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PLANT DIVERSITY CONTRIBUTIONS OF RIPARIAN AREAS IN WATERSHEDS OF THE NORTHERN LAKE STATES, USA

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Abstract. In most forested watersheds, riparian areas constitute a small proportion of the total land area, yet their contributions to overall plant diversity can be significant. However, little information is available on which portion of riparian areas (defined as functional ecotones comprising all fluvial landforms, including floodplains, terraces, and connecting hillslopes) contribute the most to plant species richness and at what scale these contributions are most evident. In order to better understand the contributions riparian areas provide to plant species richness in forested watersheds, we examined herbaceous ground-flora richness and similarity from 56 reaches in eight different valley types (defined as unique combinations of stream order, surficial geology, and stream-valley constraint) across the northern Lake States, USA. We analyzed these data at two scales: (1) at the individual reach scale; and (2) at the watershed scale by pooling individual reaches by valley type. At the reach scale and regardless of valley type, there is not significant (<50%) species similarity among landforms; however, levels of species richness are not significantly different among the floodplain, terrace–slope complex landforms (e.g., terraces, connecting hillslopes), and adjacent uplands. This suggests that individual reaches (representing an individual riparian area) may not provide significant contributions to overall plant species richness. However, when individual reaches are pooled by valley type, the floodplains are almost always more species rich than the terrace–slope complex and upland landforms, suggesting that the environmental heterogeneity associated with a variety of individual reaches can be responsible for greater species richness provided by riparian areas at the watershed level. Our results also suggest that floodplains are not the only riparian landform that adds significantly to the overall plant diversity of watersheds, especially in areas with broad, unconstrained valleys. In these systems, the terrace–slope complex landforms comprising a series of broad fluvial terraces and connecting slopes have significantly higher species richness than the adjacent uplands. Consequently, it is apparent that, to maintain plant diversity at both local and regional levels, efforts should focus on all fluvial landforms of the riparian area, not just their floodplains. This is particularly relevant when management of riparian areas uses fixed-width riparian management zones (RMZs). In our study areas, 33 m-wide RMZs (the recommended width in each of our study states) often failed to include fluvial landforms beyond the floodplain. The consequence is that areas of increased species richness and/or unique plant assemblages in the watershed may receive inadequate protection during forest-management operations.

Key words: floodplain; fluvial landforms; forested-watershed plant diversity; northern Lake States, USA; plant diversity; riparian areas and species richness; riparian management zone; species–area curves; stream-valley morphology; watershed management.

INTRODUCTION

In many regions, riparian areas constitute a small proportion of total watershed area, yet they play a prominent ecological role that far exceeds their areal extent. At local scales, riparian areas act as ecotones between aquatic and terrestrial ecosystems, while at landscape and watershed scales, riparian areas function as both boundaries and corridors between terrestrial and aquatic ecosystems, controlling the flux of energy and nutrients as well as biotic interchanges (Gregory et al. 1991, Crow et al. 2000). Riparian areas are characterized by gradients of change in many factors and at many scales, including microclimate, soil texture and fertility, flood frequency and duration, and depth to water table (Gregory et al. 1991, Brosofske et al. 1997, Lyon and Sagers 1998, Ilhardt et al. 2000, Naiman et al. 2000). The result is a complex environment characterized by frequent disturbances and a diverse array of habitats that are believed to promote higher levels of plant (Brinson and Verhoeven 1999, Naiman et al. 2000) and animal (Ross and Baker 1983, Décamps et

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al. 1987, Doyle 1990) species diversity, compared to upland and aquatic ecosystems.

Although many researchers believe that the contribution of riparian areas to plant diversity often exceeds the proportion of the landscape they occupy (Brinson and Verhoeven 1999, Ferreira and Stohlgren 1999, Crow et al. 2000), empirical tests of this hypothesis are rare. Those studies that have examined the contributions of riparian areas to plant diversity often have focused only on floodplains (e.g., Salo et al. 1986, Nilsson et al. 1994, Ferreira and Stohlgren 1999, Bornette et al. 2001) and have ignored the potential contributions of other fluvial landforms (e.g., low and high terraces, connecting slopes) to plant diversity. Gradients in several of the factors that characterize the riparian ecotone, e.g., microclimate, disturbance, and water availability, certainly extend beyond the floodplain (Kovalchik and Chitwood 1990, Brosofske et al. 1997, Ilhardt et al. 2000). Thus, one would anticipate that fluvial landforms outside of the floodplain should contribute to the hypothesized levels of increased plant diversity in riparian areas. Additionally, these contributions most likely vary with differences in stream order and stream-valley characteristics, as levels of plant diversity are thought to be mediated by hierarchical landscape factors, such as stream order, surficial geology and stream valley constraint, the unique combination of which we define here as a "valley type" (see review in Pregitzer et al. 2001). For example, in wide, unconstrained stream-valley types typical of many landscapes of the glaciated Great Lakes region changes in vegetation are often abrupt and occur across a variety of stream-valley landforms, including terraces and connecting slopes (Goebel 2001). This change in vegetation may be in response to different ecosystem processes occurring across these ecotones (Gosz 1993) well beyond the extent of the floodplain. Consequently, it is possible that other fluvial landforms, beyond the floodplain, may provide unique habitats that promote higher plant diversity in riparian areas.

Many researchers also hypothesize that the increased plant diversity in riparian areas is apparent only when examined at larger spatial scales. For example, Brinson and Verhoeven (1999) hypothesize that it is cumulative environmental heterogeneity at the watershed scale that results in higher levels of plant diversity than the adjacent uplands. Oftentimes the processes (e.g., hydrologic, geomorphic) operating along a longitudinal gradient in a watershed vary widely (Benda et al. 1998, Montgomery and Buffington 1998, Amoros 2001), resulting in a mosaic of different patches or habitats that likely support a wide array of different plant communities and promoting higher plant diversity at the watershed scale than at local or individual-reach scales (e.g., portions of streams with similar stream-valley and streambed characteristics; often between 100 and 300 m long). However, we know of no empirical studies that have examined specifically the influence of scale on patterns of plant diversity in riparian areas, except for those that have focused exclusively on floodplain environments (e.g., Bendix 1994, Amoros 2001).

Beyond developing a deeper understanding of riparian ecology, there are clear management implications related to these two hypotheses (i.e., the contribution of riparian areas to plant diversity often exceeds the proportion of the landscape they occupy, and increased plant diversity in riparian areas is apparent only when examined at larger spatial scales). Increasingly, management of riparian areas in forested watersheds incorporates a riparian management zone (RMZ) in an attempt to protect habitat and maintain functional linkages between aquatic and terrestrial systems (Blinn and Kilgore 2001). RMZs typically extend a fixed distance from a stream or river (e.g., 33 or 66 m) and are largely invariant to changes in stream-valley geomorphology, beyond modest increases in width with increasing slope (Blinn and Kilgore 2001). While fixed-width RMZs may protect some riparian functions, their efficacy at capturing important habitat and, consequently, protecting areas of increased species diversity is poorly documented. Moreover, managers often use RMZs in a watershed with little regard for the cumulative effects of habitat alteration on riparian plant community composition and structure. Determining the upland extent of increased plant diversity and unique plant assemblages across riparian areas, relative to the boundary of fixed-width RMZs, and determining the scale at which diversity contribution is most evident, will help clarify the often-contentious issue of RMZ efficacy at riparian area protection (Ilhardt et al. 2000, Blinn and Kilgore 2001).

We examined species richness and similarity of herbaceous ground-flora communities along riparian ecotones in a variety of valleys located in both first-order and higher-order stream systems of the northern Lake States, USA. Our overall goal was to better understand the contributions of riparian areas to plant diversity in forested watersheds, the influence of scale on these contributions, and the potential for RMZs to sustain these contributions. Specifically, we address the following questions: (1) Do fluvial landforms, including those beyond the floodplain, have higher plant species diversity than the uplands, regardless of the stream order or stream-valley type? (2) At what scale (within reach, among reach, or watershed) are diversity contributions most evident among different stream orders and stream-valley types? (3) How effective are RMZs at protecting areas of high plant species diversity at both reach and watershed scales among different stream orders and stream-valley types?

METHODS

Study watersheds

We studied three large watersheds in the northern Lake States, USA (Fig. 1). All watersheds are located

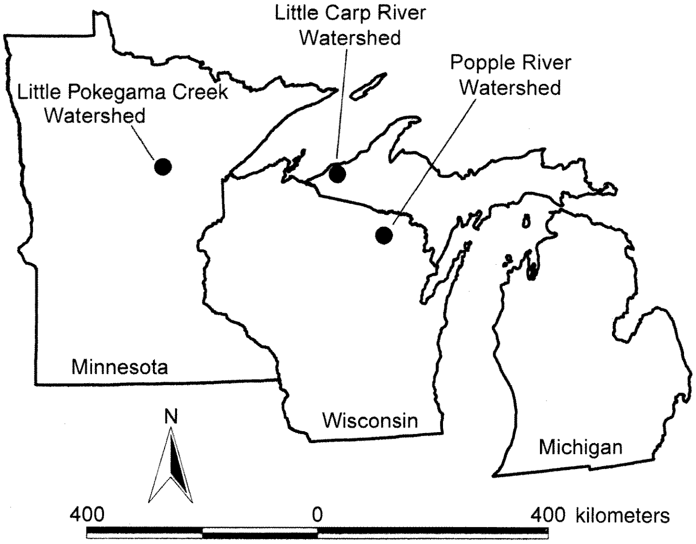

FIG. 1. Study watershed locations in the northern Lake States, USA.

within the Laurentian Mixed Forest province (212) that extends across northeastern Minnesota, northern Wisconsin, the entire Upper Peninsula of Michigan, and the northern half of Lower Michigan (Keys et al. 1994). The region has a humid-continental climate; annual precipitation ranges from an average of 58 to 69 cm in the western portion of the study area to 66 to 91 cm in the eastern portion (Keys et al. 1994). Mean annual temperature ranges from 3°C to 7°C. Our study watersheds occur within three geomorphic subsections: (1) Little Pokegama Creek Watershed–Chippewa Plains of the Northern Minnesota Drift and Lake Plains (212N), comprised of gently rolling lowlands and glacial features such as broad outwash and till plains; (2) Little Carp River Watershed–Lake Superior Clay Plains of the Southern Superior Uplands (212J), with broad, flat plains comprised of Wisconsian lake silts, clays, and sands; and (3) Popple River Watershed–Brule and Paint Rivers Drumlinized Ground Moraine of the Southern Superior Uplands (212J), comprised of gently rolling ground moraine, drumlins, and broad outwash plains (Keys et al. 1994). The characteristics of each study watershed are summarized in Table 1.

Study design and data collection

We define riparian areas from a functional standpoint, as ecotones that influence stream habitat and ecosystem processes and, conversely, that are influenced by stream hydrology and microclimate. Under this definition, the riparian area is not limited strictly to floodplains or low terraces that flood frequently. Rather, our definition includes higher terraces (although still of fluvial origin), and even slopes connecting terraces with the upland, since these landforms are connected functionally to streams through organic-matter input, sediment and nutrient filtering or uptake, and in some cases shading. Moreover, research has shown that this broad terrestrial setting is influenced by microclimatic conditions of even small, first-order stream systems (Brosofske et al. 1997) and by infrequent large-magnitude floods (Palik et al. 1999). As such, we believe high terraces and slopes are best considered distinct from the upland environment, and as part of the riparian ecotone, but also distinct from the floodplain. Our approach to sampling and data analysis, described below, reflects the ecotonal structure of the riparian area; i.e., we contrast floodplains to the upland and, separately, we contrast a combined terrace–slope complex to the uplands.

We identified a total of eight different valley types associated with both first-order and higher-order streams (Table 1) in the three study watersheds based upon geologic substrate and valley constraint (ratio of stream bankfull width to valley floor width; sensu Fetherston et al. 1995). The fluvial landforms that comprise the different riparian areas reflect this geomorphic variability, with a floodplain along the stream channel and a complex of terraces and slopes that occur between the floodplain and the adjacent uplands. This terrace–slope complex includes low and high terraces, as well as slopes between terraces, between a terrace and the floodplain, or between a terrace and the upland. The lateral width of the terrace–slope complex varies considerably among valley types, being most narrow in the constrained and bedrock-controlled valley types and most broad in the unconstrained valley types, including those in the clay lake-plain valley type.

In each valley type we identified individual study reaches (~150–300 m long) that represent a portion of a stream-valley type (~1–10 km long) and have similar stream-valley characteristics and streambed features (e.g., stream order and stream type; Table 1). In each reach we established three to seven transects that extended from the stream edge to at least 40 m into the

TABLE 1. Hydrologic and geomorphic properties of northern Lake States (USA) riparian study sites.

Name and location	Number of reaches	Stream order†	Geologic type‡	Valley constraint	Valley type§
Little Pokegama Creek Watershed, Minnesota					
Upper	2	1	EM	constrained	EMC
Middle	4	1	EM	constrained	EMC
Lower	5	1	EM	constrained	EMC
Little Carp River Watershed, Michigan					
Greenstone Falls Creek	2	1	BC	constrained	BCC
Mirror Lake Creek	2	1	BC	constrained	BCC
Upper Little Carp River	3	2	BC	constrained	BCC
Middle Little Carp River	4	3	BC	constrained	BCC
Lower Little Carp River	4	3	LP	constrained	LPC
Popple River Watershed, Wisconsin					
Upper Morgan Creek	2	2	OP	unconstrained	OPU
Lower Morgan Creek	2	2	OP	constrained	OPC
Upper N. Branch Popple River	2	2	OP	unconstrained	OPU
Middle N. Branch Popple River	4	2	GM	unconstrained	GMU
Lower N. Branch Popple River	2	2	GM	constrained	GMC
Upper Riley Creek	2	2	OP	constrained	OPC
Lower Riley Creek	2	2	OP	constrained	OPC
Upper Rat Creek	2	2	GM	unconstrained	GMU
Lower Rat Creek	2	2	GM	constrained	GMC

† Horton's stream-order designation (McCuen 1998).

‡ Geologic types: EM = end moraine; BC = bedrock controlled; LP = lake plain; OP = outwash plain; GM = ground moraine.

§ Valley types: EMC = constrained end moraine; BCC = constrained bedrock controlled; LPC = constrained lake plain; OPU = unconstrained outwash plain; OPC = constrained outwash plain; GMU = unconstrained ground moraine; GMC = constrained ground moraine.

uplands on one side of the stream, with transects arrayed perpendicular to streamflow. We determined the location of the first transect by selecting a random distance from the beginning of the upstream boundary of the study reach. Successive transects were located randomly from the first transect, but at least 15 m apart in the downstream direction. Using bankfull elevation as the reference point, we used a level transit and standard surveying procedures to determine the location for each ground-flora sample plot and valley landform boundary. Sample plots were located along each transect at fixed distances, with at least one sample plot per landform; individual transects had between 4 to 13 plots, depending on the valley width. In each sample plot (0.5 m^2 in Minnesota, 1.0 m^2 elsewhere), we recorded the presence or absence of all herbaceous species during the summer (June–August) of 1998 for the Popple River (Wisconsin) and Little Pokegema Creek (Minnesota) watersheds, and during the summer of 1999 for the Little Carp River (Michigan) watershed. We focused our efforts on the herbaceous ground flora, as woody plant species richness is often low in these northern hardwood forest ecosystems (Goebel 2001) and herbaceous species are thought to be better phytometers of environmental changes (Barnes et al. 1998).

Data analysis

Prior to analyses, individual sample plots along each transect were grouped into one of the following landform classes: floodplain, terrace–slope complex, or upland (Fig. 2). We grouped terraces and slopes into one class because individual transects and reaches did not consistently contain each of these different landforms (e.g., terraces and connecting slopes). Comparisons of diversity among landform classes were analyzed within individual reaches, among reaches of a similar valley type, and at the watershed scale by pooling all reaches of a similar valley type.

We summarized herbaceous ground-flora diversity as species richness, the most direct and simplest way to measure species diversity (Whittaker 1972). As comparisons of species richness among landform classes at the within-reach and among-reach scale were conducted by individual valley type, there was no need to normalize species-richness values for differing sample plot sizes (0.5 m^2 in Minnesota, 1.0 m^2 elsewhere). Additionally, we calculated Jaccard's coefficient to quantify species similarity among landform classes. Jaccard's coefficient (J) was calculated as

$$J = A/(A + B + C) \quad (1)$$

where A = the number of species found in both paired landform classes, B = species in landform class 1 but not in landform class 2, and C = the number of species found in landform class 2 but not in landform class 1. The similarity coefficient ranges from 1.0 for complete similarity to 0.0, indicating no similarity or shared species; we present these data, however, as a percentage ranging from 100% for complete similarity to 0%, indicating no similarity or shared species.

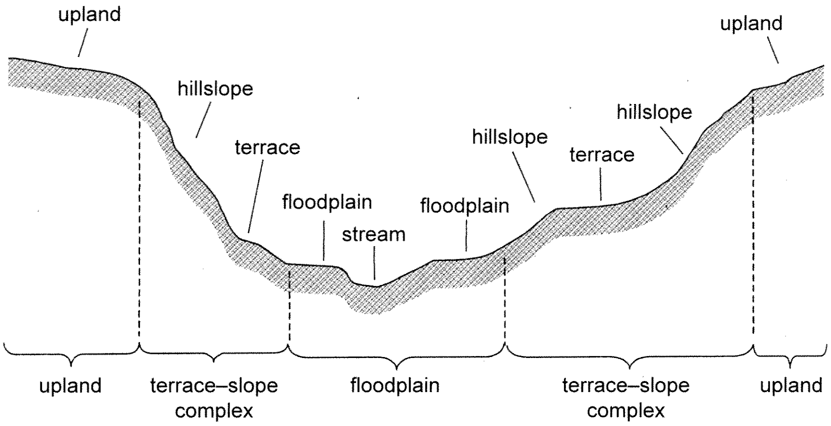

FIG. 2. Stream-valley schematic showing typical arrangement of different landforms and landform classes (floodplain, terraces, connecting slope and upland) across riparian ecotones. The width of riparian ecotone from the stream channel to the top of the connecting slope is variable, ranging from 0–50 m in narrow, constrained valleys to 0–300 m in broad, unconstrained valleys.

We tested for differences in species richness among landforms using a complete-block repeated-measures ANOVA (Gill 1978, SAS Institute 1989), where individual transects (within-reach scale) or reaches (among-reach scale) are the blocks and landform was the repeated measure. A repeated-measure model is appropriate because we sampled the riparian ecotone at multiple locations in space and these locations are always arrayed in a nonrandom pattern (i.e., a floodplain is always positioned before a fluvial terrace or connecting slope, which is always positioned before the upland). We formulated a set of a priori contrasts to test the following hypotheses at two scales, including within individual reaches and among reaches of a similar valley type: (1) floodplains have higher species richness than the adjacent uplands; and (2) terrace–slope complex landforms have higher species richness than the adjacent uplands. Our level of replication was low in some instances (i.e., some reaches were sampled more intensively than others). Therefore, to assess deficiencies in replication we calculated the power of each ANOVA. We assumed contrasts with a power of 0.80 had a sufficient sample size and requisite statistical power to detect differences among the landform classes.

We pooled data from each reach to examine differences in species richness among landforms at the watershed scale. From these pooled data, we generated species–area curves for each landform class and estimated the total species richness for each landform class at the watershed scale using the jackknife method described in Palmer (1990). Species richness (R) is calculated as

$$R = S + r^1(n - 1)/n \qquad (2)$$

where S = the observed number of species from pooled samples, r^1 = the number of species occurring in an individual sample unit of the pooled samples, and n = the number of pooled sample units. This nonparametric sampling approach produces a more accurate and less biased estimate of species richness when subsampling a larger area (Palmer 1990). We used PC-ORD software (McCune and Mefford 1999) to generate the species–area curves and to calculate the variance associated with each level of a curve. We used these results to plot 95% confidence intervals ($\text{CI} = 1.96 \pm \sqrt{\text{variance}}$) for each curve. We assumed species richness to be significantly different among different landform classes at the watershed scale when confidence intervals did not overlap at or near the asymptote of the species–area curve. Additionally, we fit a line to each of the species–area curves using the natural log-log transformation of

$$S = cA^z \qquad (3)$$

where S is the expected number of species in area A, z is the instantaneous rate by which species richness increases with an incremental increase in area, and c is the expected number of species in a unit area (Arrhenius 1921). We then compared the coefficients of the species–area curves, among landform classes, within each valley type (i.e., curves with similar coefficients suggest similar species–area relationships). Although several different models have been proposed for describing the species–area relationship (e.g., power function, random-placement model, exponential model, extreme-value model), no one model adequately quantifies this relationship in all instances (McGuinness 1984, He and Legendre 1996). Because the power function is perhaps the most common way to describe the species–area relationship, we used this model specifically to compare the *relative* contributions to plant diversity provided by various landform classes in each watershed.

Finally to assess the effectiveness of riparian management zones (RMZs) at protecting areas of high spe-

TABLE 2. *Herbaceous species richness (mean with 1* SE *in parentheses) and ANOVA results by landform class among stream reaches by valley type (end moraine or bedrock controlled) and for individual reaches of headwater streams in the northern Lake States, USA.*

	Landform class			ANOVA†				Contrasts‡	
Reach	Floodplain, FP	Terrace slope, TS	Upland, UP	df	*F*	G-G	H-F	FP vs. UP	TS vs. UP
End moraine									
Upper Little Pokegama Creek (MN)									
Reach 1§	5.2 (0.7)	3.1 (0.3)	3.3 (0.5)	6	8.07*	0.06	0.04	9.17*	0.02
Reach 2	5.6 (1.0)	4.6 (0.4)	4.1 (0.6)	7	0.92	0.78	0.69	0.89	2.93
Middle Little Pokegama Creek (MN)									
Reach 1§	6.7 (1.0)	5.0 (0.5)	4.6 (0.5)	7	2.69	0.09	0.09	2.95	0.68
Reach 2§	6.8 (0.8)	5.4 (0.5)	5.2 (0.6)	6	1.84	0.19	0.18	2.42	0.21
Reach 3	7.1 (1.0)	6.0 (0.7)	7.4 (0.7)	7	0.79	0.81	0.76	0.08	1.75
Reach 4	7.7 (1.0)	5.9 (0.4)	5.7 (1.2)	6	1.06	0.29	0.28	1.02	0.21
Lower Little Pokegama Creek (MN)									
Reach 1	9.4 (0.7)	7.3 (0.4)	6.6 (1.4)	5	2.63	0.12	0.11	3.73	0.51
Reach 2	6.5 (0.8)	6.0 (0.5)	5.1 (0.6)	6	0.91	0.81	0.79	1.11	0.88
Reach 3	8.8 (1.5)	8.0 (0.1)	6.4 (0.6)	4	1.70	0.23	0.17	2.46	5.40
Reach 4	10.3 (0.5)	9.2 (0.7)	8.2 (1.2)	7	1.37	0.42	0.40	2.79	0.55
Reach 5§	12.8 (0.7)	7.1 (0.7)	5.8 (1.2)	6	26.15*	0.03	0.02	16.71**	1.31
Among reaches§	7.9 (0.7)	6.2 (0.5)	5.7 (0.4)	11	15.74*	0.03	0.02	17.42**	3.73
Bedrock controlled									
Mirror Lake Creek (MI)									
Reach 1§	7.4 (0.6)	4.9 (1.1)	3.0 (0.7)	4	7.81*	0.02	0.06	15.64*	11.63*
Reach 2	5.2 (1.4)	3.5 (1.2)	2.0 (0.7)	4	3.29	0.15	0.11	4.16	1.28
Greenstone Falls Creek (MI)									
Reach 1	4.8 (0.6)	5.1 (0.5)	6.1 (0.4)	4	5.14*	0.07	0.05	9.30	3.69
Reach 2	4.2 (0.8)	4.6 (0.3)	4.9 (0.6)	4	0.31	0.69	0.74	0.39	0.11
Among reaches§	5.4 (0.5)	4.5 (0.4)	4.0 (0.5)	4	2.56	0.12	0.11	2.98	1.13

Notes: MN = Minnesota, MI = Michigan. End-moraine richness values are based on 0.5-m^2 plots; bedrock-controlled richness values are based on 1.0-m^2 plots.

* $P < 0.05$; ** $P < 0.01$.

† Repeated-measure adjusted probabilities (G-G = Greenhouse-Geisser and H-F = Huynh-Feldt) are included for comparison.

‡ Values included are F statistics of planned contrasts.

§ Power of ANOVA > 0.80.

cies diversity, at both the reach and watershed scales, we first determined the width of the RMZ for each valley type as prescribed by state guidelines for each study area (33 m RMZ in all cases regardless of state, valley type, or stream size). We then determined the location of the RMZ boundary by landform class for each reach of a given valley type (e.g., percentage occurrence of the RMZ that includes portions of the floodplain, terrace–slope complex, or upland landform class).

RESULTS

Within individual reaches by valley type

There was considerable variability in species richness among landform classes in each of the first-order streams we sampled, regardless of valley type (Table 2). The ANOVA results reflect this variability, as few significant differences at the individual-reach scale were detected. Only three of the fifteen individual reaches showed a significant difference in species richness between the floodplain and the uplands, or the terrace–slope complex and the upland ($P < 0.05$; Table 2). However, when we considered only those reaches with the requisite statistical power, 60% (3 of 5) had a significant difference in species richness between the floodplain and the uplands, or the terrace–slope complex and the upland ($P < 0.05$; Table 2).

As with the first-order streams, there were few differences in species richness at the individual-reach scale for the second-order or larger stream systems (Table 3). Approximately 22% of the total reaches (7 of 31) have significantly higher species richness on the floodplains than the adjacent uplands (60% or 9 of 15 when only comparisons with requisite statistical power are considered), while <13% (4 of 31; 19% or 3 of 16 with requisite statistical power) of the individual reaches had significantly higher species richness on the terrace–slope complex than the adjacent uplands ($P < 0.05$).

Although we did not always observe differences in species richness among landforms at the individual-

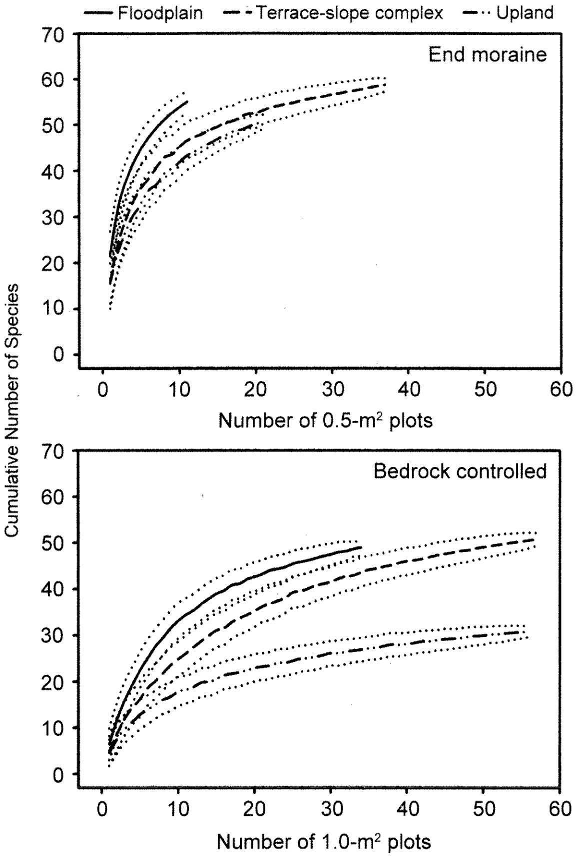

FIG. 3. Species–area curves by landform and valley type for first-order streams based on 0.5-m^2 plots sampled in the end moraine valley type and 1-m^2 plots in the bedrock-controlled valley type. Dotted lines represent 95% confidence intervals around each curve.

reach scale, there was consistently low species similarity among landforms in both the first-order (Table 4) and higher-order (Table 5) streams. Among first-order streams, only reach 4 in Middle Pokegama Creek, and reaches 2 and 3 in Lower Pokegama Creek, share >50% of the species from one landform class to another. Among the higher-order streams, only reaches in the constrained bedrock-controlled and clay lake-plain valley types share more than half of the species among landforms (Table 5). In some instances, such as the reaches in Upper Rat Creek in the constrained ground moraine valley type, ground-flora communities shared no species (i.e., species similarity was 0%) between the floodplain and upland landforms, and shared <25% of the species occurring on the terrace–slope complex and upland landforms (Table 5).

Among reaches by valley type

When all individual reaches were pooled by valley type, we found consistent significant differences in species richness across riparian ecotones ($P < 0.05$). For example, richness on the floodplains of first-order steams in the end-moraine valley type was 7.9 ± 0.7 species/0.5 m^2 as compared to 5.7 ± 0.4 species/0.5 m^2 in the adjacent upland (mean ± 1 SE) (Table 2). Similar results were observed in the first-order streams of the bedrock-controlled valley type. When we pooled reaches by valley type for the higher-order streams, we found that the floodplains had higher richness than the adjacent uplands in all cases except for the unconstrained valleys in the outwash plain ($P < 0.05$; Table 3). For example, in the constrained valleys of the ground-moraine valley types in Wisconsin, floodplains on average have over twice the number of herbaceous species per 1.0 m^2 (9.1 species) than the uplands (4.0 species) ($P < 0.01$; Table 3). Both the unconstrained valleys of the outwash plain and the bedrock-controlled valley types have significantly higher species richness on terrace–slope complex landforms than in the adjacent uplands ($P < 0.01$; 7.4 vs. 4.4 species and 5.3 vs. 3.9 species, respectively; Table 3), as does the constrained ground-moraine valley type ($P < 0.05$; 5.6 vs. 4.0 species; Table 3).

In first-order streams, when we pooled individual reaches within valley types, patterns in species similarity among landforms differed from those within individual reaches. For example, the terrace–slope complex and upland landforms in both first-order valley types had similar species compositions (species similarity >50%; Table 4), compared to low similarity between these landforms when examined at the reach scale. In higher-order streams, pooling individual reaches by valley type generally resulted in similar species-similarity patterns among landforms as at the reach scale, with the exception of the bedrock-controlled valley type (species similarity = 74.1%; Table 5).

Watersheds by valley type

Differences in total species richness among landforms at the watershed scale were similar to those seen when individual reaches were pooled by valley type (Fig. 3). In both of the first-order valley types, the floodplains have higher richness than the adjacent uplands, and on average the terrace–slope complex landforms have similar richness to the floodplains. For instance, the jackknife estimates for total species richness of the floodplain and terrace–slope complex landforms of the end-moraine valley type are ~67 and 69 species, respectively, vs. 60 species for the uplands (Fig. 3; Table 6). The coefficients of the species–areas curves also differ among landforms, including the floodplain and the terrace–slope complex landforms. Both the floodplain and terrace–slope complex landforms have similar initial species richness values when one 0.5-m^2 plot is examined ($c = 25.04$ and 23.49, respectively), but the slope of the floodplain species–area curve is higher than that of the valley floor ($z = 0.34$ and 0.26, respectively), suggesting that initially there is a higher rate of increase in ground-flora species per unit area

TABLE 3. Herbaceous species richness (mean with 1 SE in parentheses) and ANOVA results by landform classes among reaches by valley types (ground marine, outwash plain, bedrock controlled, or clay lake plain) and for individual reaches of second-order or higher streams in the northern Lake States, USA.

	Landform class			ANOVA†				Contrasts‡	
Reach	Floodplain, FP	Terrace slope, TS	Upland, UP	df	*F*	G-G	H-F	FP vs. UP	TS vs. UP
Ground moraine, constrained valleys									
North Branch Popple River (WI)									
Reach 1	11.2 (2.5)	7.6 (0.4)	6.0 (3.0)	3	2.09	0.28	0.26	1.89	0.13
Reach 2	11.6 (0.5)	7.3 (0.4)	7.7 (2.0)	3	5.19	0.15	0.15	5.12	0.01
Reach 3§	8.7 (0.5)	5.7 (0.8)	2.7 (0.9)	3	24.84**	0.04	0.03	32.83*	30.00**
Reach 4§	11.2 (0.5)	6.1 (0.5)	4.7 (1.5)	3	12.45*	0.04	0.02	13.97	1.24
Upper Rat Creek (WI)									
Reach 1§	7.0 (0.6)	3.6 (0.4)	2.0 (1.5)	3	4.82	0.15	0.13	5.77	0.69
Reach 2§	5.7 (0.3)	3.6 (0.8)	1.7 (0.9)	3	6.96*	0.12	0.12	16.00	1.69
Among reaches§	9.1 (0.6)	5.6 (0.4)	4.0 (0.8)	6	40.02**	0.01	0.01	49.08**	5.88*
Ground moraine, unconstrained valley									
North Branch Popple River (WI)									
Reach 1§	8.3 (1.1)	5.8 (0.9)	3.3 (0.7)	3	5.12	0.13	0.08	28.48	3.00
Reach 2§	8.3 (0.7)	2.2 (0.2)	4.0 (0.9)	3	26.21**	0.02	0.01	63.26*	2.81
Upper Rat Creek (WI)									
Reach 1§	7.8 (0.6)	6.5 (0.6)	4.3 (0.4)	3	10.12*	0.04	0.03	34.90*	6.04
Reach 2	7.0 (0.7)	5.3 (0.9)	3.8 (0.4)	3	26.22**	0.01	0.01	42.08*	9.00
Among reaches§	7.8 (0.4)	5.0 (0.6)	3.9 (0.3)	4	21.33**	0.01	0.01	129.03**	2.52
Outwash plain, constrained valleys									
Morgan Creek (WI)									
Reach 1	13.0 (1.2)	10.5 (0.8)	13.0 (1.2)	3	4.44	0.16	0.12	0.01	57.76
Reach 2	8.0 (0.1)	10.2 (0.4)	11.7 (2.7)	3	1.65	0.33	0.33	1.89	0.42
Upper Riley Creek (WI)									
Reach 1§	12.8 (0.4)	4.8 (1.9)	4.5 (1.3)	3	9.39*	0.07	0.03	25.00*	0.01
Reach 2§	12.3 (0.4)	6.0 (0.5)	4.7 (1.9)	3	10.50*	0.08	0.06	15.91	0.32
Lower Riley Creek (WI)									
Reach 1§	7.2 (0.9)	3.6 (0.8)	3.0 (1.7)	3	4.66	0.15	0.13	4.22	0.29
Reach 2	7.3 (0.8)	5.3 (0.5)	2.3 (0.8)	3	8.07*	0.05	0.04	15.79	4.48
Among reaches§	10.3 (0.8)	6.7 (0.7)	6.4 (1.2)	6	8.53**	0.01	0.01	8.84**	0.07
Outwash plain, unconstrained valleys									
Upper N. Branch Popple River (WI)									
Reach 1	6.1 (0.3)	8.0 (0.9)	4.7 (0.9)	3	5.92	0.09	0.06	4.54	28.02
Reach 2	4.7 (0.2)	7.8 (0.4)	6.0 (1.2)	3	5.77	0.14	0.14	0.99	6.37
Morgan Creek (WI)									
Reach 1	5.2 (0.6)	7.9 (1.0)	4.7 (0.9)	3	3.18	0.15	0.15	0.15	4.86
Reach 2	4.9 (0.6)	5.9 (1.0)	2.3 (0.7)	3	57.19**	0.01	0.01	90.25**	144.92**
Among reaches§	5.2 (0.3)	7.4 (0.5)	4.4 (0.6)	4	18.05**	0.01	0.01	1.56	48.21**
Bedrock controlled									
Upper Little Carp River (MI)									
Reach 1§	12.9 (0.6)	7.9 (1.3)	5.8 (0.6)	8	20.00**	0.01	0.01	75.84**	3.74
Reach 2§	12.5 (0.8)	8.6 (1.3)	5.6 (0.7)	8	9.38**	0.01	0.01	29.09**	3.65
Reach 3	7.7 (1.6)	3.4 (0.7)	3.7 (0.9)	3	3.89	0.17	0.12	6.86	0.05
Middle Little Carp River (MI)									
Reach 1	4.4 (1.7)	2.6 (0.3)	2.7 (0.2)	8	0.96	0.40	0.36	1.05	0.02
Reach 2	2.0 (0.9)	2.7 (0.3)	2.5 (0.3)	8	0.39	0.63	0.66	0.23	0.12
Reach 3§	16.0 (2.1)	7.4 (0.2)	2.5 (0.6)	3	36.86**	0.03	0.03	78.11**	52.12*
Reach 4§	10.5 (1.0)	4.1 (0.2)	3.0 (0.3)	3	82.24**	0.02	0.01	104.32**	121.00**

TABLE 3. Continued.

Reach	Landform class			ANOVA†				Contrasts‡	
	Floodplain, FP	Terrace slope, TS	Upland, UP	df	F	G-G	H-F	FP vs. UP	TS vs. UP
Clay lake plain									
Lower Little Carp River (MI)									
Reach 1	3.3 (1.3)	5.5 (0.9)	4.3 (1.2)	4	0.66	0.50	0.53	0.17	1.42
Reach 2	13.2 (5.7)	4.7 (1.0)	7.8 (0.7)	3	1.58	0.34	0.34	1.08	5.82
Reach 3§	14.7 (1.2)	3.7 (0.4)	4.7 (0.7)	3	49.54**	0.02	0.01	42.86*	15.08
Reach 4§	6.9 (1.6)	4.1 (0.3)	4.4 (0.7)	8	3.39	0.10	0.10	5.12	0.19
Among reaches§	8.4 (1.5)	4.5 (0.3)	5.0 (0.5)	4	5.91**	0.03	0.02	6.69*	1.08

Notes: MI = Michigan, WI = Wisconsin. Richness values are based on 1.0-m^2 plots.

* $P < 0.05$; ** $P < 0.01$.

† Repeated-measure adjusted probabilities (G-G = Greenhouse-Geisser and H-F = Huynh-Feldt) are included for comparison.

‡ Values included are F statistics of planned contrasts.

§ Power of ANOVA > 0.80.

on the floodplain than on the terrace–slope complex landforms (Table 6). Additionally, even though the floodplains are more species rich than the adjacent uplands at the smallest observed level (0.5 m^2), both appear to increase in species richness at similar rates (Table 6). Similar trends are observed for the bedrock-controlled watershed, except that the uplands increase in richness at a slower rate than the floodplains (Table 6).

When we examined the larger stream systems at the watershed scale, we again observed similar patterns in total species richness as when individual reaches were pooled by valley type (Fig. 4). In general, the floodplains of the larger stream systems are the most species rich, while the uplands have the lowest levels of species richness. For example, the jackknife estimate of species richness for the floodplain of the constrained ground-moraine valley type is 64.6 species and only 48.8 and 27.6 species for the terrace–slope complex and upland landforms, respectively (Table 6). The two exceptions are the unconstrained outwash plain and bedrock-controlled valley types. In these valley types the jackknife estimates of species richness between the floodplain and terrace–slope complex landforms are similar (Table 6). However, in the bedrock-controlled valley type the floodplains increase in richness at a much faster rate than terrace–slope complex landforms (e.g., species–area curves have higher slope values; $z = 0.60$ and 0.41 for the floodplain and terrace–slope complex landforms, respectively).

Effectiveness of riparian management zones

For first-order streams, the locations of RMZ boundaries with respect to landform class (e.g., floodplain, terrace–slope complex, upland) suggest that RMZ widths are usually adequate for encompassing areas of higher species richness and unique plant assemblages (as shown by the low species similarity) relative to the adjacent uplands. In these systems, a 33-m-wide RMZ always includes the species-rich floodplains, and extends to include the terrace–slope complex landforms over 50% of the time and uplands over 33% of the time (Fig. 5). For higher order streams the RMZ may be inadequate for protecting plant diversity. While RMZs always include the entire floodplain, they fail to include

TABLE 4. Herbaceous species similarity between landform classes for individual reaches and among reaches by two valley types for first-order streams in the northern Lake States, USA.

Reach	Species similarity (%)	
	FP-UP	TS-UP
End moraine		
Upper Little Pokegama Creek (MN)		
Reach 1	21.3	18.9
Reach 2	2.5	35.1
Middle Little Pokegama Creek (MN)		
Reach 1	7.1	34.8
Reach 2	5.9	35.7
Reach 3	14.0	35.6
Reach 4	23.4	50.2
Lower Little Pokegama Creek (MN)		
Reach 1	2.6	31.7
Reach 2	22.8	63.2
Reach 3	20.5	58.7
Reach 4	26.3	1.7
Reach 5	6.0	7.1
Among reaches	19.7	53.0
Bedrock controlled		
Mirror Lake Creek (MI)		
Reach 1	29.5	16.8
Reach 2	16.3	48.6
Greenstone Falls Creek (MI)		
Reach 1	9.1	46.9
Reach 2	22.9	41.5
Among reaches	32.0	64.3

Notes: Landform classes: FP = floodplain; TS = terrace–slope complex; UP = upland landforms. State abbreviations: MN = Minnesota, MI = Michigan.

TABLE 5. Herbaceous species similarity between landform classes for individual reaches and among reaches by valley type for second-order or higher streams in the northern Lake States, USA.

Reach	Species similarity (%)	
	FP-UP	TS-UP
Ground moraine, constrained valleys		
North Branch Popple River (WI)		
Reach 1	37.3	46.7
Reach 2	25.6	47.4
Reach 3	8.2	23.9
Reach 4	3.9	19.9
Upper Rat Creek (WI)		
Reach 1	38.0	4.0
Reach 2	32.5	3.1
Among reaches	26.9	29.4
Ground moraine, unconstrained valleys		
North Branch Popple River (WI)		
Reach 1	0.3	6.3
Reach 2	18.3	5.6
Upper Rat Creek (WI)		
Reach 1	0.6	23.6
Reach 2	0.0	16.5
Among reaches	7.5	33.6
Outwash plain, constrained valleys		
Morgan Creek (WI)		
Reach 1	24.2	34.7
Reach 2	30.6	23.2
Upper Riley Creek (WI)		
Reach 1	5.2	18.1
Reach 2	7.3	30.6
Lower Riley Creek (WI)		
Reach 1	0.0	40.0
Reach 2	0.0	35.3
Among reaches	12.1	35.5
Outwash plain, unconstrained valleys		
Upper North Branch Popple River (WI)		
Reach 1	0.0	13.3
Reach 2	0.0	8.2
Morgan Creek (WI)		
Reach 1	2.8	23.0
Reach 2	2.2	11.8
Among reaches	1.6	25.3
Bedrock controlled		
Upper Little Carp River (MI)		
Reach 1	29.9	64.3
Reach 2	10.3	49.9
Reach 3	29.6	33.5
Middle Little Carp River (MI)		
Reach 1	5.8	57.3
Reach 2	7.3	73.7
Reach 3	10.1	14.6
Reach 4	38.1	31.5
Among reaches	18.6	74.1
Clay lake plain		
Lower Little Carp River (MI)		
Reach 1	0.0	32.5
Reach 2	10.1	54.1
Reach 3	0.0	24.2
Reach 4	4.9	46.3
Among reaches	6.1	40.2

Notes: Landform classes: FP = floodplain; TS = terrace-slope complex; UP = upland landforms.

the terrace–slope complex landforms in both unconstrained valley types, and only include the terrace–slope complex landforms 50% of the time in the clay lake-plain valley type and 67% of the time in the constrained ground moraine, constrained outwash plain, and bedrock-controlled valley types (Fig. 6). Only in the clay lake-plain valley type did RMZs include portions of the uplands 50% of the time, while upland landforms were included 33% of the time in the constrained ground moraine, constrained outwash plain, and bedrock-controlled valley types (Fig. 6).

DISCUSSION

In many regions, riparian areas, and especially floodplains, contribute significantly to plant diversity of a watershed by providing unique habitat (e.g., Salo et al. 1986, Nilsson et al. 1994, Pollock et al. 1998, Ferreira and Stohlgren 1999, Amoros 2001). Little is known, however, about how individual riparian areas contribute to plant diversity, how fluvial landforms outside of the floodplain contribute, and at what scale these contributions become evident. One might assume that the greater area associated with the terrace–slope complex and upland landforms, regardless of scale, should result in higher plant species richness relative to the floodplains. Our results, however, demonstrate the opposite regardless of the scale examined, as the floodplains at the reach and watershed scale have either significantly higher, or similar, species richness compared to the terrace–slope complex and upland landforms. Our results also suggest that an individual reach may not significantly increase plant species richness relative to upland forest in the watershed. However, there does appear to be a cumulative effect of adding individual riparian areas together, as predicted by Brinson and Verhoeven (1999), resulting in increased herbaceous species richness at larger scales.

The most likely mechanism responsible for greater plant species richness is environmental heterogeneity associated with riparian areas when examined at larger scales (e.g., among reaches, valley types). This heterogeneity is typically not present at the individual-reach scale. Spackman and Hughes (1995), Bendix (1997), Pollock et al. (1998), Ferreira and Stohlgren (1999), and Amoros (2001) all suggest that variability in duration, depth, and spatial extent of flooding may increase species diversity at the landscape scale by maintaining a variety of disturbed sites (sensu intermediate-disturbance hypothesis; Huston 1994) and thus increasing landscape-scale heterogeneity. In other words, adding individual riparian areas together (each responding to a variety of different hydraulic conditions such as depth, slope, and velocity) forms a longitudinal gradient of stream-valley conditions that increases environmental heterogeneity substantially above that occurring at small spatial scales, especially on floodplain landforms. Such patterns occurring on floodplains have also been suggested by other authors,

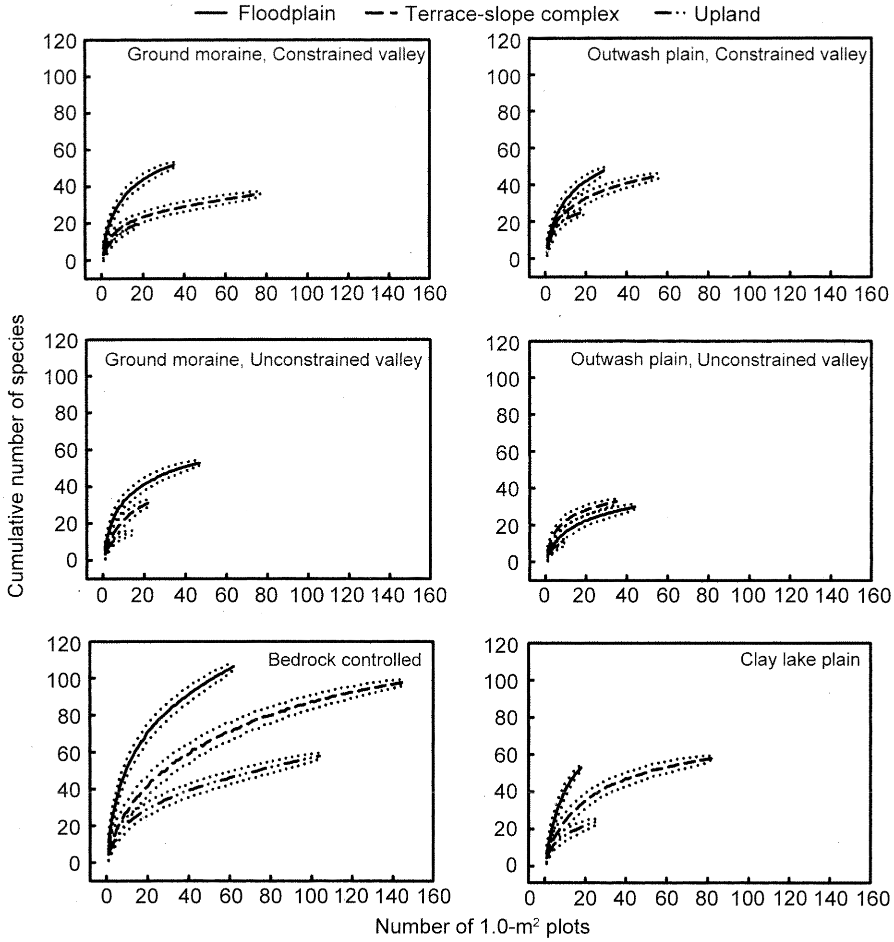

FIG. 4. Species–area curves by landform and valley type for higher-order streams. Dotted lines represent 95% confidence intervals around each curve.

including Bendix (1994), Parker and Bendix (1996), and Bendix and Hupp (2000).

At the scale of an individual reach, plant communities on the floodplains and portions of the terrace–slope complex, particularly low terraces, likely originate through primary succession, becoming relatively stable in composition over time. Many researchers have observed this pattern along both small-stream and river systems (e.g., Hupp and Osterkamp 1985, Hupp 1992, Bendix 1997, 1999) as well as larger river systems (e.g., Kalliola et al. 1991, Amoros 2001); point bars and abandoned channels provide suitable colonization sites for shade-intolerant species and the development of early successional forests often embedded in a matrix of mature forest. However, because streams adjust continually to changing environmental conditions throughout the watershed, new sites available for primary succession are created along the entire stream network. Thus, when riparian areas are viewed as the cumulative sum of all reaches in a watershed, their contributions to plant diversity can be significant.

This does not mean that individual riparian areas do not make important contributions to plant diversity in other ways. While our results demonstrate that species richness does not change consistently across the riparian ecotone at the reach scale, the composition (and likely the structure) of the ground-flora community often changes dramatically. In all but a few instances, we observed low species similarity from the floodplain, across the terrace–slope complex, and into the uplands at small spatial scales. Although not presented here, opposite trends in overstory composition across these riparian ecotones was observed at similar scales, with low overstory species richness (usually <8 woody overstory species) and high species similarities among the floodplain, terrace–slope complex, and upland landforms (Goebel 2001, Palik et al. 2003). As both overstory and understory composition and structure are important factors regulating the type and quality of habitat for many animals (Pregitzer et al. 2001), the low species similarity that occurs in the ground-flora communities across riparian ecotones may be an important

TABLE 6. Jackknife estimates of herbaceous species richness and regression coefficients by valley type for first-order and higher-order streams in the northern Lake States, USA.

Landform by geologic type	Jackknife estimate of species richness	Regression coefficients† c	z
First-order streams			
End moraine			
Floodplain, FP	67.0	25.04	0.34
Terraces slope, TS	69.7	23.49	0.26
Upland, UP	60.5	18.86	0.34
Bedrock controlled			
FP	60.6	12.13	0.41
TS	63.8	9.37	0.43
UP	38.9	7.69	0.35
Higher-order streams			
Ground moraine, constrained			
FP	64.6	12.12	0.42
TS	48.8	7.90	0.35
UP	27.6	4.35	0.54
Ground moraine, unconstrained			
FP	64.7	12.96	0.38
TS	42.5	6.08	0.54
UP	17.8	4.79	0.45
Outwash plain, constrained			
FP	63.5	10.64	0.45
TS	57.8	10.92	0.36
UP	32.7	8.05	0.40
Outwash plain, unconstrained			
FP	39.8	9.23	0.37
TS	41.7	5.74	0.44
UP	12.8	4.03	0.43
Bedrock controlled			
FP	144.4	19.68	0.41
TS	123.8	11.68	0.43
UP	82.8	7.85	0.43
Clay lake plain			
FP	72.8	9.82	0.60
TS	72.8	9.95	0.41
UP	31.7	5.79	0.44

† Definitions: c = intercept coefficient; z = slope coefficient; see Eq. 3.

feature that regulates the diversity of other organisms, such as amphibians and ground-nesting birds.

Our results also demonstrate the contributions to plant diversity provided by fluvial landforms other than floodplains, particularly at larger spatial scales. While the processes of formation are complex, the plant communities of many terrace–slope complexes represent the interaction of current hydrologic forces such as severe floods, as well as historical geologic processes that created the landforms (Verry 2000). This interaction often results in unique environmental conditions that may favor higher plant diversity. In one particularly interesting example, the terrace–slope complex landforms of unconstrained valleys in the outwash plain of the Popple River watershed in Wisconsin (USA) have higher levels of species richness than the floodplains. While the floodplains in these systems are quite extensive, they are also inundated frequently. The result is a plant community dominated by a dense matrix of *Carex stricta* and *Leersia oryzoides* tussocks that often inhibit the germination and survival of other plant species. In contrast, low terraces, while only slightly higher in elevation than floodplains, are out of the direct influence of annual flood events. The result is a diverse ground flora dominated by perennial forbs, pteridophytes, and graminoids.

While our results serve to underscore that it is the cumulative effect of adding reaches (each with different physical characteristic) that is responsible for many of the contributions of riparian areas to plant diversity in forested watersheds, it is difficult if not impossible to make broad generalizations about species-richness patterns beyond trends observed at the among-reach or valley-type scale. Smaller headwater and constrained valleys typically have narrow floodplains and sharper transitions across the riparian ecotone. Conversely, broad, unconstrained valley types have a variety of environments along the valley floor that may promote the development of species-rich plant communities.

Management implications

In the northern Lake States, as well as many other regions, most organizations and agencies have devel-

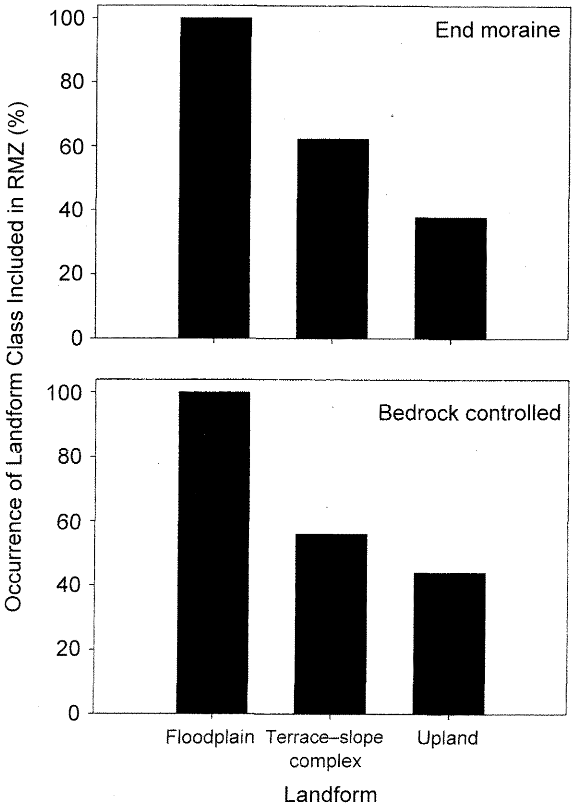

FIG. 5. Percentage occurrence of the extent of the riparian management zone (RMZ) by landform and valley type for first-order streams.

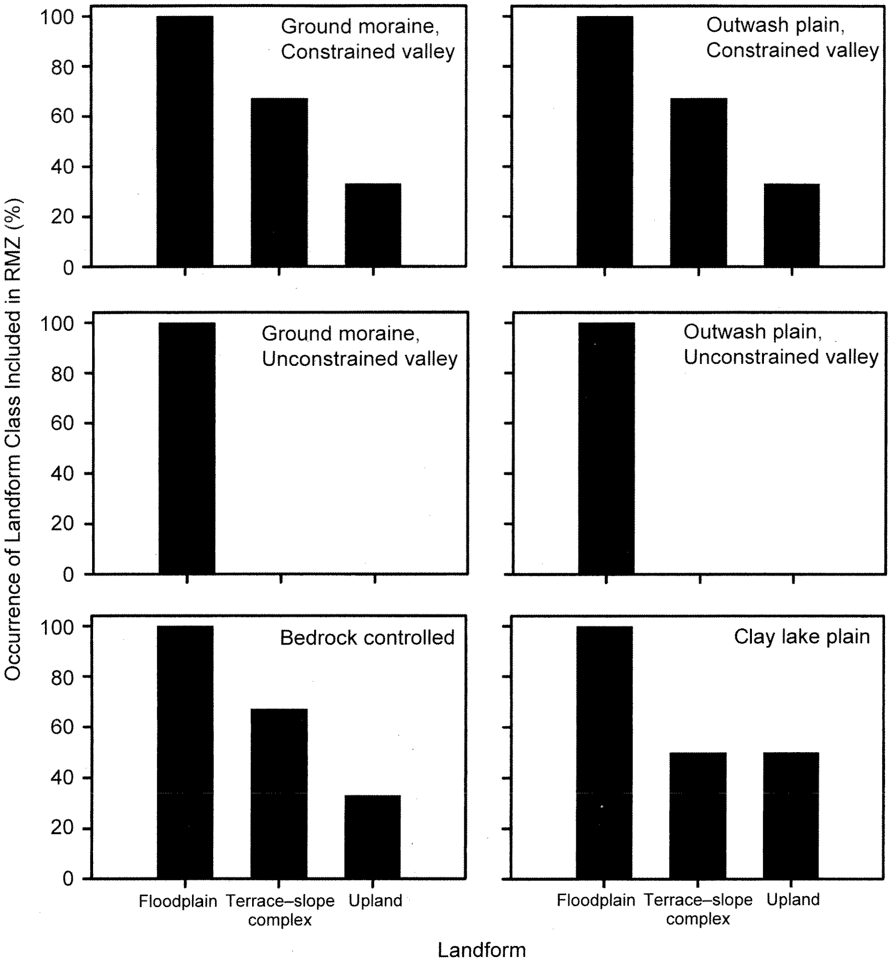

FIG. 6. Percentage occurrence of the extent of the riparian management zone (RMZ) by landform and valley type for higher-order streams.

oped riparian-forest management guidelines. These guidelines usually include identification of a riparian management zone (RMZ) and modification of management practices within the RMZ to better protect aquatic ecosystems and adjacent terrestrial habitat. While the primary intent of RMZs often is to reduce sediment delivery to streams and lakes (Blinn and Kilgore 2001), their role is expanding to include maintenance of a broad array of functional linkages (e.g., shading, organic-matter flux, habitat for riparian-dependent species) between aquatic and terrestrial segments of the riparian ecotone (Palik et al. 2000). Although the specific details of riparian management guidelines differ among regions and organizations, RMZ widths of 30–60 m along each side of a stream are common (Blinn and Kilgore 2001). This width is often invariant in the face of differences in reach and stream-valley characteristics, like stream order or floodplain width (deMaynadier and Hunter 1995) and is determined without regard for the lateral extent of different riparian functions (Gregory 1999, Palik et al. 2000). Consequently, there is great uncertainty about the efficacy of RMZs at protecting riparian areas and the functional linkages between aquatic and terrestrial components of the landscape.

Our results support the contention that current prescriptions for RMZ delineation in the northern Lake States may be inadequate for maintaining plant diversity at multiple scales, particularly in larger stream systems. For example, our results show that floodplains are not always the only important geomorphic feature of riparian areas that contributes to increased plant diversity. Moreover, RMZs often fail to include landforms outside of the floodplain, especially in broad, unconstrained stream valleys. Consequently, we suggest that to protect riparian plant diversity at local scales, the structure and functional sustainability of areas beyond the floodplain (i.e., terraces and slopes) should be considered.

Additionally, our results support the hypothesis that it is the cumulative effect of different riparian habitats that result in increased plant diversity. Consequently, managers need to ensure that a sufficient amount of riparian habitat (at the reach scale) in a variety of successional stages (from disturbed to undisturbed) is maintained to ensure that the full complement of riparian plant species and assemblages are sustained. This suggests that RMZ planning and implementation should be conducted with a watershed perspective in mind, taking into account the variability associated with different types of stream systems and spatial arrangement of different seral stages of riparian forest, to better ensure that the diversity of riparian habitats and riparian plant assemblages are afforded some protection.

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