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ARTICLE

Influence of Flooding and Landform Properties on Riparian Plant Communities in an Old-Growth Northern Hardwood Watershed

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Abstract In most forested landscapes, the organization of plant communities across stream valleys is thought to be regulated by a complex set of interactions including flooding, landform properties, and vegetation. However, few studies have directly examined the relative influence of frequent and infrequent flooding, as well as landform properties, on riparian plant community organization in moderately or deeply entrenched stream valleys where the magnitude and extent of frequent flooding may be constrained by local stream valley characteristics. Our approach, which we applied in an old-growth northern hardwood watershed, integrated detailed plant community surveys with a GIS and watershed surface hydrology model that allowed us to model water surface elevation associated with different flood magnitudes and recurrence intervals for specific locations across the old-growth watershed. Our results show that irrespective of stream valley geomorphology, the ground-flora exhibits a high rate of species replacement across the stream valley at low elevations, which are the most susceptible to frequent and more extreme infrequent flooding. However, over 50 % of the major shifts in ground-flora community composition and almost all of the shifts in overstory composition occur beyond the direct influence of flooding, especially in the high-gradient moderately and deeply entrenched stream valleys. In these areas, landform boundaries and changes in the environmental properties associated with these boundaries appear to be the primary factors controlling changes in vegetation across the stream valley.

Keywords Flooding · Ecotones · Fluvial landforms · Hydrologic modeling · Northern hardwood forest ecosystems · Great Lakes

Introduction

In regions dominated by rivers, lakes, and streams, forests along these water bodies provide many important ecological services critical to maintaining watershed productivity and sustainability (Swanson et al. 1988; Gregory 1999; Naiman et al. 2005). These forests regulate the flux of energy, nutrients, and biotic interchanges between aquatic and terrestrial ecosystems (Gregory et al. 1991; Ilhardt et al. 2000; Naiman et al. 2000), and consequently have been described as functional ecotones (Gregory et al. 1991; Hupp and Osterkamp 1996; Ilhardt et al. 2000). Due to their dynamic position on the landscape, these forests are often characterized by gradients of change in many factors, including microclimate, soil drainage and fertility, and flood frequency and duration (Gregory et al. 1991; Brosofske et al. 1997; Ilhardt et al. 2000). These gradients promote unique and highly diverse plant communities when compared with the adjacent uplands (Brinson and Verhoeven 1999; Naiman et al. 2000; Goebel et al. 2003a) and provide many functional connections between aquatic and terrestrial systems (e.g.,

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large wood and other particulate organic matter inputs that drive aquatic food webs in heterotrophic systems) (Goebel et al. 2003b; Holmes et al. 2010).

Most models of riparian forest development suggest that flooding, landforms, and vegetation are intimately interconnected, and are the primary factors regulating plant community composition and structure (Yarie et al. 1998; Bendix and Hupp 2000; Ilhardt et al. 2000; Osterkamp and Hupp 2010). Flooding clearly controls vegetation development in riparian forests by influencing the dispersal, germination, establishment and mortality of plant species (Hupp 1983; Swanson et al. 1988; Bendix and Hupp 2000). Flooding also results in increased erosion along with sediment transport and deposition, which creates and maintains habitat for a variety of different plant species (both early-, mid-, and late-successional species) that are either resistant to flooding or are able to recover quickly following flooding disturbance (Pickett and White 1985; Auble et al. 1994; Reice 1994). Infrequent flooding, usually associated with high stream flow events that inundate large areas of stream valley bottoms, also results in major rearrangements of sediment, creating new channels or drastically modifying existing channels and floodplains (Bendix and Hupp 2000). These infrequent floods also transport larger materials such as coarse sediment, boulders and large wood through the stream network, disturbing the stream valley environment further and providing potential refuges for different organisms during future floods (Palik et al. 1998; Swanson et al. 1998; Bendix and Hupp 2000). Prolonged saturation of soils across stream valleys also accompanies flooding and these effects are often regulated by local topographic and physiographic conditions (Kozlowski 1984), favoring species that are able to tolerate the prolonged periods of hydric soil conditions that often accompany flood waters (Baker and Barnes 1998; Baker and Wiley 2004; Holmes et al. 2005).

The effects of flooding are mediated by properties of valley floor landforms (floodplain, terraces, and connecting slopes) (Baker and Barnes 1998; Pabst and Spies 1998; Baker and Wiley 2004) which regulate the specific response of vegetation across stream valleys to flooding by controlling inundation depths and duration (Hupp 1983; Viereck et al. 1993). Additionally, microsite differences across valley floor landforms result in unique physical and chemical soil characteristics in response to the interaction between water table depth, surface flooding, and upland disturbances (e.g., fire, landslides, wind) that affect the composition, structure, and successional development of stream valley plant communities (e.g., Viereck et al. 1993; Baker and Barnes 1998; Pettit and Naiman 2007; Mouw et al. 2009). Riparian vegetation also functions to regulate flooding and landform properties, especially early successional species that have been shown to aid in the development of floodplain landforms (Corenblit et al. 2009). These interconnected factors exert a strong influence on the composition and structure of riparian plant communities due, in large part, to the species-specific tolerance to varying degrees of inundation and habitat disturbance (Franz and Bazzaz 1977; Hupp 1983; Hupp and Osterkamp 1985; Auble et al. 1994). As the distance from and elevation above the bankfull channel increase, the direct and indirect impacts of flooding on plant communities decreases (Bendix 1999). Conversely, the direct and indirect impacts of upland disturbances and hillslope processes such as the accumulation of colluvium at the base of the valley wall, and subsequent changes in soil moisture regimes and nutrient availability that affect plant competition and succession, are thought to increase in importance beyond the floodplain (Pabst and Spies 1998; Holmes et al. 2005; Goebel et al. 2006).

Despite the recognition that flooding, landform properties, and riparian vegetation are important interconnected factors regulating plant communities across stream valleys, little information on the relative importance of each on plant communities is available in large part because of the interdependence and complexity among factors (Osterkamp and Hupp 2010). This is particularly true for many low-order streams and rivers in the glaciated Lake States region where streams and rivers are often underfit and moderately to deeply entrenched in response to post-glacial streamflows and the lowering of lake surface levels (Verry 2000), which results in plant communities along the valley floor that are not directly influenced by flooding (Goebel et al. 2006). Such relationships demonstrate the importance of the geomorphic setting which constrains the physical stream valley characteristics and landform properties.

In this paper, we examine the relative importance of flooding and landform properties on organizing plant communities across stream valleys of an old-growth northern hardwood forest watershed in the northern Lake States, U.S.A. As the old-growth riparian and upland forests of the Little Carp River watershed have never been logged, the observed relationships reflect the long-term interactions among hydrogeomorphic processes, properties of stream valley landforms, and riparian vegetation without the added complication from human-mediated disturbances. We hypothesize that the observed patterns in riparian plant communities in this glacially modified landscape reflect the interactions between hydrogeomorphic forces and vegetation, and major differences in the riparian plant community responses are due to shifts in the balance between allogenic physical controls (e.g., streamflow, sedimentation, nutrient availability) and autogenic controls (e.g. facilitation, competition, succession). While disentangling these complex interactions is challenging (Osterkamp and Hupp 2010), we began this process by examining the following questions: 1) How important are both frequent (recurrence interval $\leq$10 years) and infrequent (recurrence interval between 11–50 years)

floods as factors regulating the organization of plant communities across different stream valley types? 2) What role do valley floor landforms beyond the floodplain (e.g., those terraces and connecting slopes beyond the influence of flooding) have on organizing plant communities across different stream valley types? 3) Do overstory and ground-flora plant communities respond in a similar manner to flooding and landform properties occurring across stream valleys and are these patterns consistent among different stream valley types?

Methods

Study Area

We conducted our research in the Little Carp River watershed (Fig. 1), a 42.2 km^2 northern hardwood-hemlock forest located in the Porcupine Mountains Wilderness State Park along the south shore of Lake Superior in Michigan's western Upper Peninsula (46°45′N, 89°47′W). The Little Carp River watershed has never been logged and is best characterized as an uneven-aged northern hardwood-hemlock forest (Lorimer and Frelich 1984; Frelich and Lorimer 1991). The climate is characterized by moderate precipitation (91 cm yr^{-1}), cold winters (January mean −7 °C), and mild summers (July mean 19 °C). Over two-thirds of the precipitation usually occurs as snow from November to April, and peak discharges along the Little Carp River and its tributaries usually occur following snowmelt in the spring (Goebel 2001).

In this landscape, the sequence of landforms includes (in order of increasing distance and elevation from the stream channel), the floodplain, low and high terraces, and connecting slopes (see Goebel et al. 2006 for a generalized sequence of landforms). We define the floodplain as the alluvial surface created by the stream under current environmental and climatic conditions that is flooded once every 1–3 years (Dunne and Leopold 1978). The formation of terraces above the floodplain often occurs in response to a variety of processes, but many terraces, including those along streams and rivers are remnants of older floodplains that have been abandoned as the stream lowered the valley by degradation, especially in relatively young glacial landscapes

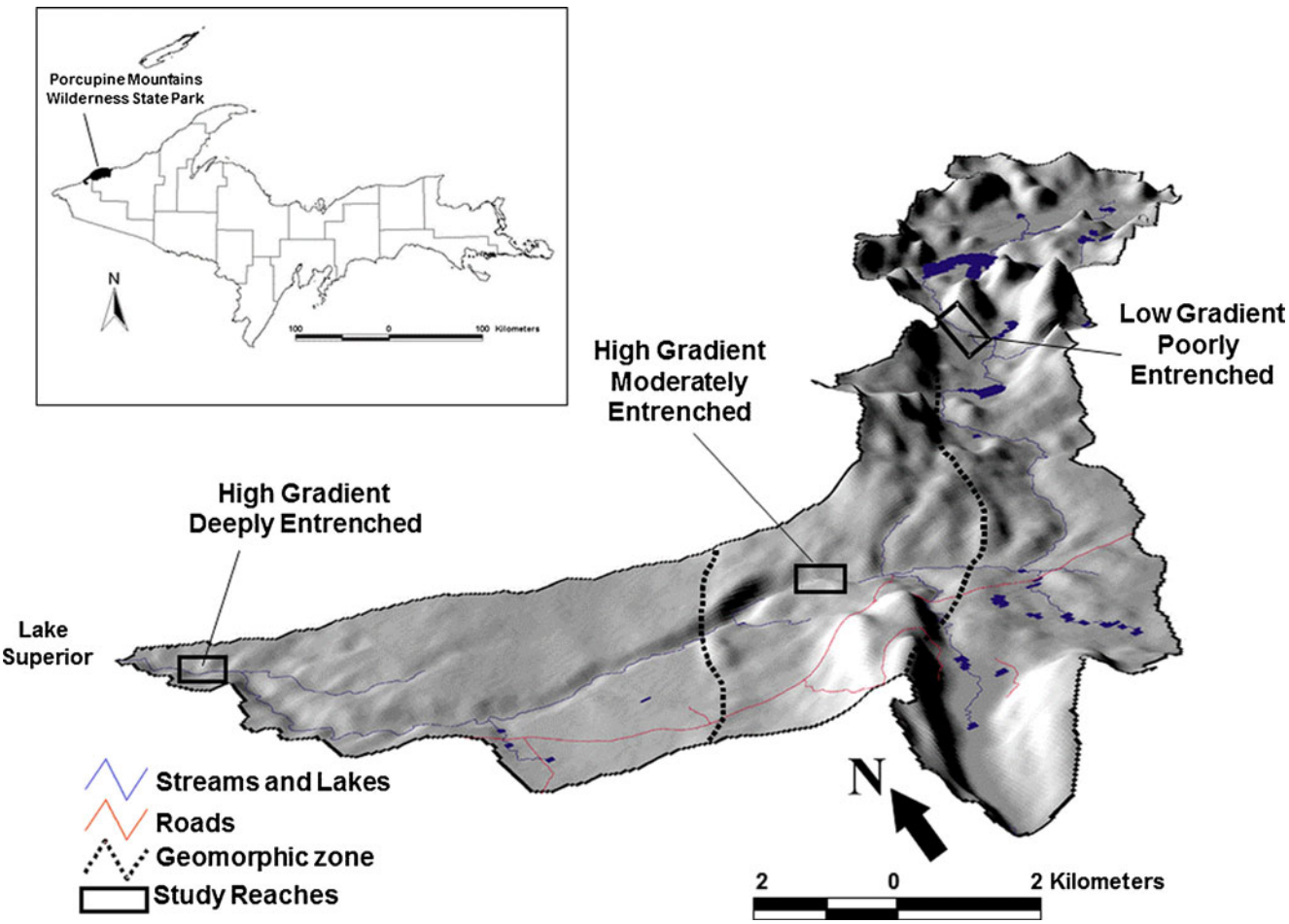

Fig. 1 Location of the Porcupine Mountains Wilderness State Park (inset) and a shaded digital elevation relief map showing location of different geomorphic settings and study reaches in the Little Carp River watershed, Upper Michigan

such as represented by the Little Carp River watershed (Howard et al. 1968). Many of these terraces and connecting slopes in the moderately or deeply entrenched stream valleys are so high above the active stream channel that they rarely flood or do not flood at all (Verry 2000).

The Little Carp River watershed is comprised of three major geomorphic settings or stream valley types (Table 1). In the upper portions of the watershed, the Little Carp River flows southwest from the headwaters between two highly resistant granitic and conglomerate ridges. The river channel in this valley type has a low-gradient (1.8 %) and is considered slightly entrenched. Extensive floodplains and wetlands dominated by *Alnus incana* L. and grass-sedge plant communities are common in this area, comprising approximately 12 % of the total watershed area. These lowland areas are dominated by poorly drained soils and often have a surface layer of organic matter less than 1 m thick. Conversely, the adjacent upland soils are shallower and rock outcrops are common. Bedrock types are amygdaloidal basalt, granite, or Copper Harbor Conglomerate at the higher elevations (Dorr and Eschman 1970).

In the middle portion of the watershed, approximately 8 km from the watershed divide, the Little Carp River changes direction, flowing northwest through a divide in the resistant conglomerate and grantitic bedrock. The gradient of the Little Carp River increases dramatically (~5 %) once it reaches this middle valley type and is characterized by large rapids and water falls where the stream is moderately entrenched and has downcut into the highly resistant bedrock. Most floodplains are quite narrow in this valley type, with terraces approximately 3–6 m above the bankfull channel and dominated by northern hardwood-hemlock forests.

Finally, the lower portions of the watershed along the shore of Lake Superior flow through a clay lake plain, a remnant of Glacial Lake Duluth that covered this portion of the watershed until ~8,000 years BP (Hough 1958). This valley type is characterized by areas with very deep deposits of silty lake bottom sediments at elevations up to 120 m over shale and sandstone bedrock (Dorr and Eschman 1970). These lower reaches of the Little Carp River have very steep slopes or valley walls (>70 %) as it flows through the clay lake plain, with valley walls that frequently collapse, resulting in large expanses of bare mineral soil along the river channel. Although the gradient is low (~2 %) and the stream channel is deeply entrenched, valley constraint in this lower valley type is less than the high-gradient, moderately entrenched valley type as a result of the broad terraces over 100 m wide (Table 1).

Table 1 Stream valley characteristics by valley type of the Little Carp River, Upper Michigan, USA

Variable	Valley type		
	Low-gradient Bedrock controlled	High-gradient Bedrock controlled	Low-gradient Clay lake plain
Channel entrenchment	Slightly	Moderately	Deeply
Channel slope (%)	1.8	4.3	1.7
Bankfull height (m)[a]	0.5	0.6	0.6
Bankfull width (m)[a]	5.8	11.3	18.3
Bankfull discharge (cms)[a]	4.7	9.4	9.7
Entrenchment ratio[a]	6.4	1.4	1.6
Valley floor width (m)[a]	148.0	122.0	223.0
Valley constraint (%)[b]	3.9	9.2	8.2

[a] Measurements taken at downstream boundary of each study reach over 3 year period

[b] Valley constraint = (bankfull width/valley floor width) * 100

General Approach

Our approach is based on a gradient analysis approach that quantifies major changes in vegetation along a complex ecotone characterized by multiple gradients, including the influence of both frequent and infrequent flooding. Similar approaches have been used by Franz and Bazzaz (1977) and Auble et al. (1994) to assess the impacts of river impoundments on inundation periods and vegetation at a single site. However, in these instances long-term stream discharge data were available, and there are many rivers and streams in North America (including those located in the Porcupine Mountains Wilderness State Park) that do not have streamflow records. We used an integrated series of modules starting at the watershed scale using a geographical information system (GIS), surface hydrology model, and long-term climate data from a nearby weather station to develop estimates of surface flow and flood frequency curves for our study streams as long-term records of stream discharge were not available (see Electronic Supplementary Materials Section A for more information on these procedures). The results of this modeling approach were then combined with detailed stream valley topographic surveys at specific locations in the watershed representing each major geomorphic setting, and a hydraulic model to determine water surface elevations for different flood recurrence intervals. Finally, water surface elevations were combined with detailed vegetation surveys to relate changes in vegetation with different flood events using differential profiles.

Data Collection and Analyses

Within each of the three major geomorphic settings, we established a study reach ranging from 150 to 300 m long.

Each reach was delineated based upon homogeneity of valley and streambed characteristics (e.g., valley width, valley shape, streambed material, and bankfull channel width) and were named based on their overall stream gradient and stream channel type. These include: low-gradient, slightly entrenched; high-gradient, moderately entrenched; and, low-gradient, deeply entrenched. Vegetation data were collected in each of the three study reaches during the summer and fall of 1999. We collected vegetation data from transects that bisected the entire stream valley, each transect extended across the stream valley and at least 40 m into the adjacent uplands on both sides, with transects arrayed perpendicular to streamflow. Eight transects were sampled in both the low-gradient, slightly entrenched and high-gradient, moderately entrenched reaches, while six transects were sampled in the low-gradient deeply entrenched reach. The elevation above and the distance from the bankfull channel were calculated by topographically surveying each transect using a Leica® TC600 total station and standard surveying procedures with bankfull elevation as the reference point. While surveying each valley-wide transect, we visually delineated and noted the boundaries between major valley floor landforms (floodplain, terraces, slope, and upland).

Along each transect, ground-flora sample plots were spaced every 5 m from the stream edge up to 20 m on each side of the river, with subsequent plots after 20 m spaced at 15 m or 30 m intervals thereafter depending on valley width (e.g., 15 m spacing for more narrow stream valleys and 30 m for wider stream valleys). In all cases, at least two sample plots were located in the adjacent upland forest. Individual valley-wide transects had 30 to 60 1-m^2 ground-flora sample plots, depending on the valley width, for a total of 441 1-m^2 ground-flora sample plots distributed across the three study reaches. In each sample plot, we recorded percent cover of all herbaceous and woody species <1 m tall using the following cover classes: <1 %, 1–5 %, 6–10 %, 11–20 %, 21–40 %, 41–70 %, and 71–100 %. Species names for both the herbaceous and woody plants follow Voss (1972, 1985, 1996). Each species was classified according to its functional lifeform guild and wetland indicator status following Herman et al. (1996).

The overstory was also sampled along each transect from a total of 274 overstory plots. We measured the diameter of all stems >10.0 cm dbh by species in a series of 100 m^2 circular plots (radius=5.64 m). The first overstory plot along each side of the valley-wide transect was located 5 m from the bankfull channel with subsequent plots located every 15 or 30 m, again depending on the valley width.

Ground-flora abundance was summarized by percent cover while overstory abundance was summarized as an importance value [IV = relative basal area (%) + relative density (%) divided by two, 100 % maximum]. Ground-flora cover and overstory datasets were analyzed with detrended correspondence analysis (DCA) to determine the interrelationships of species and sites along riparian areas within individual study reaches of the Little Carp River valley. Although DCA has potential limitations as a gradient analysis technique when examining more than one axis (McCune and Grace 2002), DCA has been shown to be a useful method for relating compositional changes across distance and elevation gradients areas associated with stream valleys (e.g., Lyon and Sagers 1998; Pabst and Spies 1998) and is an appropriate technique to summarize beta diversity, or species turnover, when considering the first axis scores only (McCune and Grace 2002). Prior to these analyses, rare species (those occurring on <5 % of the plots, <22 of 441 plots) were omitted from the ground-flora dataset (91 of 161 species), as were the species of unknown identity (28 of 161 species), while 6 of the 14 overstory species occurred on less than 5 % of the overstory plots (<15 of 271 plots) and were excluded from the ordination analyses. We used distance from the bankfull channel and elevation above bankfull channel as surrogates for flooding gradients across the riparian areas, and used regression analyses to describe the best-fit distribution of plant species communities as expressed by the DCA first axis site scores to both the distance from the bankfull channel and elevation above the bankfull channel individually using SAS ver. 9.3 software (SAS, Cary, NC). In all instances, a non-linear model was selected as the best fit, however, only those stream valley types that had a significant ($P<0.01$) relationship between the DCA first axis site scores, and the distance from and elevation above the bankfull channel, are presented.

Differential profiles developed using moving window analyses (Hobbs 1986; Ludwig and Cornelius 1987; Johnston et al. 1992) were used to identify the location, width, and magnitude of vegetation change along each of the 22 valley-wide transects. To develop each differential profile, we used DCA to quantify the vegetation change across individual transects, however, unlike the DCAs of each valley type, we used the entire ground-flora dataset (no species were removed from the dataset) of each individual valley-wide transect. Next, we placed a two sample-window over a data set of sequential DCA first axis scores and measured the dissimilarity (squared Euclidean distance or SED) between window halves, moving to the next set of values to produce a series of dissimilarity values between window halves along the entire transect. These dissimilarity values were plotted against distance from and elevation above the bankfull to channel to generate a differential profile (*sensu* Hobbs 1986; Johnston et al. 1992) based on the first axis DCA scores as the first axis was consistently highly correlated with distance from and elevation above the bankfull channel in all valley types. Similar analyses were conducted with the overstory data set. Points along a transect with the highest SED represent locations where there is the greatest change in plant community composition across the stream valley, while the width and

strength of the vegetation change can also be determined by examining the structure of the differential profile. For example, abrupt changes in vegetation appear as high, narrow peaks, while gradual changes in vegetation appear as wider and more gradual peaks.

To identify whether shifts in plant community composition (defined as a change in SED greater than 50) are related to either frequent (recurrence intervals <10 years) or infrequent (recurrence intervals between 10–50 years) flooding, the lateral extent of the different flood events estimated using the HEC-RAS (see Electronic Supplementary Materials Section A for more information) were compared with each differential profile graphically. Such an approach allowed us to identify whether vegetation change corresponds with the extent of frequent flooding or infrequent flooding. Similar graphical analyses were conducted to determine if shifts in plant community composition were associated with landform properties by comparing peaks along the differential profiles with landform boundaries that were determined from topographic surveys of each transect. Finally, because the threshold SED value we selected is subjective, we conducted the same graphical analyses using a SED value of less than 25 and greater than 100 to assess the sensitivity of the different gradients to SED value.

Results

Patterns in Ground-Flora Composition

We identified a total of 161 ground-flora species (87 forbs, 34 graminoids, 12 pteridophytes, and 28 woody shrub and tree species). Of the 161 species sampled, only 26 % (43 species, see Electronic Supplementary Materials Section B for complete list) occurred on more than 5 % of the sample plots (22 of 441 sample plots). DCA ordinations suggest that sample plots and species are associated with distance and elevation above the stream channel, and these patterns are similar in all three study reaches (see Electronic Supplementary Materials Section C for DCA ordinations diagrams). Obligate wetland and facultative wetland graminoid and pteridophyte species such as *Leersia oryzoides* (L.) Sw., *Carex stricta* Lam., *Thelypteris phegopteris* (L.) Slosson., and *Athyrium felix-femina* L. dominate the near-stream end of the ecotone represented by the first DCA axis of all three ordinations, while as the distance from and elevation above the bankfull channel increases, these species give way to more upland species, including *Acer saccharum* Marsh., *Maianthemum canadense* Desf., *Trientalis borealis* Raf., *Dryopteris intermedia* L., and *Carex arctata* Boott., all considered upland facultative or upland obligate species.

The distribution of DCA Axis 1 scores are best fit by decay functions that decline sharply as distance from the bankfull channel increases beyond ~20 m in the low-gradient, slightly entrenched reach (d.f.=157, F=265.45), ~40 m in the high-gradient, moderately entrenched reach (d.f.=156, F=2137.02), and ~60 m in the low-gradient, deeply entrenched reach (d.f.=125, F=2435.75) (Fig. 2). Beyond these distances DCA first axis scores became more stable, suggesting less change in the plant community composition beyond this threshold. The regression analyses of DCA first axis and elevation above the bankfull channel also suggest that the composition of the ground-flora communities becomes more stable at elevations ~5 m above the bankfull channel in the low-gradient, slightly entrenched reach (d.f.=157, F=467.75), ~10 m above the bankfull channel in the high-gradient, moderately entrenched reach (d.f.=156, F=1183.82), and ~15 m above the bankfull channel in the low-gradient, deeply entrenched reach (d.f.=125, F=368.56) (Fig. 2).

Patterns in Overstory Composition

A total of fourteen overstory species were sampled, however only eight of these species occurred on more than 5 % of the total overstory plots (see Electronic Supplementary Materials Section B for complete list). The distribution of overstory sample plots and species is related to distance from and elevation above the bankfull channel as in the ground-flora DCA ordinations (see Electronic Supplementary Materials Section C for DCA ordinations diagrams). The distribution of overstory species reflect these relationships, with some areas farther from the stream channel of the low-gradient, slightly entrenched stream valleys dominated by *Acer saccharum*, *Fraxinus nigra* L., *Abies balsamea* L., and *Betula allegheniensis* L., while those areas closer to the stream and the wetter portions dominated by *Alnus incana*. Similar differences are observed in the high-gradient moderately entrenched stream valleys, as *Acer rubrum* L. and *Tsuga canadensis* L. dominate the near-stream environment, while *Acer saccharum* and *Betula allegheniensis* dominate the upland end of the riparian ecotone. Only in the high-gradient, moderately entrenched reach (Fig. 3) did we observe a significant relationship between DCA Axis 1 site scores and distance (d.f.=103; F=85.89) and elevation above (d.f.=103; F=34.21) the bankfull channel. No significant relationships among overstory DCA Axis 1 scores and distance from and elevation above the bankfull channel were observed in the low-gradient, slightly entrenched reach and the low-gradient, deeply entrenched reach.

Factors Influencing Vegetation Change Across Stream Valleys

The differential profiles of the 22 individual valley wide transects suggest both flooding and landform properties

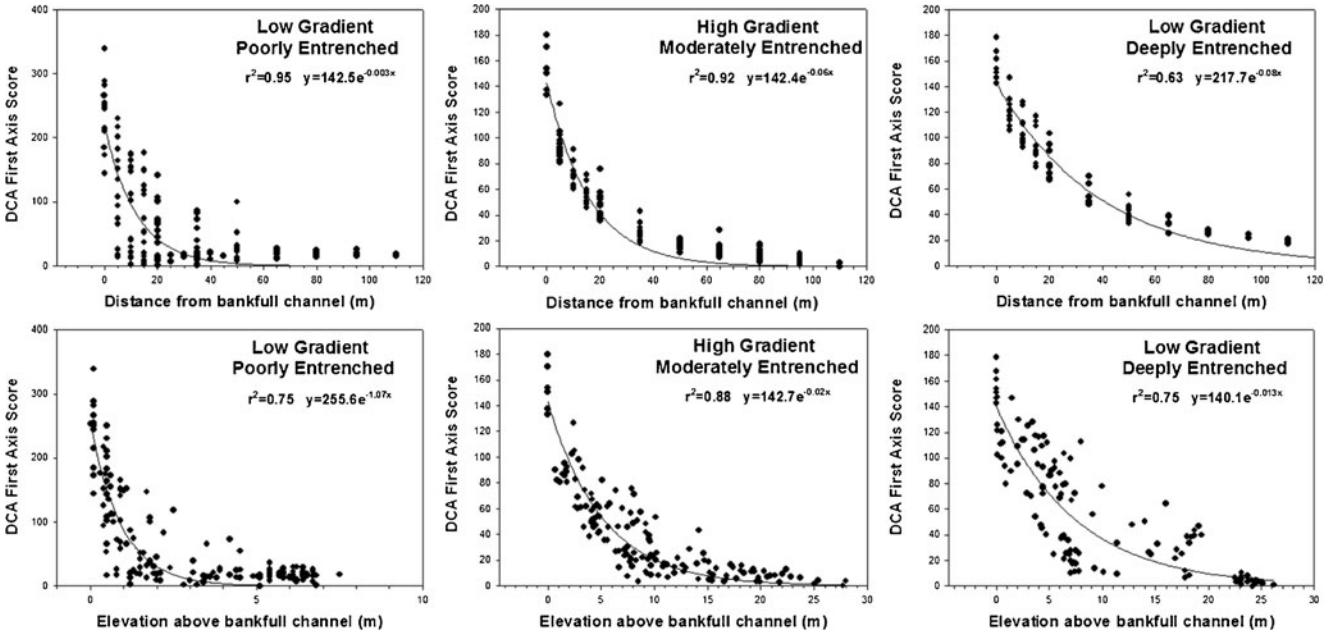

Fig. 2 Ground-flora DCA Axis 1 ordination scores in relation to distance from the bankfull channel and elevation above the bankfull channel for different stream valley types of the Little Carp River. Regression equations are significant at $P<0.01$

influence the composition of the vegetation across the stream valleys of the Little Carp River watershed (Figs. 4 and 5). When we examine the sensitivity of the SED value selected to determine where a major change in plant community composition occurs, we find that using a more conservative or more liberal criteria (SED_{100} or SED_{25}, respectively), the results do not change considerably. Consequently, we feel confident that the SED_{50} value to quantify a shift in community composition to be an appropriate cutoff value.

Approximately half of the shifts in ground-flora composition in the low-gradient, slightly entrenched reach are associated with flooding, most of which are associated with infrequent flooding rather than frequent flooding (36 % and 16 %, respectively, Fig. 4). In the high-gradient, moderately entrenched and deeply entrenched reaches, approximately 30 % of the shifts in ground-flora composition are associated with flooding. However, these shifts are more commonly associated with infrequent flood events in the high-gradient, moderately entrenched reach (22 %), while those in the low-gradient, deeply entrenched reach tend to be associated with frequent flooding (21 %). Landform properties also appear to be important factors regulating plant community composition, as the majority of shifts in ground-flora composition are associated with landform boundaries in both high-gradient reaches, and landforms are the second highest factor associated with plant community change in the low-gradient, slightly entrenched reach (Fig. 4). In all cases, over 20 % of the observed shifts in ground-flora composition are associated with a factor other than flooding or landform boundary.

A characteristic valley wide transect for each reach is illustrated in Fig. 6; in all cases, the two-dimensional profile (elevation v. distance) of each stream valley is plotted with the SED values for the first transect-scale DCA axis of the ground-flora (solid line) and overstory (dashed line) DCA ordinations; more significant changes in the vegetative composition are represented by the taller and narrow peaks. In the examples presented, we observed changes in ground-flora communities that were associated with frequent and infrequent flooding both in the high-gradient moderately entrenched and the low-gradient deeply entrenched reaches. These changes are often abrupt (as reflected by the tall and narrow peaks) and are confined within the fluvially-active portion of the stream valley which is narrow in these high-gradient stream valleys. However, ground-flora species turnover associated with flooding in the low-gradient, slightly entrenched reach tends to be more gradual as represented by the broader peaks in SED than those typically observed in the high-gradient reaches (Fig. 4). Other shifts in ground-flora composition are also observed in all three reaches, however, these shifts occur beyond the influence of flooding and are primarily associated with a landform boundaries (Fig. 4), such as those associated with the transition between the terraces and terrace slopes.

Fewer shifts in the overstory are related to flooding under the less conservative criteria (SED >50), as none of the changes in overstory composition observed in the three different valley types is related to frequent flooding (Fig. 5). Furthermore, no major changes in overstory composition are related to infrequent flooding, except for in the

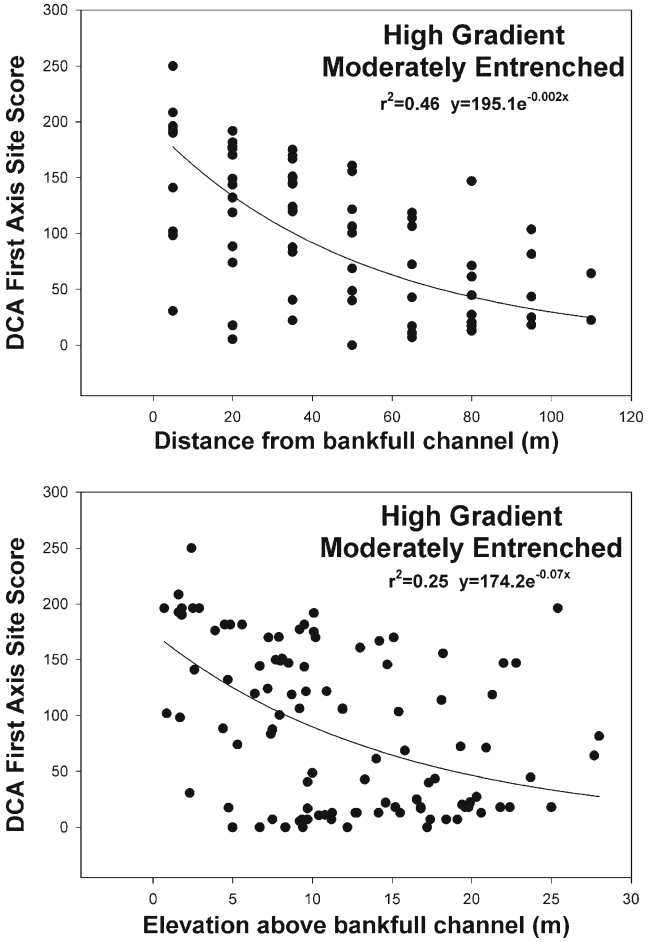

Fig. 3 Overstory DCA Axis 1 ordination scores in relation to distance from the bankfull channel and elevation above the bankfull channel for the high-gradient, moderately entrenched stream valley type of the Little Carp River. Regression equations are significant at $P<0.01$

low-gradient, slightly entrenched system where 22 % of the shifts in overstory composition are related to infrequent flooding (Fig. 5). Most changes in the overstory across the riparian ecotones are associated with valley floor landforms or the boundaries between valley floor landforms (55–71 %). Examples of these patterns are presented in Fig. 6, and the infrequent flooding associated with these low-gradient stream valley types usually results in a shift in the abundance from *Acer rubrum*, and *Abies balsamea* to an overstory community dominated by *Alnus incana*.

Discussion

Influence of Flooding on Plant Communities

We observed high rates of change in the composition of the ground-flora within a few meters of the channel in high-gradient, moderately entrenched and low-gradient deeply entrenched stream valleys, and similar high rates of change in the ground-flora occur at upwards of 30–40 m from the active channel in the low-gradient, slightly entrenched stream valley. Based upon the application of our hydrologic model to these stream valleys, these changes are most likely associated with flooding. Our results also suggest that the role of flooding in driving riparian plant community dynamics is mediated by the characteristics of the stream valley and is more important in the slightly entrenched stream valleys than in the moderately entrenched and deeply entrenched stream valleys. This is in large part due to the narrow lateral extent of both frequent and infrequent flooding in these entrenched stream valleys.

Although others have suggested that frequent flooding is one of the most important drivers of riparian vegetation dynamics (e.g., Bendix and Hupp 2000), we suggest that in slightly entrenched stream valleys of the Little Carp River changes in plant community composition are more likely associated with infrequent flood events rather than frequent flooding. As with the moderately and deeply entrenched stream valleys, the lateral extent of frequent flooding in the slightly entrenched stream valleys of the Little Carp River is constrained. However, the lateral extent of infrequent flooding can be more extensive, impacting an area up 30 to 40 m away from the bankfull channel. In these areas, the temporal and spatial variation in flow energy associated in these flooded areas may be high (Bendix 1999) and result in a mosaic of local microhabitats with unique environmental conditions that support different riparian plant communities. Dick and Gilliam (2007), for example, found considerable spatial variability in both soil organic matter content and nitrification levels across a floodplain of southwestern West Virginia, and these factors were determined to be important drivers of abrupt plant community change. Additionally, flooding may affect the spatial heterogeneity of habitat and plant communities through hyporheic exchange. Areas with significant upwelling and connection with groundwater sources have been shown to exhibit higher levels of dissolved nitrogen and carbon (Ford and Naiman 1989), leading to increased growth rates and niche space for riparian plants (Mouw et al. 2009). The importance of these factors on plant communities is beyond the scope of the current study and future studies are needed to investigate these potential interactions and controls on the spatial heterogeneity of plant communities across these different stream valley types.

There is also evidence that plants themselves can have a dramatic influence on shaping the properties of fluvial landforms, especially areas directly influenced by flooding. Plants often affect sediment deposition by increasing roughness and site-specific flow energy, and have been shown to accelerate the process of island formation in larger riverine systems (Gurnell et al. 2001). In dynamic systems such as

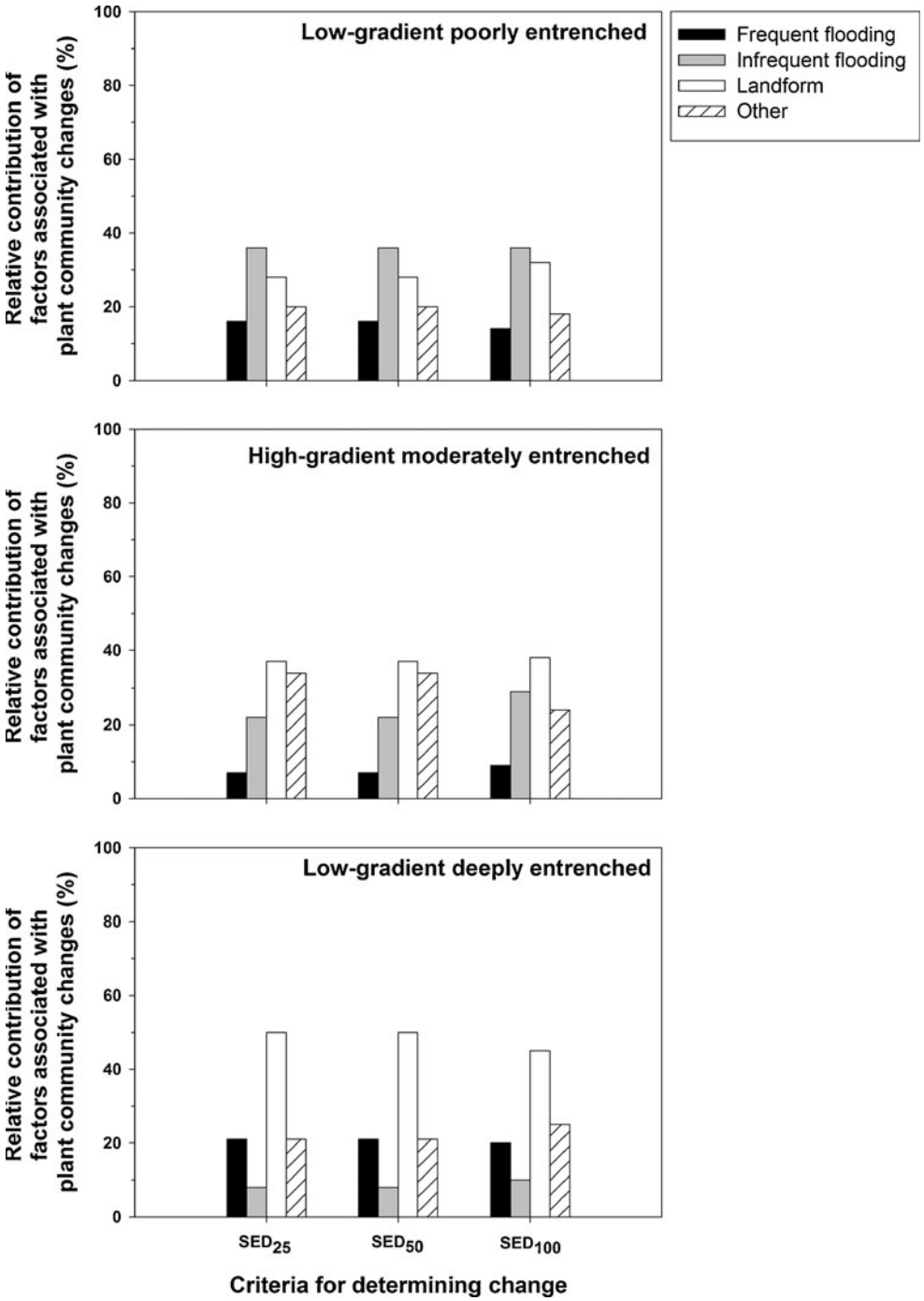

Fig. 4 Relative contribution (%) of different factors associated with major changes in ground-flora vegetation across riparian ecotones of the Little Carp River watershed. See text for explanation of SED values

the slightly entrenched stream valleys of the Little Carp River, the negative and positive feedbacks between floodwaters, sediment, and plants themselves across the stream valley impacted by infrequent flooding are likely responsible for a complex and shifting mosaic of habitat, and corresponding differences in plant communities, as evidenced by the abrupt changes in plant community composition between areas impacted and not impacted by infrequent flooding. It is possible that a similar dynamic is occurring in the moderately and deeply entrenched stream valleys, but on a much smaller scale than examined in the current study and limited to the near-stream environment or within the entrenched channel.

Influence of Landform Properties on Plant Communities

Despite the importance of flooding in the near-stream environment, there are other factors that influence the distribution of ground-flora and overstory species across these stream valleys of the Little Carp River. In the high-

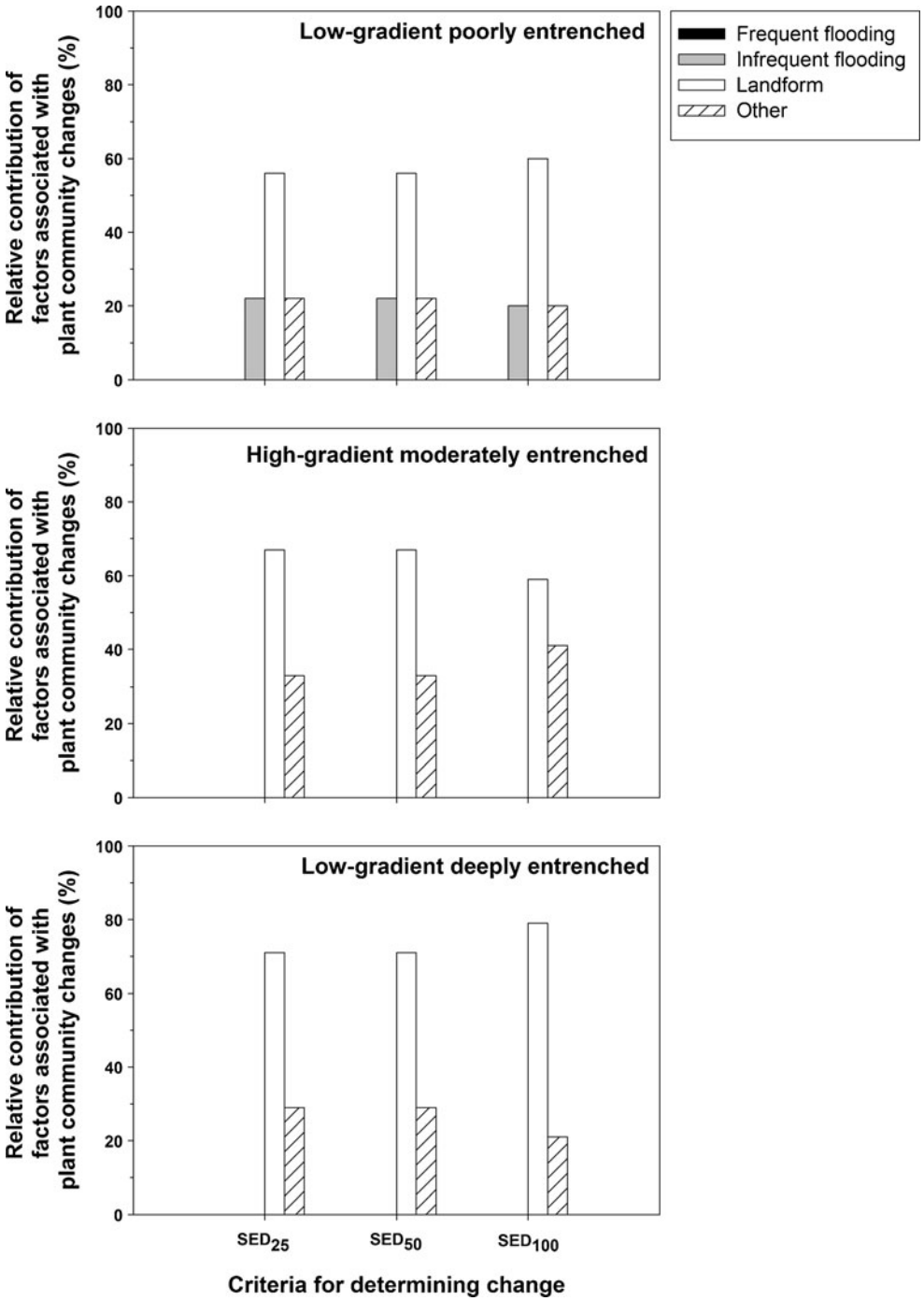

Fig. 5 Relative contribution (%) of different factors associated with major changes in overstory vegetation across riparian ecotones of the Little Carp River watershed. See text for explanation of SED values

gradient, entrenched stream valleys no shifts in the overstory composition, and less than 30 % of the major shifts in ground-flora vegetation, can be attributed to either frequent of infrequent flooding. However, our analyses show that the plant community composition along the valley floor often changes considerably well beyond the influence of flooding, and in many cases these changes are associated with either landform boundaries or factors not measured in this study but likely associated with autogenic processes (e.g., changes in light conditions associated with canopy gaps on terraces or hillslopes; *personal observation*). In these entrenched stream valley types, the greatest changes in vegetation are often associated with the boundaries between high, abandoned terraces and adjacent slopes. Processes associated with these landforms, such as the accumulation of colluvium at the bottom of slopes likely increases the water holding and nutrient capacity of these soils, and changes the microclimatic conditions of the site. The influence of seeps, of which little is known in these systems, may also affect riparian plant communities via connections with groundwater sources.

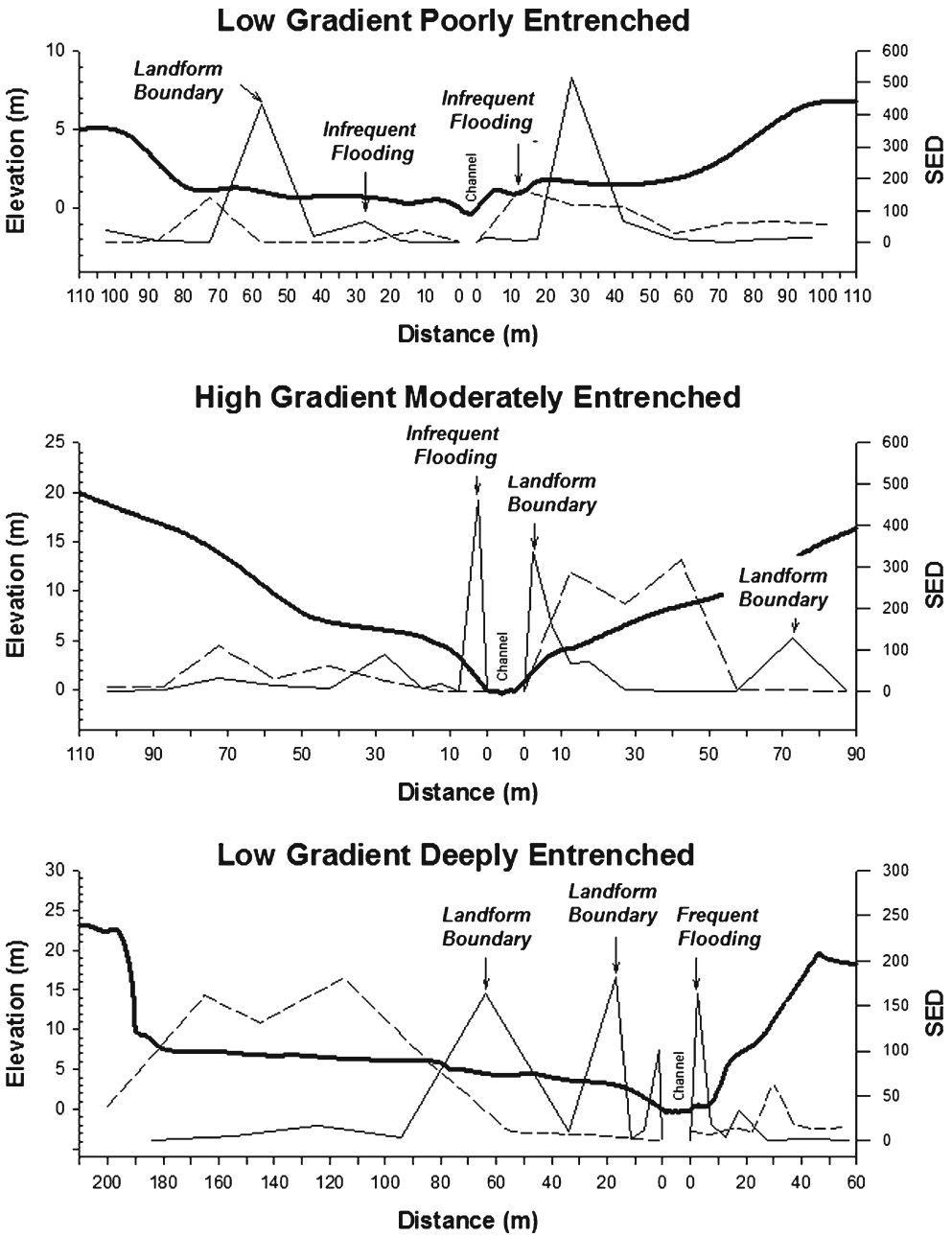

Fig. 6 Representative differential profiles of ground-flora (*solid lines*) and overstory (*dashed lines*) Squared Euclidean Distance (SED) values plotted against elevation (*bold lines*), showing significant composition shifts for different valley types of the Little Carp River watershed. Changes in vegetation change associated with frequent flooding, infrequent flooding, or landform boundaries are noted (if not labeled than other factor was responsible for the change), abrupt shifts appear as high, narrow peaks, while gradual shifts appear as wider and more gradual peaks. Landform boundaries determined on the ground during topographic surveys. Higher SED values indicate a greater change in plant community composition

Thus, the primary physical drivers of vegetation change across large portions of valley floor in high-gradient and entrenched stream valleys of the Little Carp River are not associated with flooding, rather they are associated with changes in landform properties or other natural disturbances (e.g., wind) and autogenic processes associated with plant succession across the stream valley.

Differential Response of Ground-Flora and Overstory Layers

We observed a differential response of overstory and ground-flora layers to the hydrogeomorphic processes and landform properties examined in this study. The only shifts in overstory composition we observed that were associated with flooding were located in the low-gradient, slightly entrenched stream systems. In these areas there are few overstory trees located along the near-stream environment and across the zone impacted by infrequent flooding. In the moderately and deeply entrenched stream valleys, streamflow energy is typically higher and the extent of floodwaters constrained as a result of stream and valley entrenchment. The result is that the overstory of these riparian areas in the Little Carp River watershed is relatively homogenous across the stream valley and adjacent uplands. Conversely, the ground-flora exhibits considerable species replacement and

sharp ecotone boundaries across the entire stream valley, including the near stream and flood-influenced environment. Although our analyses suggest that both the groundflora and overstory are likely responding to similar landform properties, the manifestation of these ecotones and vegetative responses (as represented by the sharp and high peaks in the differential profiles, Fig. 6) appear to be operating at different positions in the landscape and at different scales throughout the watershed. While species turnover in the ground-layer appears to occur frequently across many of the stream valleys and these changes are associated with flooding and changes in landform properties, shifts in overstory composition are almost always associated with landform boundaries and outside of the influence of flood waters. While live woody vegetation has been shown to exert a strong influence on the topographic surface of floodplains and is a critical component driving biogeomorphological succession (Opperman et al. 2008; Francis et al. 2009; Corenbilt et al. 2010) and is likely functioning in a similar manner in the slightly entrenched stream valleys of the Little Carp River, the overstory in the moderately and deeply entrenched stream valleys appears to be less influential in driving riparian vegetation dynamics. However, we have observed large accumulations of in-stream large wood in these moderately and deeply entrenched stream valleys (Morris et al. 2007), and such accumulations have been shown to dramatically affect the topographic surface and habitat conditions within the bankfull channel (Gurnell et al. 2005).

Conclusions

Our study illustrates the importance of hydrogeomorphic factors, landform properties, and vegetation in regulating the organization of the floristically diverse plant communities associated with glacial landscapes. In general, our results support our hypothesis that in low-order streams of the Great Lakes region major differences in the riparian plant communities across stream valleys are due to shifts in the balance between allogenic and autogenic controls. This balance between physical and ecological processes appears to be regulated by the geomorphic structure of the stream valley and the relative importance each plays in terms of driving vegetation dynamics varies laterally across the stream valley. However, the role flooding and landform properties have on regulating the spatial heterogeneity of nutrient availability and interactions with the hyphoreic zone, and how these factors regulate the distribution and abundance of riparian plants across stream valleys, remain slightly understood.

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