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Riparian Vegetation Patterns in Relation to Fluvial Landforms and Channel Evolution Along Selected Rivers of Tuscany (Central Italy)

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Riparian vegetation distribution patterns and diversity relative to various fluvial geomorphic channel patterns, landforms, and processes are described and interpreted for selected rivers of Tuscany, Central Italy; with emphasis on channel evolution following human impacts. Field surveys were conducted along thirteen gauged reaches for species presence, fluvial landforms, and the type and amount of channel/riparian zone change. Inundation frequency of different geomorphic surfaces was determined, and vegetation data were analyzed using BDA (binary discriminate analysis) and DCA (detrended correspondence analysis) and related to hydrogeomorphology. Multivariate analyses revealed distinct quantitative vegetation patterns relative to six major fluvial geomorphic surfaces. DCA of the vegetation data also showed distinct associations of plants to processes of adjustment that are related to stage of channel evolution, and clearly separated plants along disturbance/landform/soil moisture gradients. Species richness increases from the channel bed to the terrace and on heterogeneous riparian areas, whereas species richness decreases from moderate to intense incision and from low to intense narrowing. *Key Words:* channel incision, floodplains, fluvial landforms, riparian zone, vegetation.

Human activity has caused repeated deforestation of riparian areas particularly in Europe (Décamps et al. 1988; Petts, Möller, and Roux 1989). In southeastern France for example, between the sixteenth and nineteenth centuries most riparian areas were devoid of woody vegetation largely due to high sediment loads and active channel braiding (Piégay, Pautou, and Bravard 2003). Subsequently, river regulation beginning in the mid 1700s involved the removal of riparian trees throughout Europe (Bravard, Amoros, and Pautou 1986; Petts, Möller, and Roux 1989; Petts 1990); these areas were then actively used for agriculture and wood (fuel) production (Petts 1997). Surviving riparian areas have undergone considerable aforestation largely due to abandonment of human activities as populations moved from rural areas to urban areas beginning with the industrial revolution through the present (Piégay, Pautou, and Bravard 2003; Rinaldi 2003). Therefore, riparian forests of the area are now a mix of natural and seminatural habitats in an agricultural setting, dominated by arable fields, improved pasture, and tree plantations (Petts 1997; Gurnell and Petts 2003).

The community organization and dynamics of vegetation on the bottomlands of large rivers are strongly governed by fluvial geomorphic processes and landforms, which are largely created and maintained by fluctuations of water discharge. The fluvial geomorphic effects of

human disturbances vary according to (1) multiple possible combination, (2) mutual adjustments of the fluvial variables, and (3) the physiographic context (Steiger et al. 2005). The likelihood of a given species vigorously growing on a particular landform is a function of (1) the suitability of the site for germination and establishment (ecesis) and (2) the ambient environmental conditions at the site that permit persistence at least until reproductive age (Grubb 1977; Zimmermann and Thom 1982; Hupp and Osterkamp 1996; Hupp and Bornette 2003). The presence of a given species on a particular landform has the potential to provide information about the hydrogeomorphic conditions of the landform. This is because the distributional pattern may be limited by the tolerance of a species for specific disturbance regimes, or stress, and consequently by tolerance for biotic interactions that prevail at this disturbance or stress level.

Investigations at the interface between fluvial geomorphology and riparian plant ecology have increased during recent decades. Various aspects of the relations between vegetation and hydrogeomorphology have been summarized in Hupp and Osterkamp (1985); Viles (1988); Thornes (1990); Gregory, Davis, and Tooth (1993); Gurnell and Gregory (1995); Hupp, Osterkamp, and Howard (1995); Hupp and Osterkamp (1996); Gurnell, Hupp, and Gregory (2000); and most recently

by Steiger et al. (2005). In particular, studies in North America, Europe, and Japan have shown that there are characteristic plant species distributional patterns for specific fluvial landforms and processes (Osterkamp and Hupp 1984; Décamps et al. 1988; Tabacchi, Planty-Tabacchi, and Décamps 1990; Gregory 1992; Naiman, Décamps, and Pollock 1993; Pautou and Arens 1994; Marston et al. 1995; Hupp and Osterkamp 1996; Bravard et al. 1997; Hughes 1997; Tabacchi et al. 1998; Nagasaka and Nakamura 1999; Bendix and Hupp 2000; Nakamura and Shin 2001; Gurnell and Petts 2003). These relations are significant and may be used to infer hydrogeomorphic conditions where gauging-station or other hydrologic information is lacking. The vegetation-landform relation may be useful also in determining stage of riparian-zone recovery following disturbance, including gravel mining and channelization operations (Hupp 1992). Substantial progress has been made in the interpretation of channel evolution through the use of conceptual models (Schumm, Harvey, and Watson 1984; Simon and Hupp 1992; Surian and Rinaldi 2003). Research by Rinaldi (2003) supports this notion, but shows that models developed in fine-grained, low-gradient systems (e.g., Simon and Hupp 1992) are not completely transferable among physically distinct physiographic regions.

Many, if not most, streams have been mildly to severely affected by human disturbance, which complicates efforts to understand riparian ecosystems. Rinaldi (2003) and Surian and Rinaldi (2003) developed a conceptual model of channel evolution (in Italy) through phases of adjustment following various land usage. This model can be used as a backdrop for plant ecological investigations, which is a central focus of the present article. Vegetation may strongly alter rates of sediment erosion and deposition, and, in large part, may be integral in the overall stability of fluvial surfaces (Hupp 1999). This is particularly evident on fluvial landforms along nonequilibrium streams during and after (recovery) channel incision (Hupp 1999) and channel narrowing (Marston et al. 1995; Friedman, Osterkamp, and Lewis 1996; Garcia-Ruiz et al. 1997; Liébault and Piégay 2001, 2002; Friedman and Lee 2002; Rinaldi 2003). The study of vegetation patterns in specific relation to these dynamic, progressively adjusting fluvial landforms is generally lacking in the literature. The objective of this paper is to describe and interpret relations between riparian-species patterns and fluvial surfaces along a series of stream reaches, representative of different channel processes, morphologies, and types of channel adjustments. We use Tuscan rivers as our study area to facilitate congruence with the Rinaldi (2003) model, which was developed specifically for streams with

a long history of human activity. The present work is significant because the application of previously tested approaches in investigation of the highly dynamic fluvial setting of Tuscany with ancient, historic, and recent human disturbance is novel. Our results may be of use to floodplain managers and planners because investigation of existing conditions may provide reasonable prediction of future conditions such as continuing incision or narrowing or approaching relative stability.

Study Area

The study area coincides with the region of Tuscany (22,991 km²), central Italy, delimited by the Northern Apennines on the Northeast side and by the Tyrrhenian Sea on the West side (Figure 1). The main rivers of the region, in their upper and middle courses, usually have reaches cutting unconsolidated marine or fluvio-lacustrine sediments, alternating with narrow bedrock-controlled reaches, whereas their terminal reaches flow on relatively wide coastal plains.

The central and southern parts of Tuscany fall within the temperate climatic zone with a dry season, the Mediterranean climate category, whereas the northern portion has some continental climate characteristics. The main morphometric, climatic, and hydrologic data for the gauging stations of the rivers investigated are reported in Table 1.

Most Tuscan rivers have been subjected to numerous human disturbances and modifications since historical times (Billi and Rinaldi 1997; Rinaldi, Simon, and Billi 1997). During the twentieth century, human disturbances included interventions at basin level (construction of weirs, variation of land use in watersheds), intense instream gravel-mining activity after World War II, and in some cases the construction of dams. In response to these disturbances, drastic channel adjustments have affected the main alluvial rivers of the region (Rinaldi 2003) and, similarly, most of the main alluvial rivers of Italy (Surian and Rinaldi 2003). Bed incision represents the dominant vertical adjustment and is common along all the investigated fluvial systems. The Arno River system is the most affected by bed-level lowering as much as 9 m (Agnelli et al. 1998; Rinaldi and Simon 1998), whereas incision generally less than 2 m is observed along rivers of the southern part of the region (Rinaldi 2003). The second type of adjustment common along most of the rivers in the region is channel narrowing. Based on measurements of channel width taken from aerial photos of 1954 and 1993–1998, 38 percent of the analyzed reaches have been affected by a narrowing greater than 50 percent of the initial

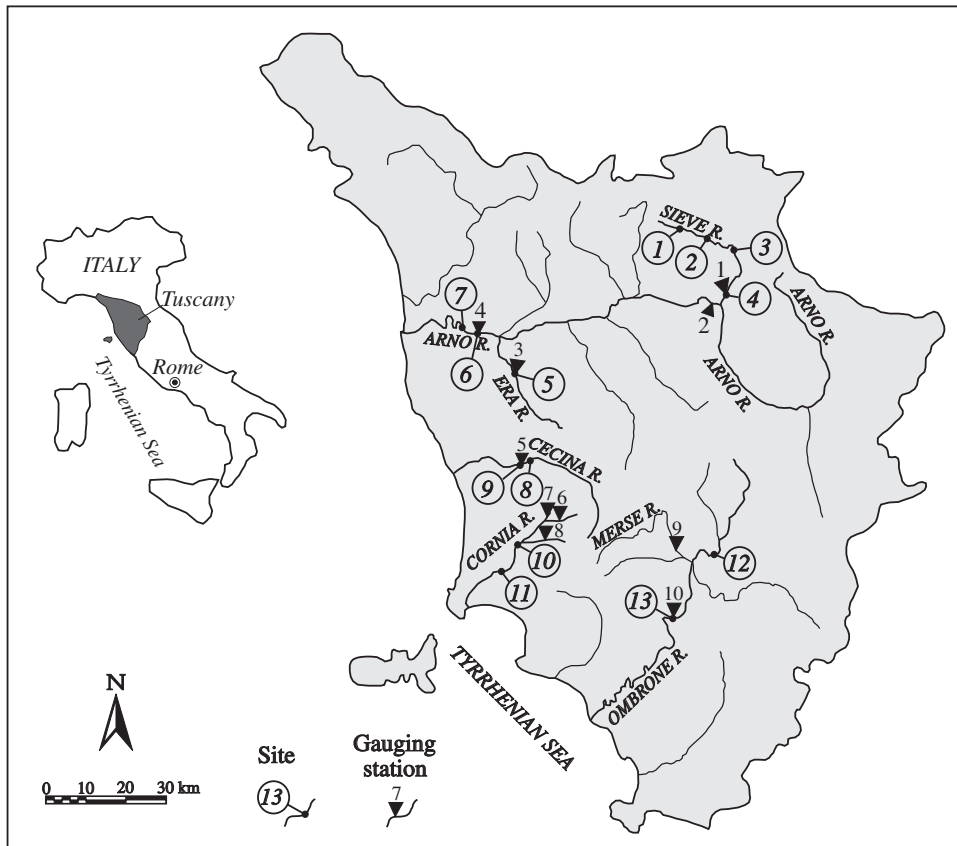


Figure 1. Study area and location of selected sites. 1: Site number; 2: gauging stations.

channel width (Rinaldi 2003). The greatest amounts of channel narrowing were observed along initially braided or sinuous channels with alternate-bar morphologies in the southern portion of the region.

Most of the study area lies in the Eurosiberiana phytogeographic region of Italy. Pedrotti and Gafta (1996) described the riparian and lowland forests of Italy and divided them into several vegetation associations. Along incised channels of Tuscany, riparian forests closest to the stream (channel edge) are dominated by the association *Salicetum albae* with *Salix alba* L. the dominant species; on higher parts of the floodplain, the *Fraxino-Quercetum roboris* association is common. This association may be mixed with the *Aro italici-Ulmetum minoris* association in more moist situations; dominant species include *Ulmus minor* Miller and *Populus alba* L. Less disturbed riparian areas may have more complex forests that include *Alnus glutinosa* L. and *Fraxinus excelsior* L. dominated associations in addition to those identified above. Throughout the region the relatively dry terraces commonly support the *Viburno-Quercetum ilicis* association; *Quercus robur* L. and *Viburnum* L. species are common along our study reaches (for more detail on these vegetation associations, see Pedrotti and Gafta 1996).

Methods

We now describe the methodologies used to collect hydrogeomorphic and plant ecological data in thirteen reaches along six rivers, and subsequent data analyses including multivariate procedures that relate species presence to fluvial landforms, site conditions (channel incision and/or narrowing), and channel type according to the Rinaldi (2003) model of channel evolution.

Hydrogeomorphic Analyses

The Arno, Sieve, Era, Cecina, Cornia, and Ombrone Rivers were visited and surveyed; reach locations are shown in Figure 1. A main criterion for site selection was the proximity of a gauging station to facilitate interpretation of the relations among fluvial landforms, species patterns, and discharges that may be responsible for various fluvial environmental features. Five of the ten gauging stations reported in Table 1 correspond to reaches sampled in this study (sites 4, 5, 6, 9, and 13; Figure 1). Near the other five gauging stations, vegetation was not sampled, although cross sections with the identification of the different surfaces were available. For each gauging station, the following standard procedure

Table 1. Morphometric, climatic, and hydrologic data for the main gauging stations of Tuscan rivers

River and gauging station	A (km ²)	L (km)	H (ma.s.l)	ΔH (m)	R (mm)	q_{mean} (m ³ /s)	Q_2 (m ³ /s)
Sieve R. (1) (1931–1993)	831	58	490	1565	1213	15.7	410.7
Arno R. (2) (1931–1993)	4083	113	450	1585	1038	56.7	1186.0
Era R. (3) (1933–1982)	355	37	225	650	1074	9.25	103.3
Arno R. (4) (1924–1982)	8186	198	330	1650	1031	97.4	1203.8
Cecina R. (5) (1935–1993)	634	53	309	1018	944	7.61	339.9
Cornia R. (6) (1954–1978)	97	19	338	785	953	0.69	51.4
Massera R. (7) (1976–1994)	58	13	222	485	861	0.50	97.2
Milia R. (8) (1970–1992)	77	24	390	815	934	0.40	45.8
Merse R. (9) (1933–1979)	483	54	365	911	1011	6.38	306.2
Ombrore R. (10) (1933–1994)	2657	80	346	1679	916	26.7	768.0

Notes: Locations of the gauging stations are shown in Figure 1.

A = drainage area; L = river length; H = average basin elevation; ΔH = difference between higher and lower basin elevation; R = average annual runoff; q_{mean} = average of mean-daily discharges; Q_2 = peak discharge with two-year return period.

was performed to define the frequency of inundation for the different geomorphic surfaces: (a) identification of the river stages inundating each surface delimited in cross section; (b) transformation of the river stage to discharge by using the rating curve for the station; (c) statistical frequency analysis of annual peak discharges and flow duration curve; and (d) determination of frequency of inundation for each surface. These estimates are referred to the lowest limit of each surface above the bed elevation. Other criteria for site selection were the representation of the main morphological channel types of the region and the inclusion of sites with past and present hydrogeomorphic processes associated with the dominant types of channel adjustments observed in the region. For the Arno and Cecina Rivers, two sites were selected a short distance apart because they can be characterized by different adjustments (i.e., vertically stable and incised for the Arno, laterally stable or migrating for the Cecina).

Field routine consisted of (1) site reconnaissance; (2) selection and establishment of a transect normal to the river channel from terrace top or hillslope to the corresponding form on the opposite bank, which contained relatively mature woody vegetation and appeared to be representative of the reach; (3) measurement of the lateral extent of the various fluvial landforms; and (4) identification and description of woody and herbaceous vegetation along the transect and on each landform surface (emphasis is on woody vegetation). Topographic cross sections were already available or surveyed later. Types and amounts of channel adjustments (Table 2) for each surveyed reach have been characterized in Rinaldi (2003), where bed-level adjustments were evaluated by available topographic profiles, specific-gauge analysis, and field evidence. Changes in channel width were measured by comparison of aerial photos (1954 and

1993–1998). Channel incision (vertical change) and narrowing were placed into low, moderate, and intense categories (Table 2).

Plant Ecological Analyses

Vegetation presence data (of woody and herbaceous plants) were collected along the transect at study sites. Plants were identified to the species taxonomic level, where possible; otherwise only the genus was recorded. Compilation of an exhaustive list, however, was not among our objectives; the goal was to identify those species that may be indicative of fluvial geomorphic site conditions and landforms. Field routine included the documentation of species growing on each of the geomorphic surfaces; a plant needed to be reproductively mature or vigorously growing for inclusion in the list. After identification, annual species were removed from further analysis because of their highly ruderal life history, as they are less likely to reflect or affect site conditions than perennial plants. Species richness or number of species present on a fluvial landform was determined and later reorganized by specific site condition and channel type (Table 2, Figures 2 and 3).

Binary discriminant analysis (BDA), a powerful tool for interpreting species-environmental interactions, was performed on the vegetation transect data (Strahler 1978; Hupp and Osterkamp 1985; Hupp 1992). BDA consists of two phases: first, the construction of contingency tables detailing the frequency (number of times a species occurred on a particular landform relative to the number of times the landform occurred in the field) distribution of each species according to each of the fluvial geomorphic landforms. Three sets of contingency tables were constructed where species presence/absence were rows and (1) landforms, or (2) categorized site

Table 2. Main morphological and sedimentological parameters and types of channel adjustments

River reach	A (km ²)	S	D ₅₀ (mm)	W (m)	D (m)	Channel adjustments		
						Vertical	Width	Type
1	289.5	0.0019	22.6	48.0	1.5	I-I	N-I	H
2	457.6	0.00064	40	28.2	1.0	I-M	N-I	H
3	519.6	0.00056	47.7	31.7	1.28	I-I	N-M	I
4	831.0	0.003	45.7	34.5	1.54	I-M	N-M	D
5	331.8	0.00112	9	16.4	1.46	I-M	N-L	D
6	8186.0	0.00027	0.4	101.8	4.54	I-L	N-L	A
7	8186.0	0.0004	0.4	114.7	4.1	I-I	N-L	I
8	630.0	0.0017	52	50.4	1.00	I-M	N-M	E
9	634.0	0.0035	58.1	56.3	1.04	I-M	N-L	F
10	195.0	0.00112	46.5	30.2	0.80	I-M	N-L	F
11	290.4	0.0041	38	48.5	1.09	I-M	N-M	E
12	760.0	0.0022	8.4	24.5	3.18	I-I	N-L	I
13	2657.0	0.0021	143.1	64.2	2.45	I-M	N-M	H

Notes: Locations of river reaches are shown in Figure 1.

A = drainage area; S = channel slope; D₅₀ = median diameter of bed sediments; W = bankfull width; D = bankfull mean depth.

Vertical adjustments: I-L = absent or limited incision, corresponding to a bed lowering less than 0.5 m; I-M = moderate incision, corresponding to a bed lowering less than 2 m; I-I = intense incision, corresponding to a bed lowering more than 2 m.

Width adjustments: N-L = limited narrowing and/or uncertain changes; N-M = moderate narrowing, up to 50 percent of the initial (1954) width; N-I = intense narrowing, above 50 percent of the initial width.

Type of adjustments: The cases from A to H refer to the classification scheme of Figure 2.

conditions, or (3) channel types were columns. Frequency data in the contingency tables were converted to standardized residuals, which places common and rare species on equal grounds (Haberman 1973). A summary table was constructed using these standardized residuals (*D* values or Haberman's *D*, a measure in terms of standard deviation away from zero where a species shows no positive or negative association) as entries, with species, identified in transects as rows and landforms as columns. Inspection of the table identified which species were most positively associated or most negatively associated with corresponding fluvial landforms. Binary data (species presence/absence) avoids possible complications (e.g., density, cover) that species interactions impose on abundance data (Strahler 1978; Zimmermann and Thom 1982) and are rapidly obtained.

The second phase of the BDA is the processing of the binary data through an ordination, detrended correspondence analysis (DCA), a commonly used ecological procedure (Gauch, Whitaker, and Wentworth 1977; Hill and Gauch 1980). DCA is a form of reciprocal averaging that has been detrended and uses a subroutine to preserve ecological distances (dissimilarity) through rescaling. The ordination produces a two-dimensional scatter diagram using axes extracted from explained variance (eigenvalue) in the original binary data matrix. Although more than two axes may be extracted, it is typically the first two, in descending eigenvalue, that explain much of the variance in the matrix. Both species and dependent variables

(landform, site condition, channel type) are scored against each axis and can be plotted to quantitatively describe similarity patterns among variables and species distributions. Three DCAs were performed on the fluvial geomorphic parameters: (1) landform (Figure 3), (2) site conditions, categorized amounts of channel incision/narrowing (Figure 2), and (3) channel type (Figure 2). These analyses reveal groups of closely associated plants or related processes and channel types; trends along the axes (gradients) may be inferred from the species (or species cluster) and parameter arrangement in the diagram.

Hydrogeomorphic Form and Process

In the following sections we describe the main types of channel adjustments and the principal fluvial landforms occurring in the study area with their attendant frequency of inundation. In doing so, we also summarize the results of our previous work (Rinaldi, Simon, and Billi 1997; Rinaldi 2003).

Channel Adjustments

A regional classification scheme (Rinaldi 2003) illustrating the main types of channel adjustments, or site conditions, is shown in Figure 2 and summarized in Table 2. Amounts of channel incision and narrowing are divided into categories (absent or limited, moderate, and intense; see Table 2 for their definitions). The scheme is

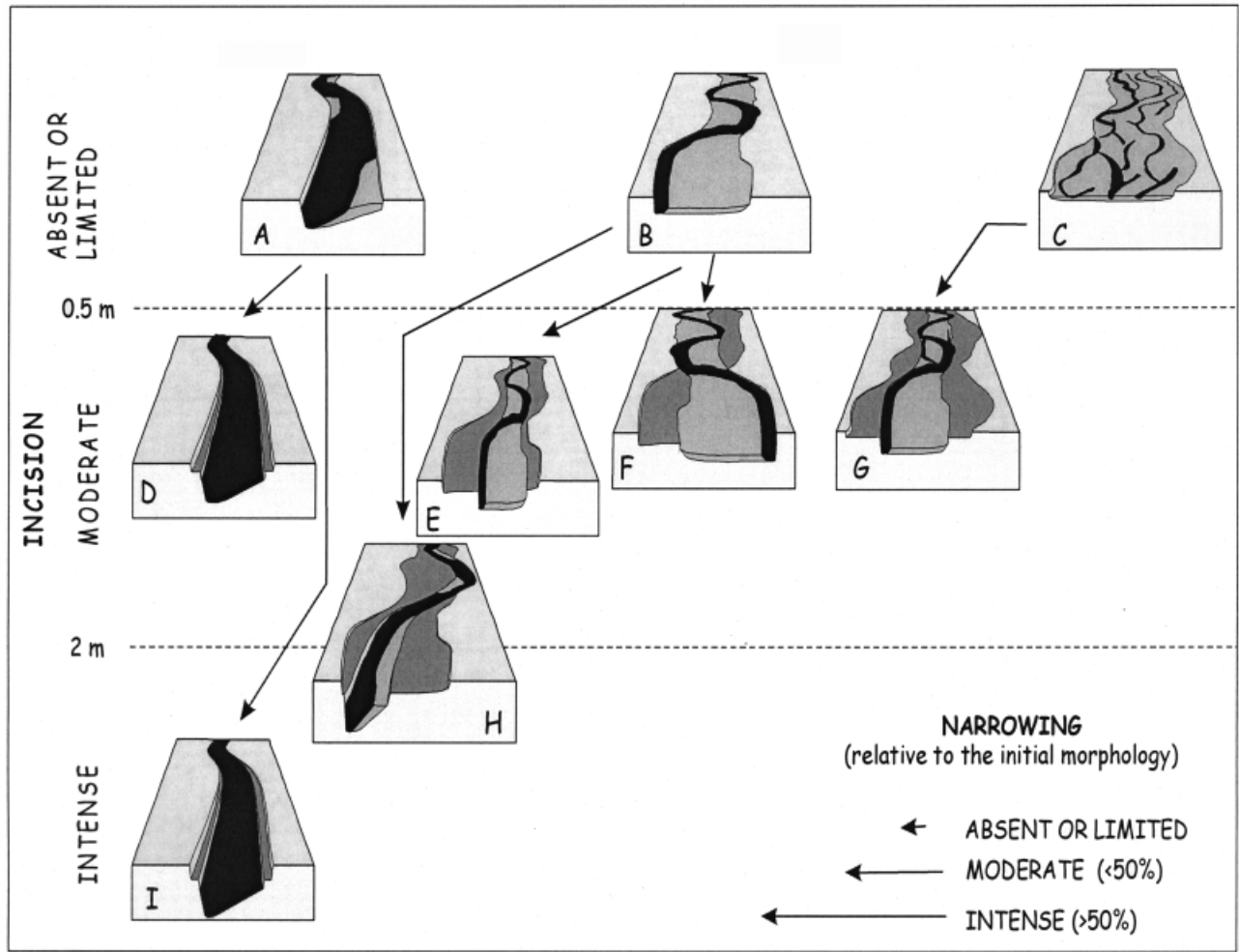


Figure 2. Regional classification scheme based on channel adjustments and morphologies (adapted from Rinaldi 2003). In black: low-water channel; in light grey: active bars; in dark grey: new or incipient floodplains derived from abandonment of previous active bars after incision. Absent/limited narrowing indicates a reduction of bankfull width less than the margin of measurement error; Moderate narrowing indicates a reduction in bankfull width lower than 50 percent of the initial width; Intense narrowing indicates a reduction in bankfull width higher than 50 percent of the initial width.

slightly extended from the original model to account for cases observed in this study (sites 4 and 5) with moderate incision and limited narrowing (type D). In particular, channel types A, B, and C (sinuous-meandering, sinuous with alternate bars, and braided, respectively) refer to channel morphologies in the 1950s, before the occurrence of the main phase of adjustments (from the 1950s to the 1980s) induced by intense sediment mining. Initially sinuous-meandering rivers (A) mostly adjusted through incision, which can be moderate (type D), or intense (type I), whereas channel narrowing was generally limited.

Conversely, initially sinuous channels with alternate bars (B) have adjusted through moderate incision combined with limited (type F), moderate (type E), or intense (type H) narrowing. For initially braided channels (C), a limited amount of incision was sufficient to cause

intense narrowing and a change in river morphology from multithread to a transitional (wandering) morphology. Wandering reaches, a common channel pattern identified in Europe, are intermediate between braided and true meandering patterns where the channel is too narrow to maintain a braided pattern, yet side and midchannel bars may occur with minor but separate flow from a dominant main channel (Kellerhals, Church, and Bray 1976). River reaches in this study are included in six (A, D, E, F, H, I) of the nine channel types depicted in Figure 2. Although examples of three categories (B, C, G) are not included, the study reaches cover a relatively wide range of types and amounts of adjustments (from absent to intense incision, and from absent to intense narrowing), and are sufficient for the scope of the present article.

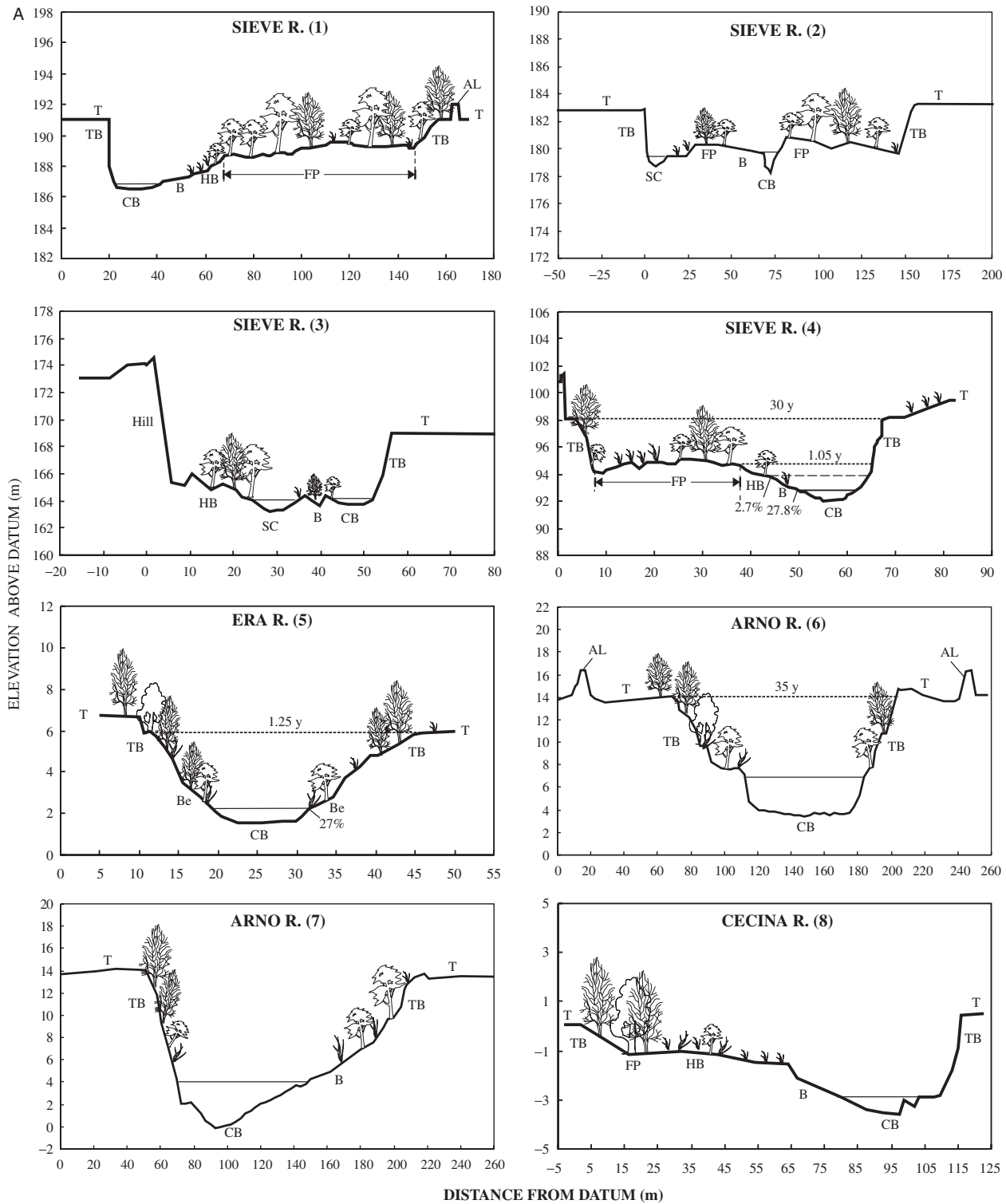


Figure 3. Riparian vegetation, geomorphic surfaces, and frequency of river stages for the selected sites. 1: Low-flow water stage (during the field survey); 2: river stage and correspondent duration (in %) equal or exceeded obtained by the flow duration curve of mean daily discharge; 3: river stage and corresponding return time (in years) determined by flow frequency analysis of annual peak discharges. Elevations for the Sieve River (sites 1 through 4) and the Arno River (sites 6 and 7) are in meters above sea level, which are used as data; for all other sites, elevations are in meters above an arbitrary datum.

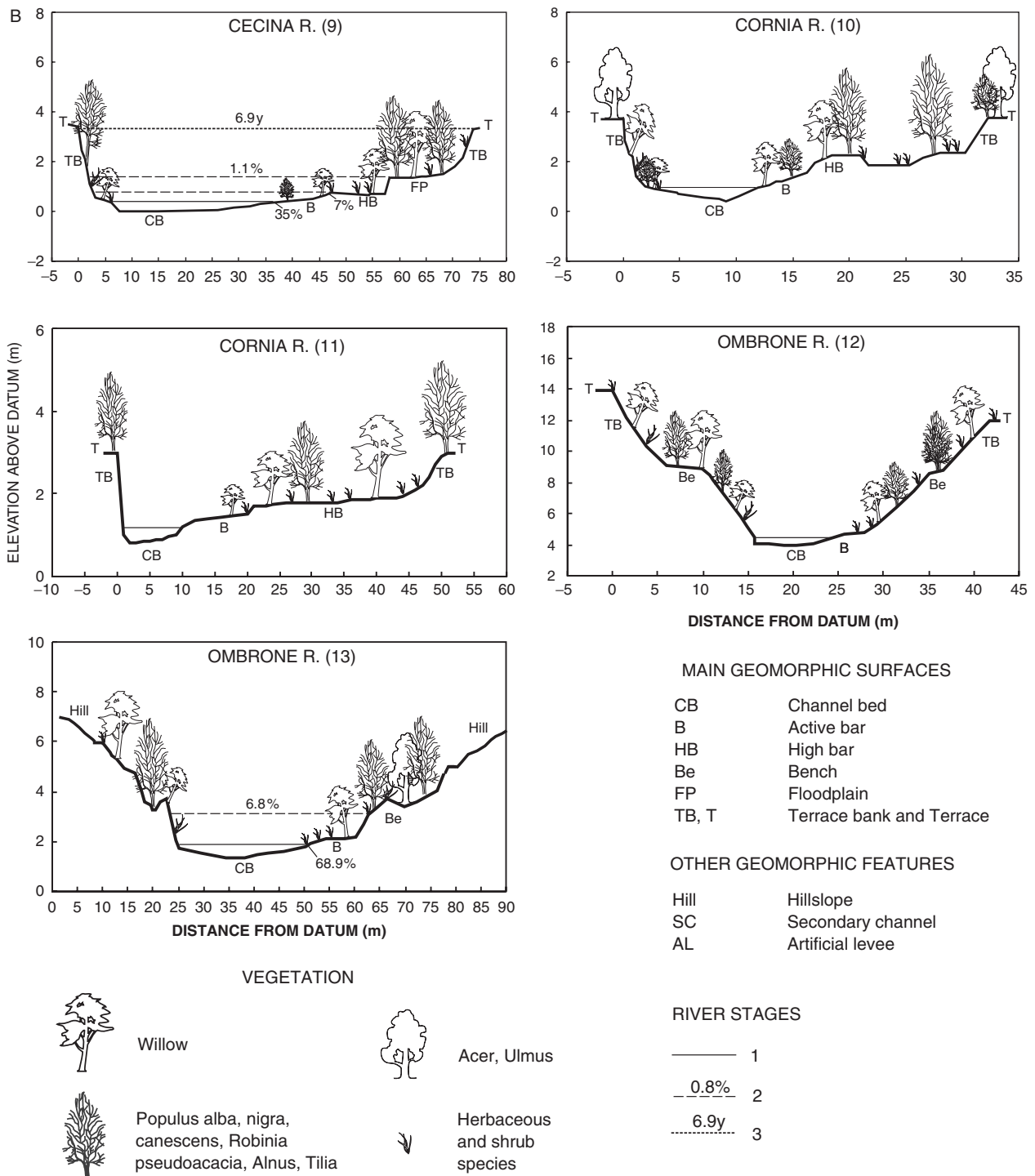


Figure 3. Continued.

Fluvial Landforms and Frequency of Inundation

Several fluvial geomorphic landforms that support vegetation were identified by field survey. Fluvial forms identified in the thirteen selected cross sections and dominant types of vegetation are shown in Figure 3. These landforms are divided into six main surfaces, from low in the cross section:

channel bed, active bar (several types), high bar, bench, floodplain, and terrace. Definitions and descriptions of these fluvial landforms follow those of Osterkamp and Hupp (1984) and Hupp and Osterkamp (1996).

River incision (most of the surveyed reaches) typically causes the previous floodplain to have a relatively high

Table 3. Frequency of inundation of different geomorphic surfaces for cross sections in correspondence of gauging stations

River and gauging station	Geomorphic surface inundations				
	Active bar (%)	High bar (%)	Bench (%)	Floodplain	Terrace
Sieve (1)	27.8	2.7		1.05	30
Arno (2)					6.7
Era (3)			27	1.25	
Arno (4)					35
Cecina (5)	35	7		1.1	6.9
Cornia (6)	45			1.6	125
Massera (7)	30.7			1.4	34
Milia (8)	42.1	2.3		1.27	64
Ombrore (9)	68.9		6.8		
Merse (10)	31.9			1.65	9

Notes: Locations are shown in Figure 1. For inundations given in percentage, the duration equaled or exceeded that obtained by the flow duration curve of mean daily discharge. For inundations not given in percentage, the number is the return period obtained by flow frequency analysis of annual peak discharges.

elevation, which functionally becomes a terrace even though there is usually little change in temporal discharge patterns. Surfaces that can be hydrologically described as new or incipient floodplains may now be recognizable at a lower elevation. Initially sinuous channels with alternate bars or braided channels, which were affected by incision and intense narrowing (Figure 2, types from E to H), typically have an incipient floodplain (with establishing vegetation) generated from previously active gravel bars. High bars show intermediate characteristics between active bars and floodplains. They are periodically reactivated by erosion during moderate flows, which are contained in the enlarged cross section of the incised channel. High bars may develop from further incision and consequent progressive colonization by vegetation of previously active bars. Initially meandering rivers that mostly adjusted through moderate to intense incision and a small amount of narrowing (Figure 2, types D and I) rarely develop a new floodplain, and in some cases a bench is present. The latter is indicated by a narrow horizontal to gently sloping surface that, in some situations, has been identified in a position proximal to the channel bed or to the terrace, and can be interpreted as a residual previous channel bar. In all cases, when this surface is present, a well-defined floodplain is not observed, a result also reported by Hupp and Osterkamp (1996).

Results from the frequency of inundation analyses for the different geomorphic surfaces are reported in Table 3 and fall within the limits described in Osterkamp and Hupp (1984). Variation of inundation frequency for the same surface along different rivers typically occurs. Active bars are frequently inundated, from the 27.8 to 68.9 percent flow duration. High bars, typically stabilized by strips of well-established woody vegetation, began as low bars during point-bar extension; incision and sediment

deposition have increased their relative elevation and now have flow durations that vary from 2.3 to 7 percent. These two types of bars (active and high) are distinguished in subsequent vegetation analyses. Floodplains, present in six sites, are subject to relatively high inundation frequency, from 1.1 percent flow duration to a return interval of 1.65 years; these surfaces are now forming after a previous stage of incision and in some cases are not yet well developed (incipient floodplains).

Inundation frequency for surfaces interpreted as terraces varies from 6.7 (Arno River) to 125 years (Cornia River). Some terraces along the Arno River have a return period of 35 years, even though the channel bottom has been artificially fixed since about 1859. Even where incision is absent, a relatively low terrace-inundation frequency occurs. This may be explained by an artificial interembankment zone historically subjected to frequent inundation that caused progressive aggradation through intensive overbank sedimentation (Rinaldi, Simon, and Billi 1997). For the two cases where a bench has been observed, flow duration is relatively high, varying from 6.8 to 27 percent.

Fluvial Landforms—Vegetation Relations

Thirty-two species of woody plants (trees, shrubs, vines) and forty-nine species of herbaceous plants growing on the alluvial surfaces were identified or noted along the study reaches. The species fall into three broad categories: (1) those species with particular affinities for specific fluvial landforms; (2) those species that normally occur in disturbed situations (successional, ruderal); and (3) those species with broad ecological amplitudes that are not indicative of any particular hydrogeomorphic condition (this includes species that are typically used for commercial and ornamental purposes, i.e., apple, plum,

corkscrew willow). Our results are organized by species presence on the six predominant fluvial geomorphic surfaces; see Table 4 for a more complete list of binomials. Nomenclature follows Mabberley (1997).

Channel Bed

The channel bed, usually composed of gravel or coarser material, typically does not support vascular plants; aufwuchs communities or algae often occur in pools or slack water areas and are indicative of relatively high nutrient loads in the water column. One site on the Era River supports a dense population of submerged aquatic vegetation (SAV).

Active Bar

Most transects were on the extension axis of point bars. The lowest part of the bar, nearest the channel, is often devoid of vegetation but may support sparse herbaceous species. Midbar locations, however, support a wide variety herbaceous plants (common are ruderal species in the genera, *Xanthium* L., *Brassica* L., *Polygonum* L., *Rumex* L., and various members of the Asteraceae). Midbar locations also support scattered *Salix* L. and *Populus nigra* L., which are indicative of bar conditions; bars along the Cecina and Cornia Rivers also support small *Tamarix gallica* L.

High Bar

High parts of the point bars and scroll ridges support dense communities of *Salix* and *Populus nigra*, typically one or the other being clearly dominant; herbaceous vegetation is unimportant. Scroll swales, on bars and near floodplain elevation, do not support substantial woody vegetation, probably as a result of high flow velocities, frequent flood scour, and relatively coarse texture; flood debris occasionally accumulates.

Bench

This surface usually occurs at elevations between high bars and active floodplains. Benches are fine-grained relic high-bar surfaces and may be found along meandering streams that have adjusted by incision and small amounts of narrowing. Although limited in extent, they are relatively stable with diverse plant communities unlike those of high bars. *Canna edulis* Ker Gawler and species of *Juncus* L. and *Mentha* L. are common in the understory with a mixed woody com-

munity of *Populus alba*, *Robinia pseudoacacia* L., *Salix*, and *Ulmus minor*.

Floodplain

Few historic floodplains remain today owing to widespread channel incision; most are composed of considerably finer material than bars and remain well below the dominant valley-bottom terrace. Along some reaches, where degradation occurred many years ago, an incipient floodplain may be developing. These surfaces support distinctly less *Salix* and *Populus nigra* than on lower surfaces (floodplain bank and bars), which are replaced by *Populus canescens* Aiton, *Ulmus*, *Alnus*, *Platanus* L., *Acer campestre* L., and other less common tree species. Relatively dense shrubs, mostly *Sambucus* L., *Viburnum* L., *Genista* L., *Alnus incana* (L.) Moench, and *Cornus* L., usually characterize the understory. By far the most common herbaceous plant is *Urtica* L., occurring in dense communities where sufficient light penetrates the canopy and the soil is nutrient rich (typically the case).

Terrace Bank and Terrace

These two features are combined because terrace tops are usually cleared for agriculture or other purposes where the vegetation is not similar to that of the terrace bank. The original floodplains of most rivers have been affected by degradation processes, which hydrologically render them terraces. The most characteristic feature of terraces is their tendency to support upland plants exclusively or in association with plants found on floodplains. Thus, particularly low terraces may support some floodplain species, such as *Platanus* and *Populus canescens*, but also have stands of *Acer*, *Robinia*, *Pinus* L., and *Quercus robur*. The latter two were not found on floodplain or lower surfaces. Conversely, no individuals of *Salix*, *Alnus*, or *Populus nigra* were found on surfaces higher than the floodplain.

Multivariate Analyses

Multivariate analyses revealed distinct quantitative vegetation patterns relative to the major fluvial geomorphic surfaces. Only woody plants and perennial herbaceous plants were retained for these analyses; annual plants are not substantially affected by the ambient hydrogeomorphic conditions on a given fluvial landform.

Table 4. Standardized residuals from binary discriminant analysis (BDA) of plant species distribution

Species	CB	B	HB	Be	FP	T
<i>Acer campestre</i> L.	−0.243	−0.93	−0.781	−0.912	0.195	2.077
<i>Acer negundo</i> L.	−0.153	−0.585	−0.491	−0.576	−0.79	1.898
<i>Achillea millefolium</i> L.	−0.108	−0.403	2.896	−0.406	−0.558	−0.749
<i>Alnus glutinosa</i> L.	−0.217	−0.83	−0.697	−0.817	2.434	0.457
<i>Alnus incana</i> (L.) Moench	−0.217	−0.83	−0.697	−0.817	0.063	1.644
<i>Bambusa vulgaris</i> Schrader	−0.153	−0.585	−0.491	−0.576	−0.79	1.898
<i>Brassica</i> L. sp.	−0.289	2.599	1.552	0.013	−1.493	−1.207
<i>Canna edulis</i> Ker Gawler	−0.347	−1.328	−1.115	0.544	1.037	2.294
<i>Centaurea</i> L. sp.	−0.108	−0.413	2.896	−0.406	−0.558	−0.749
<i>Chenopodium</i> L. sp.	−0.108	2.433	−0.347	−0.407	−0.558	−0.749
<i>Corylus avellana</i> L.	−0.153	−0.594	−0.491	−0.576	0.79	1.867
<i>Cyperaceae</i> Juss.	−0.108	2.433	−0.347	−0.406	−0.558	−0.479
<i>Daucus carota</i> L.	−0.187	−0.717	3.157	−0.706	−0.97	−0.092
<i>Dipsacus</i> L. sp.	−0.187	2.58	−0.603	−0.706	0.396	−1.303
<i>Echium vulgare</i> L.	−0.152	−0.585	4.104	−0.576	−0.79	−1.067
<i>Eleocharis</i> R. Br. sp.	−0.107	2.396	−0.347	−0.406	−0.558	−0.762
<i>Fraxinus excelsior</i> L.	−0.153	−0.585	−0.491	−0.576	0.88	0.418
<i>Galium</i> L. sp.	−0.187	−0.718	−0.603	−0.706	1.763	−0.092
<i>Genista tinctoria</i> L.	−0.217	−0.601	−0.933	−0.817	1.249	0.071
<i>Hedera helix</i> L.	−0.187	−0.718	−0.603	−0.706	−0.97	2.329
<i>Hypericum</i> L. sp.	−0.153	−0.585	4.104	−0.576	−0.79	−1.062
<i>Juncus</i> L. sp.	−0.217	2.032	−0.697	2.076	−1.122	−1.507
<i>Mentha</i> L. sp.	−0.243	1.635	−0.78	1.678	−0.195	−1.689
<i>Papaver</i> L. sp.	−0.187	−0.717	3.157	−0.706	0.396	−1.303
<i>Plantago</i> L. sp.	−0.153	1.431	1.806	−0.576	−0.79	−1.062
<i>Platanus orientalis</i> L.	−0.108	−0.413	−0.347	−0.406	0.558	1.339
<i>Polanisia dodecandra</i> Raf.	−0.153	1.431	1.806	−0.576	−0.79	−1.062
<i>Populus alba</i> L.	−0.266	0.152	0.48	1.367	−0.408	−0.992
<i>Populus canescens</i> Aiton	−0.429	−0.133	−0.519	−0.09	0.281	0.342
<i>Populus nigra</i> L.	−0.444	−0.235	0.242	0.549	1.344	−1.474
<i>Potamogeton crispus</i> L.	9.309	−0.413	−0.347	−0.406	−0.558	−0.749
<i>Potamogeton</i> L. sp.	9.309	−0.413	−0.347	−0.406	−0.558	−0.749
<i>Quercus robur</i> L.	−0.153	−0.585	−0.491	−0.576	−0.79	1.9
<i>Robinia pseudoacacia</i> L.	−0.414	−1.584	−1.33	0.807	1.09	0.56
<i>Rosa</i> L. sp.	−0.217	−0.83	−0.697	−0.817	0.063	1.644
<i>Rubus</i> L. sp.	−0.398	−1.523	−0.358	0.134	−0.05	1.386
<i>Rumex crispus</i> L.	−0.153	−0.585	1.806	0.576	0.88	−1.06
<i>Salix alba</i> L./ <i>eleagnos</i> Scop. ^a	−0.603	1.667	0.652	1.175	0.176	−2.52
<i>Salix matsudana</i> Matsuda	−0.107	−0.413	−0.347	−0.406	1.8	−0.75
<i>Sambucus nigra</i> L.	−0.153	−0.585	−0.491	−0.576	−0.79	1.898
<i>Senecio</i> Kodiz sp.	−0.108	−0.413	2.896	−0.406	−0.558	−0.749
<i>Smilax</i> sp. L.	−0.153	−0.585	−0.491	−0.576	−0.79	1.898
<i>Tamarix gallica</i> L.	−0.266	2.5	0.48	0.181	−0.408	−1.854
<i>Ulmus minor</i> Miller	−0.108	−0.413	−0.347	2.471	0.6	−0.749

Notes: CB = Channel bed; B = active bar; HB = high bar; Be = bench; FP = floodplain; T = terrace.

^aThe genus *Salix* includes the species shown above and *S. purpurea* L., which occurred occasionally but was not distinguished separately in the field. *Amorpha fruticosa* L. was common along several reaches, but due to an error in abbreviations in the field its inclusion in this analysis was not considered reliable.

Binary Discriminate Analysis, BDA Landforms

Binary discriminate analysis was performed for forty-five plants shown in Table 4. As previously described, positive standardized residuals (*D* values) indicate a “preference” for a plant to grow on a specific landform, whereas a negative residual indicates “avoidance” for the

landform. Only residuals with an absolute value of at least 1 (at least one standard deviation) are considered an important relation. For example, it is apparent that *Acer campestre* is rarely found on surfaces lower than the terrace, where it may be common; similarly, *Salix eleagnos* may be common on bars and benches but absent on terraces (Table 4). Residuals for twelve representative

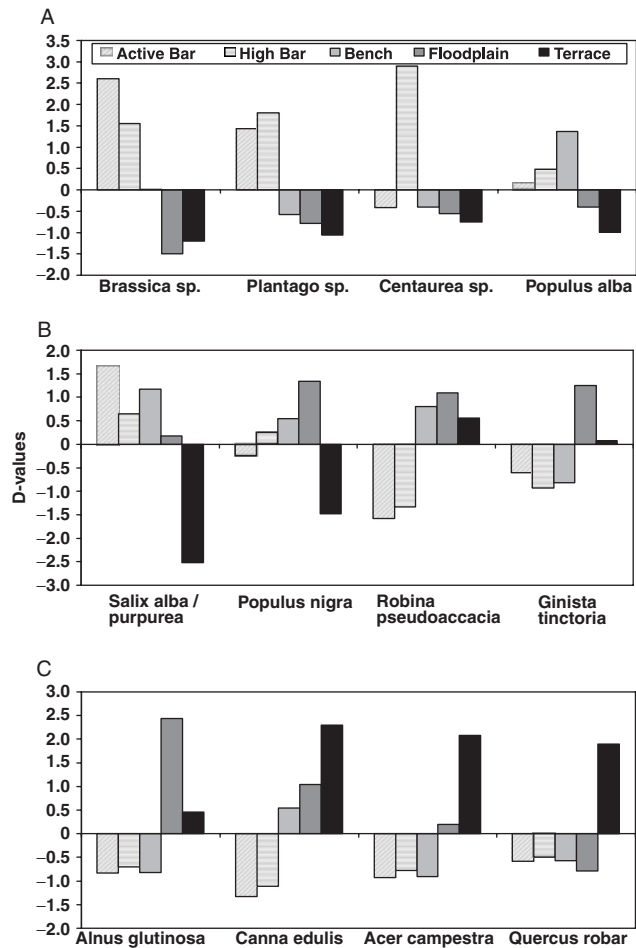


Figure 4. Diagram of D values for selected species distinguished by fluvial landform. Positive numbers indicate a “preference” for a given landform, whereas negative numbers indicate an “avoidance” (D values that do not have an absolute value of near 1 or greater should not be considered significant).

plants are depicted in Figures 4A–4C. From *Brassica* (Figure 4A) through *Quercus robur* (Figure 4C), plants, in sequence, indicative of active bars, high bars, benches, floodplains, and terraces are shown. Species shown in Figure 4A are highly ruderal herbs with the exception of *Populus alba*. This group, which includes woody species of *Salix* (Figure 4B), occurs in the highly dynamic environment of active and high bars. Note that the woody species *P. alba* and *Salix* also occur on benches (Figures 4A and 4B). A second group of species are pioneer plants (all woody) on stabilizing surfaces, namely the benches and floodplains, including *P. nigra*, *R. pseudoacacia*, and *Genista tinctoria* L. The tendencies for ruderal species to (1) persist in geomorphically dynamic environments (Hupp 1992; Marston et al. 1995; Bravard et al. 1997; Tabacchi et al. 1998; Bendix and Hupp 2000), such as active bars, and (2) potentially enhance stabilizing processes like

sedimentation (Hupp 1992; Tabacchi et al. 1998; Friedman and Lee 2002) are supported by these results.

BDA Site Conditions

Although geomorphic form cannot be separated from geomorphic process, BDA data can be analyzed in ways that facilitate process/form interpretation. Geomorphic changes affect the structure of fluvial surfaces that are riparian habitats through a range of occurrence frequencies and hydrogeomorphic conditions. The separation of the general data set by species presence in regard to sites (rather than landforms) and separating site conditions (incision/narrowing intensity) into categories (Low, Moderate, and Intense) yields a focus on fluvial process (Hupp 1992). Selected species’ D values derived from this data rearrangement are shown in Figure 5A. Considering only positive D values (Figure 5A), certain species clearly prefer/tolerate varying amounts of incision and narrowing. *Ulmus minor*, *Acer campestre*, and *Tamarix gallica* tend to grow at sites with moderate channel incision and narrowing by having positive D values for these conditions and negative D values for most of the other condition combinations (Figure 5A). These species occur where there has been moderate geomorphic activity (accretion during narrowing) and where they remain relatively moist (less incision leaving high water tables). Thus, these species may have relatively high water-availability requirements. Similarly, *Quercus robur*, *Alnus glutinosa*, and *Robinia pseudoacacia* are common at sites of intense channel incision and narrowing (Figure 5A). These species require relatively stable, high, and dry sites, which indicates that the active incision and narrowing (intense) processes nearest the channel have long since left floodplain and terrace areas where these species dominate. The impact of incision on the water table, though incompletely understood, may play an important role in the distribution of many riparian species (Friedman, Osterkamp, and Lewis 1996; Bravard et al. 1997; Hupp 1999; Bendix and Hupp 2000). The rather ubiquitous species of *Salix* and *Populus*, early-woody plant colonizers of disturbed fluvial systems, generally did not have high D values in this analytical arrangement. This observation suggests that these species respond less to past geomorphic activity than simply to the presence of suitable active landforms (bars and bench), where these species are dominant.

BDA Channel Type

The conceptual model (Figure 2) of channel types as they change through time in response to natural and

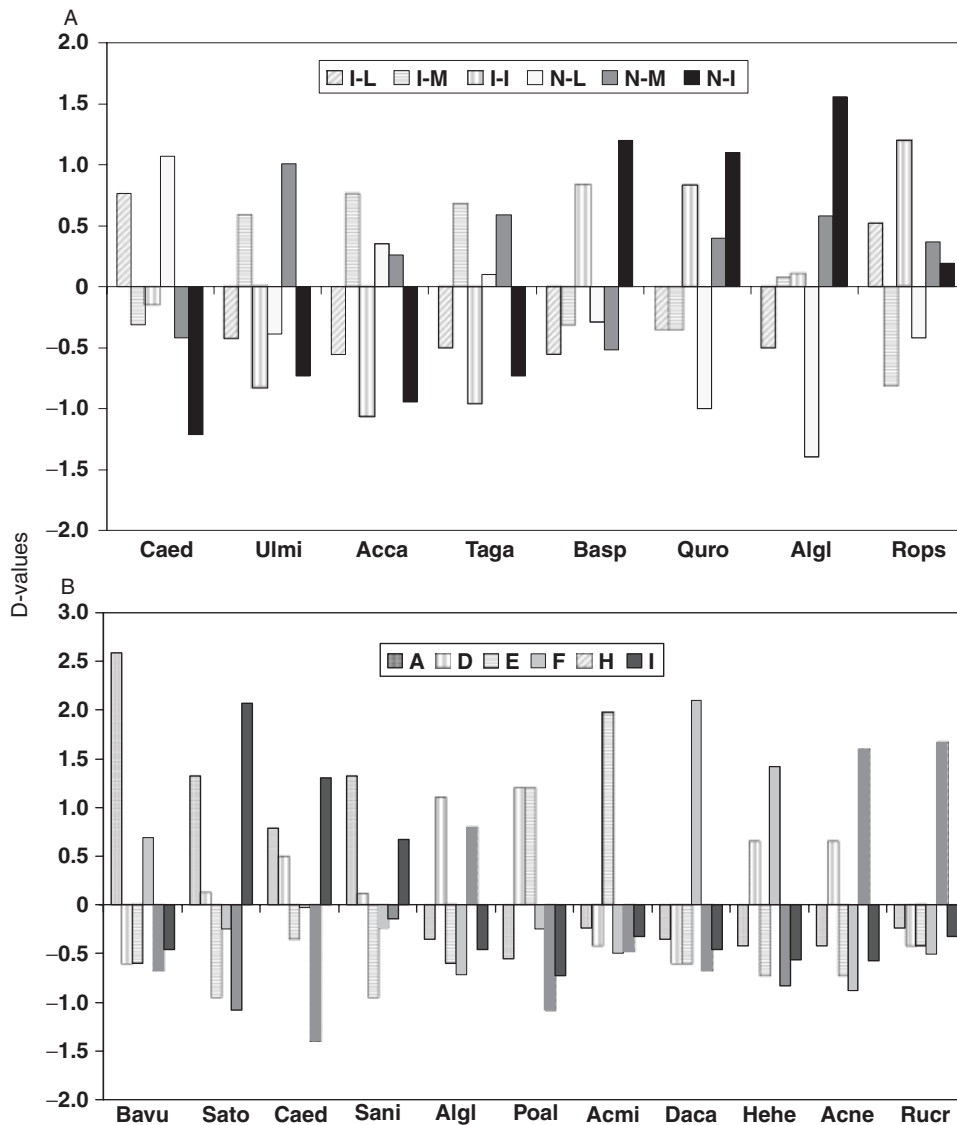


Figure 5. (A) D values for selected species analyzed against site conditions (I-L = low, or limited incision; I-M = moderate incision; I-I = intense incision; N-L = low, or limited narrowing; N-M = moderate narrowing; N-I = intense narrowing). Species are abbreviated as Caed-*Canna edulis* Ker Gawler, Ulmi-*Ulmus minor* Miller, Acca-*Acer campestre* L., Taga-*Tamarix gallica* L., Basp-*Brassica* L. species, Quro-*Quercus robur* L., Algl-*Alnus glutinosa* L., Rops-*Robinia pseudoacacia* L. (B) D values for selected species against channel type; see Figure 2 for description of channel type. Species are abbreviated as Bavu-*Bambusa vulgaris* Schrader, Sato-*Salix matsudana* Matsuda, Caed-*Canna edulis* Ker Gawler, Sani-*Sambucus nigra* L., Algl-*Alnus glutinosa* L., Poal-*Populus alba* L., Acmi-*Achillea millefolium* L., Daca-*Daucus carota* L., Hehe-*Hedera helix* L., Acne-*Acer negundo* L., Rucr-*Rumex crispus* L.

human impacts (Rinaldi 2003) can be investigated for patterns in vegetation distribution relative to channel type. This rearrangement of the data permits interpretation of the role geomorphic trends, relative to channel adjustment, play in the type of vegetal community present at a given channel type or stage (Hupp 1992). Conversely, analysis of vegetation and ambient geomorphic form may allow for an accurate estimation of channel history and trend prediction. Selected species' D values derived from this analysis are shown in Figure 5B; only channel types A, D, E, F, H, and I (Figure 2) were included. In this analysis, D values were generally of a greater magnitude (Figure 5B) than in the process analysis (Figure 5A), suggesting a strong influence of channel type on vegetation patterns. Moving from left to right in Figure 5B, species with a "preference" for channel types A through I are indicated. *Bambusa vul-*

garis Schrader ex Wendl, *Salix matsudana* Matsuda, *Canna edulis*, and *Sambucus nigra* have, with few exceptions, positive D values for channel types A, D, and I (as will be shown later, in Figure 7A). D and I types are derivatives of the basic sinuous-meandering, A, channel type (Figure 2) differentiated mainly by degree of incision and not by channel narrowing. Thus, lateral processes have been limited in these cases, which limits the amount of new horizontal fluvial surfaces upon which plants can establish. The species listed above are not truly riparian plants, instead they are indicative of human disturbance but in high and dry conditions (typically invasive plants growing near the edges of agricultural areas on terraces). The remaining species (truly riparian) characterize channel types E, F, and H, which are derived from meandering channels (B, Figure 2) and have a broad range of fluvial surfaces: accreting point bars,

benches, floodplains, and terraces, which suggests considerable narrowing and a complex fluvial landscape. These channel types provide for developed microtopographic heterogeneity and hydraulic connectivity (Tabacchi, Planty-Tabacchi, and Décamps 1990; Bornette, Amoros, and Lamouroux 1998; Hupp and Bornette 2003), which may facilitate substantial riparian biodiversity (Naiman, Décamps, and Pollock 1993; Pautou and Arens 1994). This complexity results from the simultaneous presence of active depositional surfaces near the channel, floodplain, and relatively stable terraces (Figure 2). Channel types E and F have had only moderate amounts of incision (the least in the present study), which may provide for a higher water table and more frequent flooding, and may explain the presence of typical riparian tree species: *Alnus glutinosa*, *Populus alba*, and *Acer negundo* L. (Figure 5B).

Ordination, Detrended Correspondence Analysis, DCA

DCA of the vegetation data shows distinct associations of plants to fluvial landforms. Two axes obtained from the ordination were strong enough to display the plant distributions in two dimensions (Figure 6A). Axes 1 and 2 explain about 73 percent of the variance (Table 5) within the original data matrix (species occurrence across landforms). The ordination clearly separates the

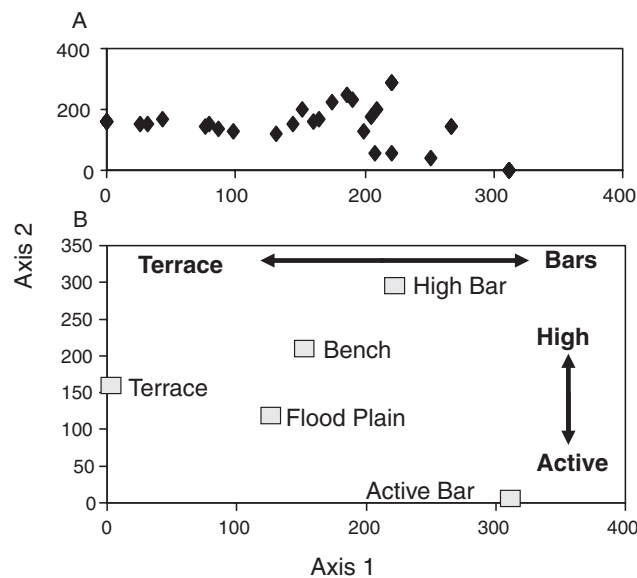


Figure 6. DCA (detrended correspondence analysis) results for species; against fluvial landforms. (A) is a plot of species; more than one species may be represented by a single point; (B) is a plot of landforms. The environmental (fluvial landform) gradients (arrows) are shown in (B), although the same gradients exist in (A).

plants along a gradient by plotting species scores against ordination axes. The greatest explained variance occurs along a landform gradient (Figure 6A), DCA Axis 1. The second axis separates plants of high bars from those of active or low bars. Each point represents a species (some points represent more than one species whose distributions were identical or nearly so). Similarly, the landforms can be plotted along the same axes (Figure 6B), allowing for the geomorphic interpretation of the species patterns. In both analyses, the closer two points are (species or landforms), the more similar they are, based on plant distributions. Axis 1 is clearly an elevation/landform gradient with terraces on one end and active bars at the other; other landforms also plotted in natural order along this descending elevation gradient (left to right, Figure 6B). Axis 2 appears to be a distinction between the two types of bars.

The DCA of site conditions (Figure 7A) suggests that process is important in species patterns, although the eigenvalues for Axes 1 and 2 only explain about 31

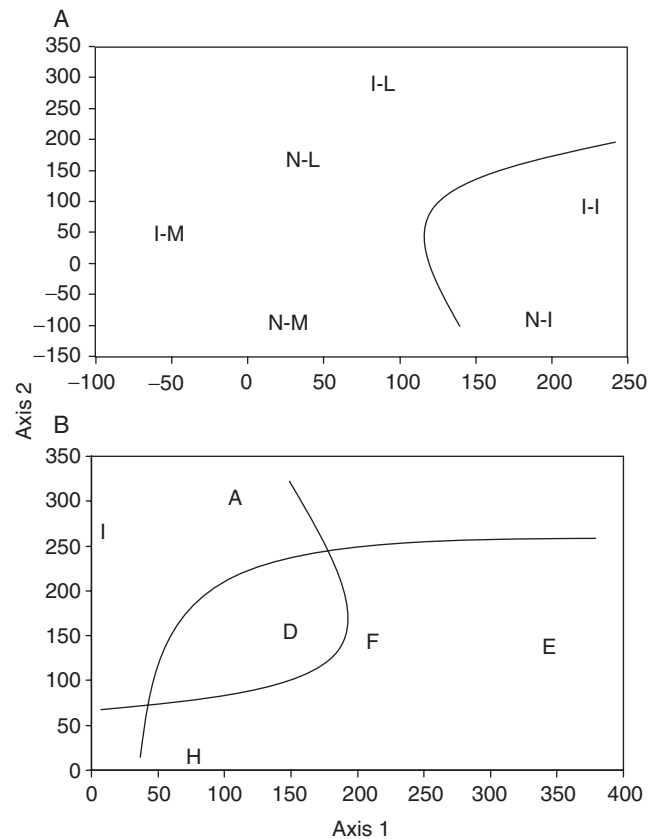


Figure 7. (A) DCA (detrended correspondence analysis) results for species against site conditions. In the lower left of the figure N-I and I-I form a distinct group as indicated by the line. (B) DCA results for species against channel type. Two relatively distinct groups are indicated by lines (1) I and A in the upper left of the figure and (2) H, F, and E in the lower or right of the figure.

percent of the original variance (Table 5). Because the initial bar colonizers, species of *Salix* and *Populus*, are not important in this data arrangement, stability is not a major gradient. It is clear that intense incision (I-I) and intense narrowing (N-I) are polar on the positive side of Axis 1 (right, Figure 7A) and all other conditions in low and moderate categories form a loose group at the other end (left, Figure 7A). Recognition of the important species in I-I and N-I reveal these to be stable sites with relatively mature/terrace species that established in the early 1950s after the abandonment of farming along many riparian areas. Axis 1 may also reflect a moisture gradient as the important species for moderate incision (I-M), moderate narrowing (N-M), and limited narrowing (N-L) are, likewise, not pioneer species but are typical of relatively moist floodplains. The left polar I-M is particularly important because the water table may remain relatively close to the soil surface. Thus, our results from all analyses suggest that moisture availability is an important factor in riparian species distribution in this region of Mediterranean climate. In humid areas like eastern North America, moisture availability is not a particularly important factor (Hupp and Osterkamp 1985) but in the semiarid Great Plains it becomes limiting (Friedman and Lee 2002). The absent or limited incision (I-L) is an outlier and is represented by only one case and not shown or used in the DCA; I-M is by far the more typical situation and most polar to I-I (Figure 7A). Axis 2 has an insignificant eigenvalue and an aberrant polar I-L, and is not interpreted further.

The DCA of channel types (Figure 7B) distinctly separates types A and I from the B-derived channel types E, F, and H. This analysis, with Axes 1 and 2 accounting for about 61 percent of the original variance (Table 5), is more explanatory than the DCA of site conditions and suggests that vegetation patterns may clearly reflect channel origin. These results suggest that channel origin (history) has a great influence on evolving fluvial landforms and their characteristic vegetation. The A-derived channel type D is intermediate between these two groups and obviously contains vegetal elements associated with both A- and B-derived channels (Figures 7A and 7B). It is not clear why this situation exists; however, the two type-D reaches are not on the

same stream (sites 4 and 5, Table 2) and are not similar in most main morphological and sedimentological parameters. Perhaps variables other than those examined here may best explain the intermediate position of type-D in this study, such as specific human impacts (Bravard, Amoros, and Pautou 1986; Liébault and Piégay 2002) or age of plant community. Few studies (Hupp 1992) have related riparian species patterns directly to stages of channel evolution.

Species Richness

Species richness, a measure of biodiversity in its simplest form, is the number of species per unit (landform, site conditions, and channel type, in this case). The riparian zone is widely known as perhaps the most

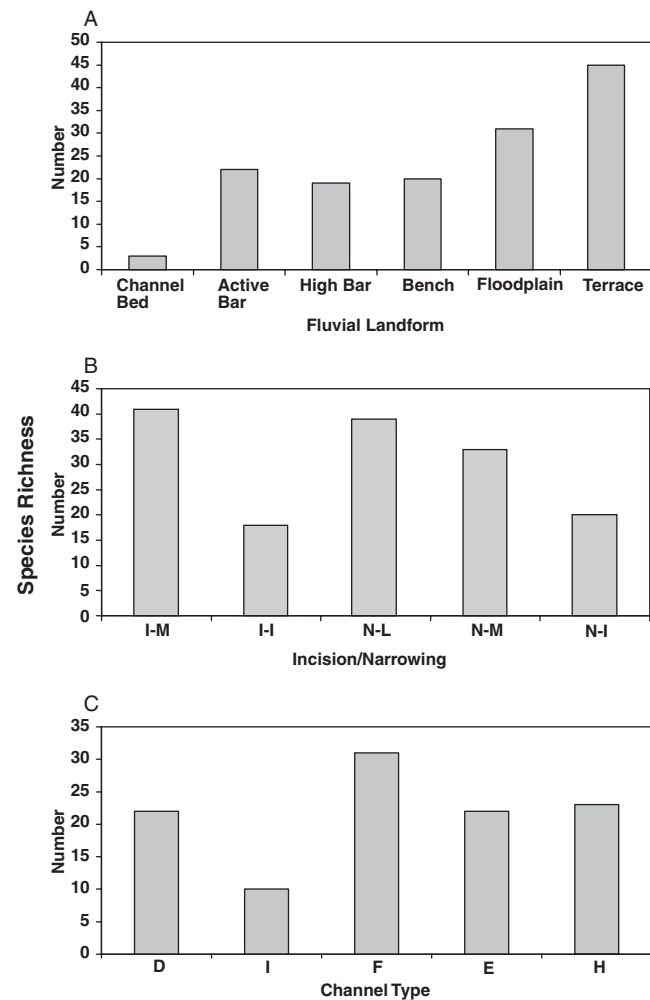


Figure 8. Species richness (total number of species) for (A) fluvial landform, (B) site conditions (degree of incision or narrowing explained in Figure 6), and (C) channel type. I-M = moderate incision; I-I = intense incision; N-L = limited narrowing; N-M = moderate narrowing; N-I = intense narrowing.

Table 5. Eigenvalues for three axes in DCAs

DCA	Axis 1	Axis 2	Axis 3
Landform species	0.58	0.15	0.07
Site conditions species	0.24	0.07	0.01
Channel type species	0.38	0.23	0.13

Note: DCA = detrended correspondence analysis.

diverse ecosystem worldwide (Nilsson 1992; Naiman, Décamps, and Pollock 1993). Inspection of the number of species for each fluvial landform (Figure 8A), each incision/narrowing category (Figure 8B), and each channel type (Figure 8C) suggests that clear trends in diversity occur along the studied reaches. Site condition Low Incision (I-L) and channel type A are not included in these analyses as only one site is represented in these cases (site 6, Table 2).

Species richness increases from the channel bed to the terrace (Figure 8A). This coincides with trends in several, related, fluvial geomorphic variables (Hupp and Osterkamp 1985) including increasing elevation from the channel, decreasing flow duration/flood return interval, decreasing sediment grain size, decreasing ambient flood intensity, and, generally, increasing landform age. The intermediate disturbance hypothesis (Connell 1978; Sousa 1984; Bornette, Amoros, and Lamouroux 1998) predicts that benches and floodplains would have the highest species richness. Where the substrate is under bedrock control, these surfaces have higher species richness than terraces (Hupp and Osterkamp 1985). Our high species richness for terraces (Figure 8A) may be related to the relative recentness of destabilizing conditions where the new surfaces have not reached the geomorphic stability necessary for the development of a diverse community (Friedman, Osterkamp, and Lewis 1996). It is also possible that the terrace species richness is an artifact of sampling, for which we had a wide range of elevations from nearly that of the mesic floodplain to xeric uplands. Further, historic and current human pressure on these terraces has lead to a wide range of habitats and patches from grazed to various states of reforestation (Décamps et al. 1988; Pautou and Arens 1994; Petts 1997); it is possible that human use of this landform may have more effect on vegetation structure than does channel adjustment. The channel bed had the lowest species richness because of its highly specialized habitat. Intermediate species richness is nearly identical for active and high bars and benches (Figure 8A). These are dynamic surfaces where, at least in central Italy (Gurnell and Petts 2003), plant persistence may be challenged by the frequent, periodic movement of the usually coarse sediment substrate. Friedman, Osterkamp, and Lewis (1996) showed that until these surfaces (during channel narrowing) can be successfully inhabited by woody vegetation, which decreases flow velocity and increases fine-sediment deposition, the development of a new floodplain and a stable, diverse, plant community is retarded.

Species richness in relation to site conditions (degree of incision and/or narrowing) showed distinct trends (Figure

8B). Intense incision (I-I) limits diversity relative to moderate incision (I-M) and can be easily interpreted. The high disturbance associated with intense incision and the general lack of diverse habitat (Figure 2) relative to moderate incision would keep species numbers low. This relation is reinforced when compared to species richness relative to channel type (Figure 8C), where type I has the lowest richness and the greatest amount of incision. The general lack of suitable fluvial substrate for riparian plants where incision has been intense severely compromises potential species richness. Conversely, the trend of decreasing species richness from low narrowing to intense narrowing (Figure 8B) is not as easily explained. Possibly intense narrowing provides a wide array of habitats as the channel regime shifts. However, if the dominant process is a rapid (a few decades) aggradation of coarse material, the subsequent fluvial surfaces may be rather homogenous features that support fewer species than do the less-disturbed streams. Recent rapid narrowing would limit the time necessary for the development of the patchy habitats normally associated with high riparian diversity (Naiman, Décamps, and Pollock 1993; Bornette, Amoros, and Lamouroux 1998; Ward et al. 2002). Similarly, the high species richness at low narrowing levels (Figure 8B) may reflect natural conditions, where there has been time for the development of many normal fluvial features that in a combination of form and process support high species diversity. Species richness relative to channel type (Figure 8C) again is easily interpreted. Inspection of Figure 2 clearly shows that channel types D and, especially, I have the least amount of area in riparian surface, which, as discussed above, inhibits diversity. Channel types F, E, and H have the greatest amount of fluvial surface and a variety of forms, which support highly diverse plant communities (Figure 8C).

Summary and Conclusions

Interdisciplinary investigations of riparian vegetation patterns in relation to fluvial geomorphic forms and processes may yield environmental interpretations that are difficult to discern using conventional approaches. Multivariate analyses revealed distinct quantitative vegetation patterns relative to the major fluvial geomorphic surfaces. One group of species, including *Brassica*, *Plantago*, *Centaurea* and *Salix alba*, is found typically in the highly dynamic environment of the active and high bars, whereas a second group of species, including *Populus nigra*, *Robinia pseudoacacia*, and *Gemista tinctoria*, is composed of pioneer plants on stabilizing surfaces (benches and floodplains). DCA of the vegetation data also showed distinct associations of plants to fluvial landforms and processes of adjustment (incision and narrowing). The ordination

separates the plants along a landform/moisture gradient, whereas the second axis separates plants on high bars from active or low bars. Certain species are found to prefer/tolerate varying amounts of incision and narrowing: in particular, *Ulmus minor*, *Acer campestre*, and *Tamarix gallica* tend to grow at sites with only moderate channel incision and narrowing, whereas *Quercus robur*, *Alnus*, and *Robinia pseudoacacia* are common at sites of intense channel incision and narrowing. Channel evolution, from original pattern through various channel types, may also exert considerable control on the development of fluvial landforms and the vegetation they support. Inspection of species richness for each fluvial landform, each incision/narrowing category, and each channel type, suggests the following main diversity trends: (1) species richness increases from the channel bed to the terrace; (2) species richness decreases from moderate to intense incision, and from low to intense narrowing; and (3) species richness is greatest on channel types with the greatest geomorphic heterogeneity, types E, F, and H.

Riparian vegetation patterns and fluvial geomorphic forms and processes are closely integrated environmental phenomena along most perennial streams. In temperate fluvial systems, water, either through streamflow conditions or groundwater availability, is the most proximal control on the distributional patterns of perennial riparian plants. Riparian vegetation may also strongly affect the rates of sediment erosion and of sediment deposition, and may be integral in the overall stability of fluvial surfaces. This is particularly evident in streams that have been disturbed by human alteration, which can lead to channel incision and/or channel narrowing. Our results show that riparian vegetation patterns even along highly human altered streams are indicative of present and ongoing fluvial forms and processes, while simultaneously reflecting stages of channel evolution following incision and narrowing.

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