GMU); (3) constrained outwash plain (OPC); and, (4) unconstrained outwash plain (OPU; Table 1). Throughout the paper, these combinations of physiographic systems and valley systems are referred to as valley types. Ground moraine valley types were located in the Argonne drumlinized ground moraine, silty, or loamy landtype association, while the outwash plain valley types were found in the Argonne Plains, loamy or silty interdrumlin outwash or Popple River Knolls loamy outwash landtype associations. All study sites were located in a landscape matrix of 70–100-year-old second-growth forests.

3. Methods

3.1. Data collection

Data were collected at nine sites in four sub-watersheds of the Popple River watershed (Fig. 2). Each site represented an individual valley type (Table 1). At each site, we collected ground-flora data from three transects located on a single side of the stream and arrayed perpendicular to streamflow. In all cases, sites were dominated by relatively undisturbed (e.g., no roads, trails, wildlife food plots) second-growth northern hardwood forest ecosystems. Transects extended from the stream edge to at least 40 m into the uplands to ensure we were beyond the functional riparian ecotone as defined by Verry et al. (2004)—the width of the valley floodprone area plus 30 m on

Table 1
Characteristics of study stream valleys in northeastern Wisconsin

Reach name	Physiographic system	Valley segment	Stream order[a]	Valley floor width (m)	Stream bankfull width (m)
Upper N. Branch Popple Rvr	Ground Moraine	Constrained	2	139	8.4
Lower N. Branch Popple Rvr	Ground Moraine	Constrained	2	92	7.3
Lower Rat Creek	Ground Moraine	Constrained	1	111	5.3
Lower N. Branch Popple Rvr	Ground Moraine	Unconstrained	2	630	6.4
Upper Rat Creek	Ground Moraine	Unconstrained	1	615	7.4
Upper Riley Creek	Outwash Plain	Constrained	2	52	5.2
Lower Riley Creek	Outwash Plain	Constrained	2	55	5.6
Upper Morgan Crk	Outwash Plain	Unconstrained	2	620	6.8
Upper N. Branch Popple Rvr	Outwash Plain	Unconstrained	2	940	7.6

[a] Horton (1945) stream order classification.

each side of the stream valley so as to encompass the important adjacent riparian functions. At each site, the location of the first transect was determined randomly beginning at the upstream boundary of the study site. Successive transects were located 15 m apart in the downstream direction. Topographic surveys of each transect were developed using a level transit and standard surveying methods with bankfull elevation as the reference point. We used these topographic surveys to calculate the distance from and elevation above bankfull channel, and a clinometer to determine the aspect of each ground-flora sample plot. Finally, boundaries between valley floor landforms were visually determined while topographically surveying the transverse geomorphic structure of each riparian area.

Sample plots (1 m^2) were located along each transect at fixed distances. Along all transects plots were spaced at 5 m intervals from the stream edge to 20 m. In the constrained stream valleys, subsequent plots beyond 20 m on each transect were located every 15 m, however because the unconstrained stream valleys were often more than 600 m wide (Table 1), subsequent plots beyond 20 m on these transects were located every 30 m. In all cases, at least two sample plots on each transect were located in the adjacent upland forest. Individual transects contained 10–16 plots, depending on valley width, for a total of 417 (1 m^2) sample plots in the study. In each sample plot, we recorded percent cover of all ground-flora species (herbaceous and woody species <1 m tall) in the following cover classes: <1%, 1–5%, 6–10%, 11–20%, 21–40%, 41–70%, and 71–100%. Additionally, we categorized species into functional plant guilds including annual forbs, perennial forbs, graminoids, pteridophytes, and woody shrubs and seedlings, and estimated the percent cover of each group. 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; USFS, 1997). Voucher specimens were collected for many species of uncertain identity; nomenclature and lifeform categories follow Voss (1972, 1985, 1996), except for pteridophytes (Gleason and Cronquist, 1991).

3.2. Data analyses

Because rare species can mask patterns in vegetation, we eliminated species occurring on less than 5% of all sample plots (19 out of 417 plots) for all floristic analyses. Additionally, the aspect of each sample plot was transformed [cos (45 − aspect) + 1] prior to analyses to assign the relatively warm and dry southwesterly slopes with a minimum value of 0, and cool and moist northeasterly slopes with a maximum value of 2 (Beers et al., 1966). Distributions of individual species relative to the hierarchical factors thought to control their distribution were examined using canonical correspondence analysis (CCA), a direct gradient analysis that uses multiple regression to examine patterns in the distribution of species as constrained by explanatory variables. CCAs were conducted separately for each of the four valley types in order to compare the effects of the transverse geomorphic structure on the distribution of ground-flora communities among different physiographic and valley segment types (i.e., individual valley types). In each CCA, the distribution of the ground-flora species was constrained by the major factors associated with the transverse geomorphic structure of the riparian ecotone, including landform class (floodplain, terrace, slope, upland), transformed aspect, elevation above bankfull channel (m), and distance from bankfull channel (m). Data were summarized in triplots that relate the individual plots and ground-flora species occurring within them with physical factors using CANOCO software (ter Braak and Smilauer, 1998). Vector length and direction indicate the strength of each physical factor in determining the distribution of sample plots and vegetation across the riparian ecotone. Categorical landform classes and their influence on the distribution of plots and species are represented as points in ordination space (ter Braak and Smilauer, 1998).

We supplemented the CCAs with Dufrene and Legendre's (1997) indicator analysis using PC-ORD (McCune and Mefford, 1995). These analyses 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 random permutations having an indicator value equal to or exceeding the observed indicator value (Dufrene and Legendre, 1997). Only those species with $P \leq 5\%$ in the indicator analysis were represented on the CCA triplots.

We also examined hierarchical influences on diversity (Shannon's index; Ludwig and Cornelius, 1987) and cover of individual lifeform guilds among the different valley types and across the transverse geomorphic gradient of the riparian ecotone. Specifically, we used an analysis of variance (ANOVA) with planned contrasts (PROC GLM; SAS Institute, 1989) to test the following hypotheses in each of the four different valley types:

1. Floodplains are more diverse and have higher percent cover of individual lifeform guilds (annuals, perennials, pteridophytes, graminoids, and woody shrubs and seedlings) than the adjacent uplands.
2. Terraces are more diverse and have higher percent cover of individual lifeform guilds than the adjacent uplands.
3. Hillslopes (i.e., valley walls) are more diverse and have higher percent cover of individual lifeform guilds than the adjacent uplands.

4. Results

4.1. Ground-flora community composition

We sampled a total of 162 species, 57 of which occurred on more than 5% of all plots. Almost half of these 162 species are perennial forbs (41%), while the remaining species are classified as woody shrubs and seedlings (26%), pteriodophytes (17%), graminoids (13%), or annual forbs (2%). Approximately one-third of these species are considered either facultative wetland

(17%) or obligate wetland (17%) species, while the remaining are classified as facultative (22%), facultative upland (24%), or upland obligate (20%) species (Table 2). Those species that were considered rare (occurring on ≤5% of the sample plots) were dominated by perennial forbs (42%), graminoids (15%), pteridophytes (14%), and woody shrubs and seedlings (13%).

4.2. *Canonical correspondence analysis*

The first two axes in each CCA explain 9–30% of the total variation in species composition (Table 3). For each valley type, there are significant correlations among the distribution of ground-flora species, landforms, and stream valley characteristics (Table 3). In all but the constrained ground moraine valley type, elevation above and distance from the bankfull channel are significantly correlated with either the first or second CCA axis ($P < 0.05$; Table 3). There are also significant correlations among the first and second axes and valley floor landforms ($P < 0.05$), suggesting that species' distributions are closely related to the transverse geomorphic structure of the riparian ecotones, regardless of the valley type (Table 3). Finally, transformed aspect is correlated significantly with either the first or second CCA axis in all four valley types, with the strongest correlations associated with the first CCA axis in the constrained valley (Table 3).

4.3. *Indicator species analysis*

Thirteen species are significant indicators of floodplains in the constrained ground moraine valley type, including obligate wetland species (*Alnus incana*, *Carex stricta*, and *Leersia oryzoides*), facultative wetland species (*Coptis trifolia*, *Equisetum sylvaticum*, *Fraxinus nigra*, and *Impatiens capensis*), facultative upland species (*Galium triflorum*, *Oxalis montana*, *Rubus strigosus*, and *Viola pubescens*) and two species not classified in terms of the wetland indicator status (*Brachyelytrum erectrum* and *Trillium grandiflorum*; Table 4). Facultative and facultative upland species are significant indicators of the terraces and slopes of the constrained ground moraine valley type (Table 4). Conversely, the floodplains of the unconstrained ground moraine valley type are dominated by three species (Fig. 3) considered significant indicator species, including the obligate and facultative wetland species (*Chamaedaphne calyculata*, *Vaccinium oxycoccus*, and *Rubus pubescens*; Table 4). A variety of facultative wetland, facultative, and facultative upland species dominate the terraces and slopes of the unconstrained ground moraine valley type, two of which are significant floodplain indicators in the constrained ground moraine valley type (*Equisetum sylvaticum* and *Oxalis montana*).

Table 2

Ground-flora species occurring on >5% of the sample plots, with lifeform guild and wetland indicator status, in riparian areas of northeastern Wisconsin

Species name	Species code	Lifeform guild[a]	Wetland indicator[b]
Abies balsamea	ABBA	WS	FACW
Alnus incana	ALIN	WS	OBL
Acer saccharum	ACSA	WS	FACU
Acer rubrum	ACRU	WS	FAC
Aralia nudicaulis	ARNU	PF	FACU
Aster macrophyllus	ASMA	PF	NI
Athyrium fillix-femina	ATFI	PT	FAC
Brachyelytrum erectrum	BRER	GR	NI
Cardamine pensylvanica	CAPE	AF	FACW
Carex arctata	CAAR	GR	NI
Carex stricta	CAST	GR	OBL
Carex trisperma	CATR	GR	OBL
Chamaedaphne calyculata	CHCA	WS	OBL
Clintonia borealis	CLBO	PF	FAC
Coptis trifolia	COTR	PF	FACW
Cornus canadensis	COCA	PF	FAC
Cystopteris fragilis	CYFR	PT	FACU
Dryopteris intermedia	DRIN	PT	FAC
Equisetum sylvaticum	EQSY	PT	FACW
Fraxinus americana	FRAM	WS	FACU
Fraxinus nigra	FRNI	WS	FACW
Galium triflorum	GATR	PF	FACU
Gymnocarpium dryopteris	GYDR	PT	FAC
Impatiens capensis	IMCA	PF	FACW
Leersia oryzoides	LEOR	GR	OBL
Lycopodium clavatum	LYCL	PT	FAC
Lycopodium obscurum	LYOB	PT	FACU
Maianthemum canadense	MACA	PF	FAC
Oryzopis asperifolia	ORAS	GR	NI
Osmorhiza claytoni	OSCL	PF	FACU
Oxalis montana	OXMO	PF	FACU
Prunus serotina	PRSE	WS	FACU
Rubus pubescens	RUPU	WS	FACW
Rubus strigosus	RUST	WS	FACU
Scutellaria epilobifolia	SCEP	PF	OBL
Scutellaria laterifolia	SCLA	PF	OBL
Scutellaria epilobifolia	SCEP	PF	OBL
Scutellaria laterifolia	SCLA	PF	OBL
Streptopus roseus	STRO	PF	FAC
Thelyptris phegopteris	THPH	PT	NI
Trientalis borealis	TRBO	PF	FAC
Trillium grandiflorum	TRGR	PF	NI
Vaccinium oxycoccus	VAOX	WS	OBL
Urtica diocia var. procera	URPR	PF	FACW
Viburnum acerifolim	VIAC	WS	UPL
Viola pubescens	VIPU	PF	FACU
Viola selkirkii	VISE	PF	NI

[a] Lifeform guilds include: AF, annual forbs; GR, graminoids; PF, perennial forbs; PT, pteidophyrtes; WS, woody shrubs and seedlings.

[b] Wetland indicator classes include: OBL, obligate wetland species; FACW, facultative wetland species; FAC, facultative species; FACU, facultative upland species; UPL, obligate upland species; NI, no indicator rating available.

Similar patterns of species distribution are observed in the outwash plain valley types (Fig. 4; Table 5). Indicator analyses reveal that 11 species are significant floodplain indicators of constrained outwash plain valley types, including five obligate wetland species (*Alnus incana*, *Carex stricta*, *Leersia oryzoides*, *Scutellaria epilobifolia*, and *S. laterifolia*), three facultative wetland species (*Equisetum sylvaticum*, *Impatiens capensis*, and *Rubus pubescens*), two facultative upland species (*Galium triflorum* and *Viola pubescens*) and one species not classified in terms of the wetland indicator status (*Viola selkirkii*; Table 5). Several different facultative wetland, facultative, and facultative upland species are characteristic of the slope and uplands of the constrained outwash plain valley type (Table 5). However, as in the ground moraine valley types,

Table 3
Summary statistics of canonical correspondence analyses (CCA) by valley type

Analysis	Ground moraine				Outwash plain			
	Constrained valley		Unconstrained valley		Constrained valley		Unconstrained valley	
	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
Eigenvalue	0.628	0.324	0.977	0.769	0.739	0.400	0.818	0.513
Species–environment correlation	0.923	0.777	0.992	0.929	0.944	0.866	0.963	0.899
Cumulative % variance								
Of species data	8.8	13.4	12.2	21.8	19.1	29.5	12.6	20.6
Of species–environment relation	44.9	68.0	33.8	60.4	48.4	74.6	43.0	69.9
Intraset correlations								
Distance	0.07	−0.01	−0.47	0.68[a]	0.64[a]	0.27	0.77[a]	−0.40
Elevation	−0.01	−0.14	−0.46	0.70[a]	0.72[a]	0.30	0.75[a]	0.53[a]
Transformed aspect	0.89[a]	−0.06	−0.69[a]	−0.19	0.85[a]	0.05	0.01	0.55[a]
Floodplain landform	−0.01	0.62[a]	0.55[a]	−0.44	−0.17	−0.44	−0.92[a]	0.13
Terrace landform	0.34	−0.24	−0.08	−0.29	–	–	0.32	−0.32
Slope landform	−0.11	−0.41	−0.26	0.35	−0.68[a]	0.21	0.53[a]	−0.35
Upland landform	−0.26	−0.01	−0.31	0.52	0.76[a]	0.19	0.50	0.47

[a] Correlation coefficients significant at $P < 0.05$.

only three species are significant floodplain indicators of the unconstrained outwash plain valley type, including *Carex stricta*, *Leersia oryzoides*, and *Cystoperis fragilis*. Unique assemblages of ground-flora species also are characteristic of the other valley floor and upland landforms, dominated by a mixture of facultative wetland, facultative, and facultative upland species (Fig. 4; Table 5).

4.4. Diversity and lifeform guilds

In all valley types, except for the unconstrained outwash plain, the ground-flora community of the floodplains was significantly more diverse ($P < 0.01$) than the adjacent uplands (Table 6). Additionally, the only significant differences in diversity detected between the terraces or slopes, and adjacent uplands were in the constrained ground moraine valley type and the unconstrained outwash plain valley type. In the unconstrained outwash plain valley type, species diversity was significantly higher on the terraces and slopes compared to the adjacent uplands ($P < 0.01$), but not significantly different between the floodplains and uplands (Table 6).

In all valley types, total ground-flora cover was significantly higher ($P < 0.01$) on the floodplain than the adjacent upland landforms, with the highest cover observed in the unconstrained ground moraine reach type (Table 6). No significant differences in total cover were observed between the terraces and uplands, or the slopes and uplands, except in the unconstrained outwash plain, where the terraces had significantly higher ground-flora cover than the uplands ($P < 0.05$; Table 6). Similar patterns were observed when total cover was partitioned into lifeform guilds. Graminoid and pteridophyte cover were both significantly higher ($P < 0.01$) on the floodplains than in the uplands in all four valley types (Table 6). While annual forb cover was low across all valley types (<1.0%), there were significant differences in perennial forb cover between the floodplain and upland landforms. Specifically, mean perennial forb cover was nearly three times higher on the floodplains than the uplands of the unconstrained ground moraine valley type ($P < 0.01$; Table 6), and twice as high in the floodplains than the uplands of the constrained outwash plain valley type ($P < 0.05$; Table 6). No differences between the terraces and the uplands, or the slopes and uplands, were observed in the different valley types, except for the unconstrained outwash plain valley type where mean cover of perennial forbs was significantly higher on the slope landform than the adjacent uplands ($P < 0.05$; Table 6). Cover of woody seedlings and shrubs was generally low (<8%) in each valley type and not significantly different among landforms, except in the constrained outwash valley type (Table 6), where woody cover was significantly higher on the floodplain (11.8%) than the adjacent upland (2.1%) ($P < 0.05$; Table 6).

5. Discussion

Hierarchy theory (O'Neill et al., 1986) provides the conceptual basis for our approach to understanding interrelationships among riparian ground-flora communities and multi-scale environmental factors. When applied to riparian landscapes, hierarchy theory predicts that the upper levels of the hierarchy (e.g., physiographic systems) constrain a complex array of hydrogeomorphic processes (e.g., flooding) that in turn mediate the dynamics of lower hierarchical levels, including stream valley shape, fluvial landforms, and plant communities (Fig. 1; Allen and Starr, 1982; Baker and Barnes, 1998; Bendix and Hupp, 2000). Consequently, a hierarchical approach to studying riparian systems is valuable for distinguishing differences in plant community composition and structure at multiple spatial scales within a regional context.

Our study of riparian areas in northeastern Wisconsin illustrates that specific patterns of ground-flora composition are mediated by hierarchical landscape factors, including valley floor landforms, and the physiographic system and valley

Table 4
Indicator analysis[a] of ground-flora species of riparian areas associated with constrained and unconstrained valleys in the ground moraine physiographic type of northeastern Wisconsin

Species name	Constrained valley				Unconstrained valley			
	FP	TR	SL	UP	FP	TR	SL	UP
Abies balsamea	2	0	13	0	10	2	9	0
Alnus incana	22^{**}	0	0	0	4	0	0	0
Acer saccharum	16	10	10	6	0	7	42^{**}	10
Acer rubrum	18	23	30	1	0	0	0	60^{**}
Aralia nudicaulis	0	0	11	1	2	0	1	7
Aster macrophyllus	–	–	–	–	0	16^{*}	0	0
Athyrium fillix-femina	9	0	1	9	2	27	0	0
Brachyelytrum erectrum	24^{**}	0	1	6	0	0	6	0
Cardamine pensylvanica	8	1	1	0	22	0	1	0
Carex arctata	8	9	1	5	6	29^{*}	1	6
Carex stricta	17^{**}	0	0	0	2	0	0	0
Carex trisperma	2	0	0	7	3	0	21	6
Chamaedaphne calyculata	–	–	–	–	50^{*}	0	0	0
Clintonia borealis	6	4	11	4	6	38^{**}	0	0
Coptis trifolia	48^{**}	1	0	0	9	0	13	0
Cornus canadensis	1	1	0	3	12	15	0	0
Cystopteris fragilis	–	–	–	–	–	–	–	–
Dryopteris intermedia	13	8	15	8	0	5	15	8
Equisetum sylvaticum	33^{**}	0	0	0	0	50^{**}	0	0
Fraxinus americana	0	0	15^{**}	0	0	40^{**}	2	9
Fraxinus nigra	39^{**}	0	0	0	6	0	0	0
Galium triflorum	15^{*}	0	0	0	6	0	0	0
Gymnocarpium dryopteris	0	33^{*}	0	0	6	3	3	5
Impatiens capensis	11^{**}	0	0	0	8	0	0	0
Leersia oryzoides	19^{**}	0	0	0	13	0	0	0
Lycopodium clavatum	4	2	15	12	0	0	28^{*}	2
Lycopodium obscurum	2	5	13	12	0	0	6	12
Maianthemum canadense	11	15	5	18	2	11	9	19
Oryzopis asperifolia	1	2	8	1	0	0	0	37^{**}
Osmorhiza claytoni	1	22^{*}	11	0	0	0	0	20^{*}
Oxalis montana	21^{**}	3	0	1	0	0	28^{**}	0
Prunus serotina	0	6	16	1	0	33^{**}	1	3
Rubus pubescens	2	0	1	12	29^{*}	0	0	0
Rubus strigosus	22^{**}	0	0	0	6	0	0	0
Scutellaria epilobifolia	–	–	–	–	2	0	0	0
Scutellaria laterifolia	7	1	0	0	–	–	–	–
Streptopus roseus	3	4	5	8	–	–	–	–
Thelyptris phegopteris	0	0	0	16^{**}	0	31^{**}	0	0
Trientalis borealis	16	9	9	2	2	9	25	6
Trillium grandiflorum	20^{**}	1	3	0	–	–	–	–
Urtica diocia var. procera	7	13	3	0	–	–	–	–
Vaccinium oxycoccus	–	–	–	–	41^{**}	0	1	0
Viburnum acerifolim	2	4	0	0	13	0	0	0
Viola pubescens	24^{**}	0	3	0	1	0	5	0
Viola selkirkii	2	6	2	10	0	0	0	13

Indicator values represent the % of perfect indication for each landform (FP, floodplain; TR, terrace; SL, hillslope; UP, upland) and are based on the species' relative abundance and relative frequency in the samples that represent each group. Significance of indicator value tested using a Monte Carlo permutation procedure.

[a] Indicator analysis based on method of Dufrene and Legendre (1997).

[*] Proportion of randomized trials with indicator value equal to or exceeding the observed indicator value by 0.05%.

[**] Proportion of randomized trials with indicator value equal to or exceeding the observed indicator value by 0.01%.

segment in which they are embedded. These relationships are similar to those observed in larger river systems of similar glacial landscapes of northern Lower Michigan (Baker and Barnes, 1998). In these larger river systems, the physiographic system was found to be an important determinant of floodplain overstory composition and floodplain ecosystem diversity. However, our results show that the physiographic system and transverse geomorphic structure not only influence vegetation and ecosystem diversity patterns of frequently inundated floodplains, but also valley floor landforms often beyond the influence of frequent flooding (e.g., terraces, slopes), regardless of the physiographic system or valley segment type. Our results are also similar to those observed along small headwater streams in northeastern Ohio (Holmes et al., 2005) and a small river in Upper Michigan (Goebel et al., 2003). In these systems, landforms located within the stream valley were more diverse

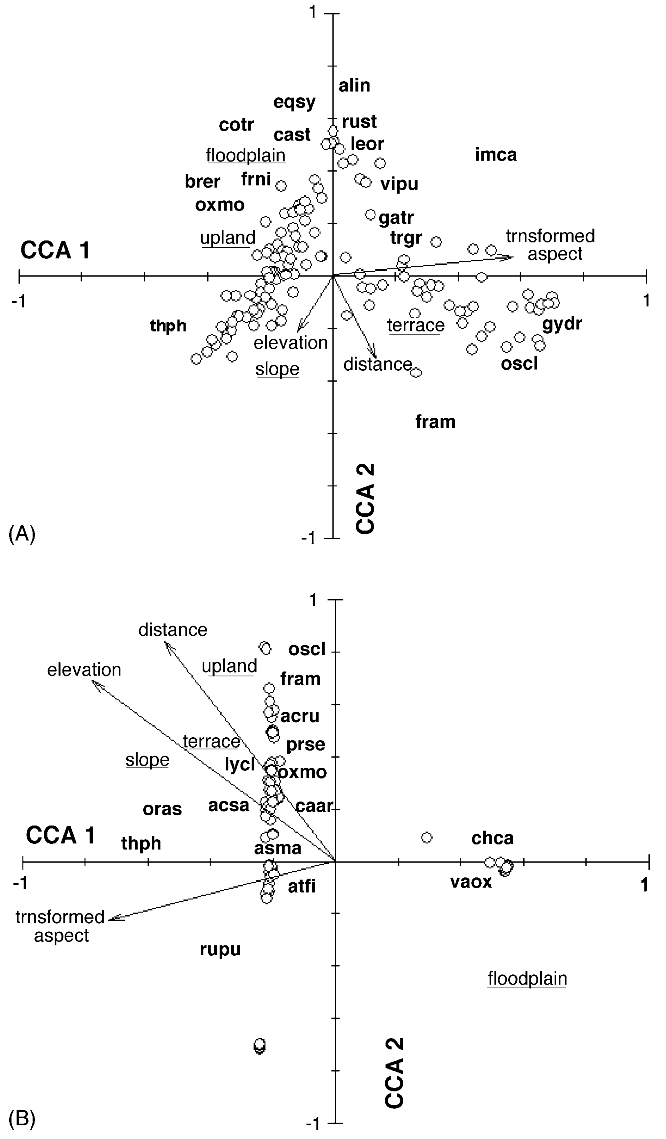

Fig. 3. Canonical correspondence analysis (CCA) relating ground-flora species of ground moraine constrained valley type (A) and unconstrained valley type (B) of riparian areas located in northeastern Wisconsin. See Table 2 for species codes.

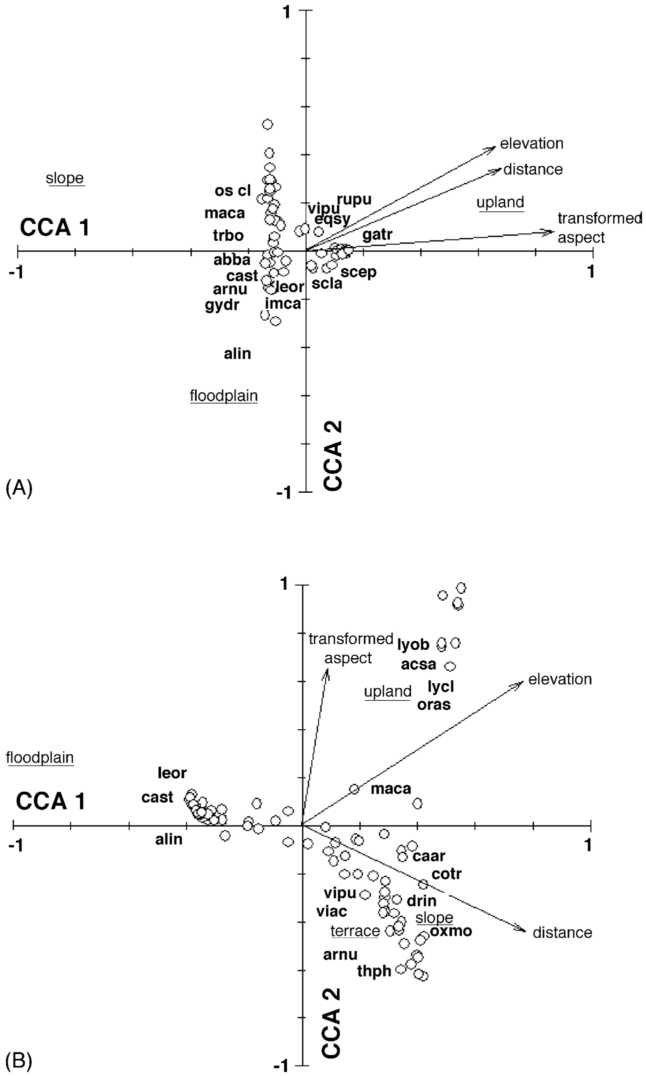

Fig. 4. Canonical correspondence analysis (CCA) relating ground-flora species of outwash plain constrained valley type (A) and unconstrained valley type (B) of riparian areas located in northeastern Wisconsin. See Table 2 for species codes.

than adjacent uplands and in most cases floodplains were more diverse and characterized by unique ground-flora species than adjacent terraces and hillslopes, especially at larger scales (Goebel et al., 2003).

5.1. Influence of hierarchical landscape properties on riparian ground-flora communities

At the watershed scale, differences between ground moraine and outwash plain physiographic systems determine patterns and arrangement of valley types and valley floor landforms. The periglacial processes that once dominated this landscape have created large valleys relative to the size and power of modern streams and rivers (Keys et al., 1994), especially in the outwash plain physiographic system and between drumlins in the ground moraine physiographic system (Fig. 5). There are locations, however, where these valleys become more narrow or constrained, such as near the end of two moraines in the ground moraine system (e.g., Lower North Branch Popple River; Fig. 5), or where glacial meltwaters down-cut through sandy surface layers in outwash, exposing different underlying till deposits that limit or confine the movements of streams across the valley floor (e.g., Rat Creek; Fig. 5).

The result is that constrained valley types have markedly different transverse geomorphic structures that are largely regulated by the physiographic system. For example, in constrained ground moraine and outwash plain valley types, riparian areas typically have narrow floodplains, with a diverse ground-flora and higher cover of graminoids and pteridophytes than other lifeform guilds favored by frequent flooding. In contrast, ground-flora communities of terraces along con-

Table 5
Indicator analysis[a] of ground-flora species of riparian areas associated with constrained and unconstrained valleys in the outwash plain physiographic type of northeastern Wisconsin

Species name	Constrained valley				Unconstrained valley			
	FP	TR	SL	UP	FP	TR	SL	UP
Abies balsamea	1	–	26^{*}	0	0	1	7	0
Alnus incana	33^{**}	–	0	0	27	1	0	0
Acer saccharum	7	–	21	31	0	1	1	47^{**}
Acer rubrum	–	–	–	–	1	4	8	0
Aralia nudicaulis	0	–	42^{**}	0	0	20^{**}	0	0
Aster macrophyllus	0	–	1	4	0	0	5	0
Athyrium fillix-femina	6	–	0	2	–	–	–	–
Brachyelytrum erectrum	0	–	15	0	0	0	5	0
Cardamine pensylvanica	12	–	1	0	2	14	3	0
Carex arctata	2	–	15	34	0	15	15	26^{*}
Carex stricta	89^{**}	–	2	0	91^{**}	0	0	0
Carex trisperma	0	–	4	0	0	7	0	0
Chamaedaphne calyculata	–	–	–	–	2	0	0	0
Clintonia borealis	–	–	–	–	0	15	5	5
Coptis trifolia	0	–	4	0	0	35^{**}	24	0
Cornus canadensis	–	–	–	–	2	22	13	2
Cystopteris fragilis	16	–	1	0	23^{*}	8	0	0
Dryopteris intermedia	13	–	7	0	1	35^{*}	25	7
Equisetum sylvaticum	25^{**}	–	0	0	0	7	7	0
Fraxinus americana	–	–	–	–	–	–	–	–
Fraxinus nigra	4	–	0	0	–	–	–	–
Galium triflorum	56^{**}	–	0	2	9	5	9	1
Gymnocarpium dryopteris	0	–	31^{**}	0	0	14	4	0
Impatiens capensis	71^{**}	–	0	0	–	–	–	–
Leersia oryzoides	58^{**}	–	0	6	80^{**}	0	0	0
Lycopodium clavatum	–	–	–	–	0	0	5	44^{**}
Lycopodium obscurum	0	–	1	6	0	0	1	48^{**}
Maianthemum canadense	0	–	16	27^{*}	0	8	7	28^{*}
Oryzopis asperifolia	0	–	14	20	0	0	6	27^{**}
Osmorhiza claytoni	0	–	3	47^{**}	–	–	–	–
Oxalis montana	–	–	–	–	0	9	42^{**}	0
Prunus serotina	1	–	7	2	–	–	–	–
Rubus pubescens	23^{*}	–	0	0	6	3	0	2
Rubus strigosus	13	–	0	0	9	16	1	0
Scutellaria epilobifolia	60^{**}	–	2	0	7	0	0	0
Scutellaria laterifolia	50^{**}	–	0	0	8	7	0	0
Streptopus roseus	–	–	–	–	0	10	1	0
Thelyptris phegopteris	0	–	11	0	0	8	21^{*}	0
Trientalis borealis	0	–	26	28	0	3	7	8
Trillium grandiflorum	0	–	7	0	–	–	–	–
Urtica diocia var. procera	–	–	–	–	13	0	0	0
Viburnum acerifolim	–	–	–	–	0	31^{**}	3	0
Viola pubescens	17^{*}	–	0	0	1	7	34^{**}	1
Viola selkirkii	18^{*}	–	1	0	0	1	4	0

Indicator values represent the % of perfect indication for each landform (FP, floodplain; TR, terrace; SL, hillslope; UP, upland) and are based on the species' relative abundance and relative frequency in the samples that represent each group. Significance of indicator value tested using a Monte Carlo permutation procedure.

[a] Indicator analysis based on method of Dufrene and Legendre (1997).

[*] Proportion of randomized trials with indicator value equal to or exceeding the observed indicator value by 0.05%.

[**] Proportion of randomized trials with indicator value equal to or exceeding the observed indicator value by 0.01%.

strained valleys of the ground moraine physiographic system (we observed few terraces along streams in constrained outwash plain valley types), and slopes in both the ground moraine and outwash plain physiographic systems, are comprised of facultative upland and obligate upland species, constrained by topographic features, such as aspect. In the unconstrained valley segments, differences in plant community composition across the riparian ecotone tend to be more subdued, as both the unconstrained ground moraine and outwash plain valley types have broad floodplains, higher terraces, and gentle slopes, or valley walls, grading into the uplands (Fig. 5). However, the floodplains of the unconstrained ground moraine valley type are characterized by more acidic, bog-like woody species (*Chamaedaphne calyculata* and *Vaccinium oxycoccus*) rather than graminoid species (*Carex stricta* and *Leersia oryzioides*).

Table 6
Analysis of variance (ANOVA) tests of ground-flora structural characteristics by valley type

	Landform[a]				ANOVA[b]			
	FP	TR	SL	UP	*F*-statistic	FP v. UP	TR v. UP	SL v. UP
Ground moraine								
Constrained valley								
Number of 1 m^2 plots	36	36	42	18				
Shannon's diversity index	2.1 (0.1)	1.5 (0.1)	1.4 (0.1)	1.1 (0.2)	17.33^{**}	39.68^{**}	6.53^{**}	3.31
Total cover	51.8 (4.4)	27.9 (3.4)	30.1 (3.1)	32.5 (7.1)	7.85^{*}	8.05^{**}	0.49	0.13
Annual forb cover	0.3 (0.2)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	1.50	2.06	0.01	0.01
Perennial forb cover	35.9 (4.2)	22.9 (3.5)	24.7 (3.0)	28.4 (6.7)	2.31	1.27	0.70	0.33
Graminoid cover	5.9 (1.5)	1.5 (0.4)	3.9 (0.9)	1.9 (0.4)	3.80^{*}	5.56^{**}	0.04	1.51
Pteridophyte cover	6.0 (1.8)	0.1 (0.1)	0.4 (0.2)	0.2 (0.2)	8.70^{*}	12.18^{**}	0.01	0.02
Woody cover	3.8 (0.8)	3.4 (0.5)	1.1 (0.3)	2.1 (0.8)	5.33	3.04	1.91	1.20
Unconstrained valley								
Number of 1 m^2 plots	18	27	15	15				
Shannon's diversity index	1.9 (0.1)	1.9 (0.1)	1.4 (0.1)	1.2 (0.1)	8.16^{*}	16.34^{**}	0.02	1.19
Total cover	86.7 (4.1)	47.1 (4.0)	32.3 (5.3)	17.9 (2.8)	12.11^{*}	29.07^{**}	2.51	2.21
Annual forb cover	0.6 (0.5)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.44	0.71	–	–
Perennial forb cover	47.0 (6.0)	24.6 (3.5)	20.4 (4.0)	12.8 (2.5)	3.71^{*}	9.34^{**}	0.17	1.76
Graminoid cover	22.7 (6.3)	11.2 (2.8)	6.4 (2.2)	0.9 (0.4)	4.15^{*}	8.79^{**}	2.60	0.25
Pteridophyte cover	12.9 (2.7)	3.8 (1.2)	0.5 (0.2)	0.2 (0.2)	6.28^{*}	10.40^{**}	0.01	0.01
Woody cover	3.6 (1.8)	7.5 (1.6)	5.1 (1.1)	4.0 (1.4)	0.37	0.62	0.85	0.11
Outwash plain								
Constrained valley								
Number of 1 m^2 plots	24	–	27	15				
Shannon's diversity index	2.2 (0.1)	–	1.5 (0.1)	1.1 (0.2)	19.88^{**}	32.88^{**}	–	2.87
Total cover	76.0 (7.3)	–	28.4 (3.5)	21.5 (5.3)	26.57^{**}	35.52^{**}	–	0.40
Annual forb cover	1.0 (0.4)	–	0.0 (0.0)	0.0 (0.0)	4.96^{*}	5.79^{*}	–	–
Perennial forb cover	26.4 (3.2)	–	14.6 (1.8)	15.1 (4.9)	4.84^{*}	4.59^{*}	–	0.12
Graminoid cover	13.0 (2.6)	–	2.4 (0.5)	3.6 (1.6)	10.98^{*}	10.25^{**}	–	0.30
Pteridophyte cover	23.7 (3.6)	–	3.1 (2.1)	0.6 (0.3)	21.21^{**}	28.39^{**}	–	0.33
Woody cover	11.8 (1.9)	–	8.3 (2.6)	2.1 (0.7)	3.85^{*}	7.69^{*}	–	3.31
Unconstrained valley								
Number of 1 m^2 plots	45	15	21	9				
Shannon's diversity index	1.5 (0.1)	1.9 (0.2)	1.8 (0.1)	1.3 (0.2)	5.04^{*}	1.55	9.28^{**}	7.22^{**}
Total cover	43.5 (3.0)	35.9 (4.9)	31.4 (2.9)	21.1 (4.4)	4.96^{*}	11.57^{**}	3.78^{*}	2.07
Annual forb cover	0.3 (0.3)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.33	0.33	–	–
Perennial forb cover	12.5 (1.5)	22.8 (2.9)	25.0 (2.6)	17.3 (3.7)	7.81	1.52	1.44	3.15^{*}
Graminoid cover	9.4 (1.7)	3.8 (0.9)	3.1 (1.0)	2.1 (0.7)	4.34^{*}	5.86^{*}	0.26	0.10
Pteridophyte cover	20.5 (2.7)	6.5 (4.0)	1.4 (0.8)	0.0 (0.0)	11.18^{*}	14.37^{**}	1.10	0.05
Woody cover	0.8 (0.3)	2.7 (1.1)	2.0 (0.4)	1.7 (0.9)	2.31	0.81	0.86	0.07

[a] Landforms include: FP, floodplain; TR, terrace; SL, slope; UP, upland.
[b] Analysis of variance using planned contrasts.
* $P < 0.05$.
** $P < 0.01$.

Within each of the valley types, patterns in ground-flora communities also reflect the existing fluvial landforms, or transverse geomorphic structure of the stream valley. Because the floodplains of the unconstrained reach types are broad and often comprised of porous sandy soils, small changes in elevation may result in distinct changes in microsite conditions that result in changes in species diversity and shifts in plant community composition. Consequently, the ground-flora species that characterize the floodplains must be able to withstand a variety of soil moisture conditions as stream and groundwater levels fluctuate, as well as a variety of hydrologic disturbances, from prolonged inundation to the force of peak streamflows. These complex edaphic and disturbance gradients may also be responsible for the patterns of species diversity we observed across the riparian ecotones of the unconstrained outwash plain. Unlike the other valley types, where the floodplains are the most diverse landform, the terraces and slopes are the most diverse landforms in the unconstrained outwash plain valley type, perhaps reflecting the fact that the floodplains of this valley type experience more frequent and intense flooding that limit the development of a diverse ground-flora when compared with the floodplains of the other valley types examined in this study (Huston, 1994; Pollock et al., 1998).

5.2. Implications for riparian management

Many natural resource organizations have developed forest management guidelines, commonly known as best manage-

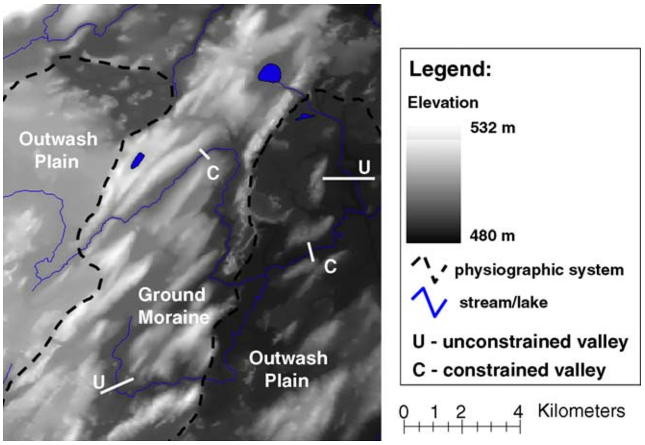

Fig. 5. Spatial patterns of major physiographic and valley systems (as represented by a 10 m digital elevation model (DEM) obtained from the U.S. Geological Survey; USGS) in the western portion of the Popple River watershed and tributaries, northeastern Wisconsin (northern half of Alvin SE USGS 7.5 min quadrangle).

ment practices (BMPs) that usually provide for some type of riparian management zone (RMZ). Forest management practices in RMZs typically are modified to help protect aquatic ecosystems and adjacent terrestrial habitat by maintaining functional linkages between aquatic and terrestrial segments of the ecotone. In Wisconsin, RMZs consist as bands of forest at least 33 m wide along each side of a navigable stream (a stream in which a canoe or small craft can float on a regular reoccurring basis) or 11 m wide on each side of a non-navigable stream (Wisconsin DNR, 1995).

In developing guidelines, the influence of hierarchical landscape properties on the lateral extent of riparian areas and consequently the delineation of RMZs is rarely considered. Our results illustrate that differences in the physiographic system, valley constraint, and arrangement of valley floor landforms result in different ground-flora communities and levels of diversity that are manifested at different spatial scales. Most RMZ guidelines, however, are inflexible to accommodate for differences related to multi-scale landscape properties (Ilhardt et al., 2000). The result is that RMZs are maintained as linear strips of forest on each side of a stream that often do not capture many of the areas of high diversity and unique plant communities associated with riparian areas. With a better understanding of how hierarchical landscape properties regulate the distribution of riparian plant communities, more ecologically appropriate RMZs could potentially be developed that help maintain many of the important functions provided by riparian areas such as biodiversity.

Based on the results of this study, we suggest that RMZ widths should be designed in a similar fashion as described by Ilhardt et al. (2000). For example, our results suggest that RMZ widths based on the approach of Ilhardt et al. (2000) would vary by valley type, with wider RMZs associated with the unconstrained valley types and more narrow RMZs applied in the constrained valley types (Fig. 5). Consequently, we suggest that RMZs designed to maintain riparian function should be variable in width rather than fixed, encompassing the valley floor landforms and valley walls, regardless of the physiographic system.

6. Conclusions

Our results for riparian areas along low-order streams in a glacial landscape suggest that composition and spatial pattern of ground-flora communities are related strongly to hierarchical landscape features of watersheds, including physiographic system (dominant glacial landform), valley type (constrained versus unconstrained), and transverse geomorphic structure (valley floor landforms). Changes in plant communities across riparian areas of constrained valley types are associated with changes in the transverse geomorphic structure of the stream valley, ultimately reflecting the influence of hydrogeomorphic processes in forming valley floor landforms. Changes in ground-flora communities of unconstrained valley types are responding not only to changes associated with the transverse geomorphic structure of the riparian ecotone, but also to more localized changes in environmental conditions that are associated with flooding and hydrologic regime. Thus, variation in riparian plant community characteristics can be explained using a nested, hierarchical landscape framework to organize and group different riparian settings based on the underlying geomorphic processes shaping stream valleys. This framework should prove useful for developing variable width RMZs that better capture the true functional extent of riparian ecotones. These RMZs should vary in width, with wider RMZs in the unconstrained valley types and more narrow RMZs in the constrained valley types.

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