

Hydrological and geomorphological impacts on riparian plant communities

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Abstract:

Riparian vegetation is affected by both flood processes and the characteristics of landforms that are shaped by floods. In many instances, species occurrence can be linked directly to specific fluvial landforms. These spatial relationships are largely due to the role of floods in the differential destruction of vegetation, in the determination of substrate characteristics, and in the transport of propagules. Major floods may, depending on the climatic context, allow for the establishment of stands of vegetation, or restart processes of plant community change. Disturbance by floods can also affect biodiversity: species richness in some watersheds is greatest where steep valley floor gradients allow for high-energy floods.

The recognition and analysis of hydrogeomorphological influences on riparian vegetation are complicated by multiple scales of environmental interactions, by the covariance of some environmental variables, and by feedbacks between vegetation and flood regimes. Copyright © 2000 John Wiley & Sons, Ltd.

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INTRODUCTION

The effects of floods on riparian vegetation are hydrological and geomorphological. Hydrological impacts include mechanical damage, saturation and propagule transport. Geomorphological impacts involve the destruction and creation of substrate. A substantial body of research relates the sometimes complex interaction of these varied flood impacts to the actual patterns of vegetation on the valley floor.

In this paper, we review some of the salient ideas that have been developed relating floods, fluvial landforms and riparian vegetation. Our concentration is on relatively high-energy streams, with no tidal influence. Low-gradient, meandering streams in broad valley bottoms may operate under different hydrogeomorphological conditions, and are not emphasized here; they are covered in varying degree in by Malanson (1993), Parker and Bendix (1996), Hughes (1997) and Hupp (2000, this volume). The proper usage of the very term 'riparian vegetation' has been subject to some debate (Hupp, 1988; Malanson, 1993). Here we follow what has become common practice in ecological literature and apply the term to vegetation growing in valley-bottom geomorphological settings, which are at least occasionally affected by floods. This discussion incorporates elements of an earlier review by Hupp (1988).

The organization and dynamics of vegetation in valley bottoms are strongly related to fluvial geomorphological processes and forms, which are largely created and maintained by fluctuations of water discharge. The likelihood of a given species vigorously growing on a particular landform is a function of (i) the suitability of the site for germination and establishment, and (ii) the ambient environmental conditions at

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the site that permit persistence at least until reproductive age (Zimmerman and Thom, 1982; Hupp and Osterkamp, 1996). Thus, the presence of a given species on a particular landform may permit considerable inference regarding the hydrogeomorphological conditions characteristic of the landform. The distributional pattern may be limited by the tolerance of a species for specific disturbance or stress regimes, as well as by tolerance for other more subtle interactions, including interspecies competition. In fluvial systems, the distribution of vegetation across landforms may be driven largely by the tolerance of species to hydrogeomorphological processes at the severe end of a stress–equilibrium gradient and by competition with other riparian species at the other end.

The remainder of this paper is organized so that we discuss first the physical aspects dominating the severe end of the gradient, discussed above, covering the fluvial system, hydrogeomorphological influences, landforms and flooding, flood impacts and scale. Next we discuss the more biological aspects of riparian plant ecology, including colonization, vegetation dynamics and biodiversity. We conclude with a section on complex causality and feedbacks between vegetation and the development of fluvial geomorphological forms.

THE FLUVIAL SETTING

Before considering the ways in which vegetation may be distributed in valley bottoms, it is worth reviewing the range of geomorphological settings upon which vegetation patterns may be overlaid. Different landforms may be likely to support different vegetation by virtue of either the processes that are active on them (principally flooding) or their physical characteristics (substrate type, proximity to groundwater, etc.).

In humid temperate settings, the suite of fluvial landforms tends to be predictable. The classic sequence includes, in order of descending elevation, terraces, the floodplain, and the features of the channel itself (Figure 1). In terms of areal extent, the floodplain is often the largest part of the riparian zone (i.e. the area occupied by riparian vegetation). The floodplain may be defined in hydrological terms as the surface that is flooded once every 1–3 years (1.5 recurrence interval on the annual series), or in geomorphological terms as the alluvial surface constructed by the river under current environmental conditions (Wolman and Leopold, 1957; Dunne and Leopold, 1978). These definitions go hand in hand, as it is assumed that the bankfull floods that are just large enough to reach the floodplain are integral to the floodplain's creation. Terraces may occur for a number of reasons (Howard *et al.*, 1968), but are usually remnants of older floodplains that have been left behind when the stream lowered the valley floor by degradation. By virtue of their higher elevation, terraces are flooded less often than the floodplain. Indeed, some upper terraces may be so high that they do not flood at all, and thus are not part of the riparian zone. Detailed terminology for features below the floodplain has received less attention, but these features are demonstrably significant as sites that support particular vegetation types (Osterkamp and Hupp, 1984; Hupp and Osterkamp, 1985).

The identification of landforms in arid valley bottoms is more problematic. Fluvial landforms in arid region watersheds tend to be transitory, subject to frequent and rapid changes (Graf, 1988a,b), resulting from the combination of flashy hydraulic regimes and abundant non-cohesive alluvial sediments that often characterize such watersheds. In these settings, the distinction between channel and floodplain features can be obscured where floods that exceed the dimensions of the main channel rise to occupy higher braided channels rather than simply spilling on to a flat floodplain; Graf (1988a) has termed this pattern a compound channel. In arid regions the assumption that the high-frequency bankfull flood plays a dominant role in shaping the floodplain becomes invalid (Baker, 1977), and the hydrological and geomorphological definitions of the floodplain can no longer be assumed to be equivalent (Graf, 1988b; Figure 2).

MECHANISMS OF HYDROGEOMORPHOLOGICAL INFLUENCE ON VEGETATION

A number of mechanisms have been recognized whereby floods and fluvial landforms affect vegetation. Perhaps the most obvious is the destruction of vegetation by floods. Plants may be broken (often resulting in

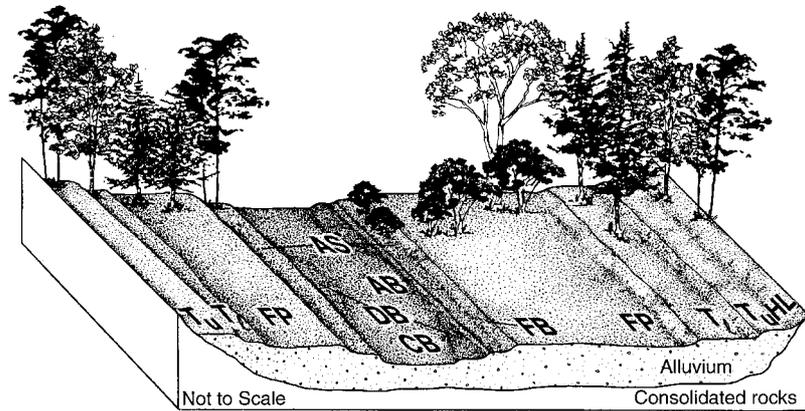


Figure 1. Diagram of fluvial landforms, including channel bed (CB), depositional bar (DB), active-channel bank (AB), active-channel shelf (AS), floodplain bank (FB), floodplain (FP), low terrace (TL), upper terrace (Tu) and hillslope (HL). Modified from Osterkamp and Hupp (1984), Hupp and Osterkamp (1985) and Hupp (1988)

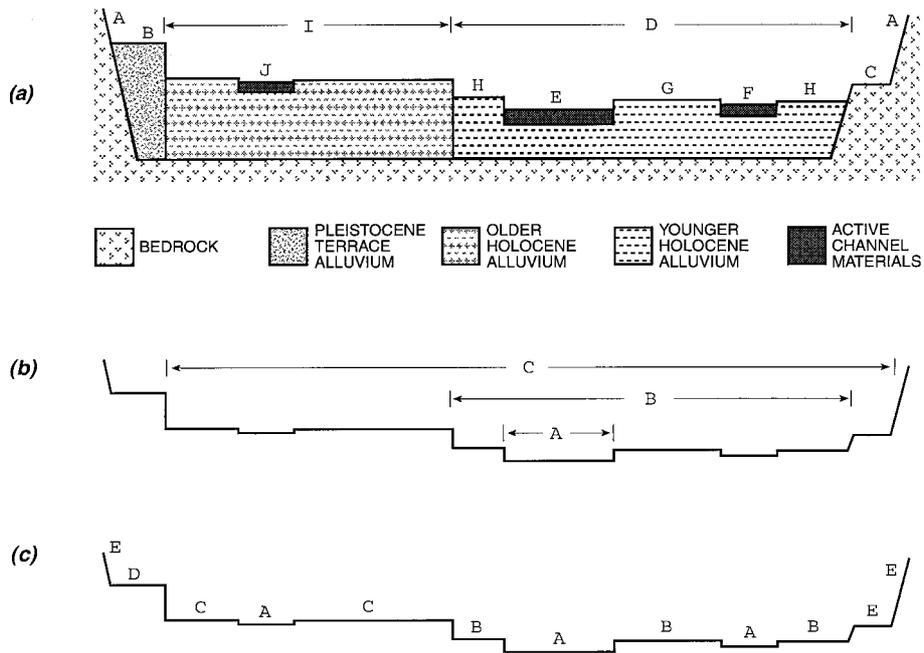


Figure 2. Varying interpretations of a schematic diagram of a cross-section of the Agua Fria River, Arizona. The diagram is not to scale, but has a vertical exaggeration of about 10:1. (a) Geomorphological interpretation relying on analysis of surface expression and subsurface materials: (A) bedrock, (B) Pleistocene terrace, (C) erosional terrace or rock bench, (D) braided channel, (E) main or low flow channel, (F) secondary channel, (G) mid-channel bar, (H) channel-side bar, (I) recent terrace, (J) overflow channel. (b) Hydrological interpretation of the cross-section shown in (a): (A) channel, (B) 50-year floodplain with channel, (C) 100-year floodplain with channel. (c) Pedologic interpretation of the cross-section shown in (a): (A) excessively well-drained floodplain soils, (B) well-drained low terrace soils, (C) well-drained middle terrace soils, (D) well-drained upper terrace soils, (E) soils developed on bedrock. Modified from Graf (1988b). *Flood Geomorphology*, Graf WL, Eds, Baker VR, Kochel RC, Pathon PC, Copyright © 1998 John Wiley & Sons, Inc. Reprinted by permission of John Wiley & Sons, Inc.

mortality) by the force of floodwaters (Bendix, 1999), or by the impact of floating woody debris or ice (Sigafoos, 1964). They may be killed by prolonged saturation of the root zone (Kozlowski, 1984). They also may be destroyed by the erosion of the substrate in which they are rooted. In any of these cases, plant species vary in their susceptibility to flood disturbance, and therefore the varying severity of flooding within the riparian zone serves to influence the spatial pattern of species composition (Hupp and Osterkamp, 1985; Bendix, 1999). Of note, mortality is not necessary for a compositional impact — species that survive but are disproportionately stressed by floods will be placed at a competitive disadvantage.

Vegetation also reflects the impact of floods in creating the conditions for seedling establishment. This may occur where floods have deposited fresh alluvial surfaces or have removed the vegetation from pre-existing surfaces (McBride and Strahan, 1984a,b; Auble and Scott, 1998). More subtly, it also may occur where floods remove organic litter, allowing colonization of species that only germinate on bare mineral soil (Yanosky, 1982). Conversely, it has been hypothesized that where floods deposit woody debris the contribution of organic matter to the soil also may affect the vegetation (Malanson and Butler, 1990). Floods also can affect colonization patterns by acting as a dispersal agent delivering propagules of riparian species to new colonization sites (Douglas, 1989; Hupp, 1992).

LANDFORMS, FLOODING AND SPECIES COMPOSITION

Whether permanent or temporary, obvious or subtle, each landform on the valley floor is distinctive in the frequency and severity of floods it experiences, as determined by its position in the valley and the local hydrological conditions. As such, they offer a setting in which to assess the effects of periodic flood disturbance on vegetation. There has been much discussion among ecologists and biogeographers regarding the role of disturbance in the development and maintenance of vegetation patterns (e.g. White, 1979; Clark, 1991; Baker, 1992). Periodic flooding may allow certain riparian communities to persist through time with consistent composition because repeated disturbance holds successional change in abeyance. Such systems have been alternately termed 'non-equilibrium' (Pickett, 1980; Pickett *et al.*, 1992) because of the suspension of successional processes, and 'quasi-equilibrium' (Bendix, 1998) because they are stable as long as the disturbance regime is maintained.

A variety of studies have suggested that characteristic variations in riparian forest composition are indeed maintained by periodic flooding (Hosner and Minckler, 1963; Osterkamp *et al.*, 1995), rather than reflecting seral recovery since the last destructive flood (Yanosky, 1982; Hupp, 1983). A detailed flood history along Passage Creek by Hupp (1982), using tree-ring analyses, found little role for succession in determining vegetation patterns on the fluvial landforms. Apparently the plant distributions are at least in part controlled by inundation frequency and susceptibility of plants to damage by floods. Vegetation growing on the flood-prone channel shelf (Figure 1) tends to have a shrub growth form with small, highly resilient stems and the ability to sprout rapidly from flood-damaged stumps (Hupp, 1983). Floodplain species are less tolerant of destructive flooding than channel-shelf species but are tolerant of periods of inundation. Conversely, terrace species may be intolerant of repeated flood damage or inundation (Hupp, 1983; Cowell, 1993).

In northern California, Harris (1987) found that low, frequently flooded landforms were dominated by Fremont cottonwood (*Populus fremontii*) and sandbar willow (*Salix exigua*). Bendix (1999) noted that *P. fremontii* attains a substantial size, which may make it relatively invulnerable, whereas *S. exigua* may survive flooding through its flexibility — and is also a rapid colonizer of flood-cleared alluvium. In Harris's study, higher, less flood-prone geomorphological surfaces were dominated by less flood-adapted species such as valley oak (*Quercus lobata*) and California black walnut (*Juglans hindsii*).

Although the recognition of riparian species *per se* is often straightforward, there have been relatively few studies documenting the relationship of species in the floodplain and below to specific hydrogeomorphological conditions. In northern Virginia, Osterkamp and Hupp (1984) and Hupp and Osterkamp (1985) have documented regionally consistent and discrete relationships between riparian vegetation patterns and the fluvial landforms depicted in Figure 1. Depositional bars, inundated about 40% of the time (Hedman *et al.*,

1972), rarely have persistent woody vegetation, but may be densely covered in water willow (*Justicia mariana*). The active-channel shelf, inundated between 10 and 25% of the time (Osterkamp and Hupp, 1984), supports a characteristic low shrub thicket (riparian shrub forest; Hupp, 1984). Typical species of the active-channel shelf include alder (*Alnus serrulata*), winterberry (*Ilex verticillata*), red willow (*Cornus amomum*), black willow (*Salix nigra*), and ninebark (*Physocarpus opulifolius*). The floodplain, with a 1- to 3-year flood recurrence interval, supports a generally diverse flora, which usually includes one or more of the following indicator species: black walnut (*Juglans nigra*), American elm (*Ulmus americana*), bitternut (*Carya cordiformis*), silver maple (*Acer saccharinum*) and hackberry (*Celtis occidentalis*). Terraces flooded less frequently than every 3 years have at least some upland oaks and hickories. The relationships between landform, flood characteristics, and species are summarized in Table I. Although species such as sycamore (*Platanus occidentalis*), box elder (*Acer negundo*), ironwood (*Carpinus caroliniana*) and green ash (*Fraxinus pennsylvanica*) are good indicators of floodplains and channel shelves, they do not completely discriminate between the two landforms.

The examples cited above emphasize not just the landforms on which species grow, but the frequency and duration with which they are flooded. It is not the landform, *per se*, which is critical, but rather the flood regime that characterizes it. In arid regions, the landform position becomes doubly critical, because it affects access to moisture as well as flood regime (Zimmerman, 1969; Birkeland, 1996). In southern California, Bendix (1999) explicitly tested the impact of floods on riparian vegetation by calculating the distribution of values of unit stream power (energy exerted per unit area — Bagnold 1966, 1977; Baker and Costa, 1987) across the valley floor, and comparing it to species composition; he further compared this relationship to the influence of height above the water table. He found that common species were sorted along an axis of stream power, but that those species that occurred on surfaces with low stream power were differentiated along a gradient of height above water table (Figure 3). The species found in locales with high stream power are either quite flexible, such as white alder (*Alnus rhombifolia*) or grow so large that mature individuals are resistant to flood damage, such as Fremont cottonwood (*Populus fremontii*). It is important to recall that some species may be common where floods are severe not because they can survive floods, but because they are rapid colonizers of flood-cleared alluvial surfaces. In southern California, seep-willow (*Baccharis salicifolia*) is a common species filling this role.

FLOOD IMPACTS IN THE CONTEXT OF SCALE

The bulk of the studies cited thus far have addressed hydrogeomorphological influences on vegetation at the scale of landforms or individual valley reaches. The importance — and the specific impact — of floods also varies with position in watersheds, and varies further between watersheds (Hupp, 1982; Baker, 1989; Tabacchi *et al.*, 1990; Bendix, 1994a,b; Parker and Bendix, 1996). Some of the reasons for such variation are hydrogeomorphological; others relate to a range of other environmental influences that constrain vegetation's response to floods.

In any valley that is confined for part of its course within bedrock gorges or has reaches where the stream gradient is controlled by bedrock, flood severity will reflect bedrock influence (Baker and Costa, 1987). Stream gradient interacts significantly and deterministically with the width, depth and velocity of floods, the factors that control flood discharge and power along a reach. Given a relatively constant discharge along a reach, variation in gradient changes the proportion each factor contributes to discharge. Changes in width, depth or velocity are related to variation in channel geometry and flood intensity. Increased stream gradient usually increases unit stream power (Figure 4; Bendix, 1997). Reaches experiencing greater unit stream power (which affects not only direct impacts on vegetation but also reworking of sediment and transport of flood debris) experience greater amounts of flood damage than reaches with gentler gradients (Sigafos, 1964; Hupp, 1982; Yanosky, 1982; Bendix, 1994a). The hydrogeomorphological variation that results from these bedrock influences has been shown to affect the distribution of riparian species in Virginia (Hupp, 1982, 1986a), Colorado (Baker, 1989), Arizona (Zimmerman, 1969) and California (Bendix, 1994a).

The very occurrence of the landforms on which riparian vegetation grows can vary in apparent response to stream gradient changes. In Passage Creek, Virginia, channel shelves, a feature more pronounced in high-gradient reaches, were found to occur farther upstream than floodplains, in apparent response to upstream increases in gradient (Hupp, 1986b). Osterkamp and Hupp (1984) suggest that different sets of hydrogeomorphological processes form the floodplain and the channel shelf, and that different suites of vegetation (floodplain forest versus channel shelf shrubs) characterize each. Along any given reach, processes that favour the development of either the floodplain or the channel shelf will dominate, such that the formation of one feature develops at least partially at the expense of the other. Stream gradient appears to be a critical factor determining which set of processes will dominate (Hupp, 1982, 1986b).

Table I. Typical vegetation on northern virginia fluvial landforms (after Hupp and Osterkamp, 1985; Hupp, 1988)

Fluvial landform	Time inundated (%)	Flood frequency	Vegetation
Depositional bar	~ 40%	–	Herbaceous species, with occasional <i>Salix</i> , <i>Platanus</i> and <i>Populus</i> seedlings
Channel shelf	10–25%	–	Riparian shrubs: <i>Alnus cerulata</i> ^a <i>Cornus amomum</i> ^a <i>Cephalanthus occidentalis</i> <i>Ilex verticillata</i> <i>Physocarpus opulifolius</i> <i>Viburnum dentatum</i> <i>Vitis riparia</i> <i>Acer negundo</i> ^b <i>Populus deltoides</i> ^b <i>Salix nigra</i> ^b <i>Ulmus rubra</i> ^b
Floodplain	–	1–3 year	Floodplain forest: <i>Carya cordiformis</i> ^a <i>Celtis occidentalis</i> <i>Juglans nigra</i> ^a <i>Staphylea trifolia</i> <i>Ulmus americana</i> ^a <i>Betula nigra</i> ^b <i>Carpinus caroliniana</i> ^b <i>Fraxinus pennsylvanica</i> ^b <i>Lindera benzoin</i> ^b <i>Platanus occidentalis</i> ^b
Terrace	–	3 year	Terrace assemblage: <i>Amelacnier arborea</i> <i>Carya tomentosa</i> ^a <i>Fraxinus americana</i> <i>Pinus virginiana</i> ^a <i>Sassafras albidum</i> <i>Quercus prinus</i> <i>Carya glabra</i> ^b <i>Cercis canadensis</i> ^b <i>Cornus florida</i> ^b <i>Kalmia latifolia</i> ^b <i>Quercus alba</i> ^b <i>Quercus rubra</i> ^b <i>Quercus velutina</i> ^b

^aSpecies with widespread distribution.

^bCommon on indicated landform, but also frequently important on other fluvial features.

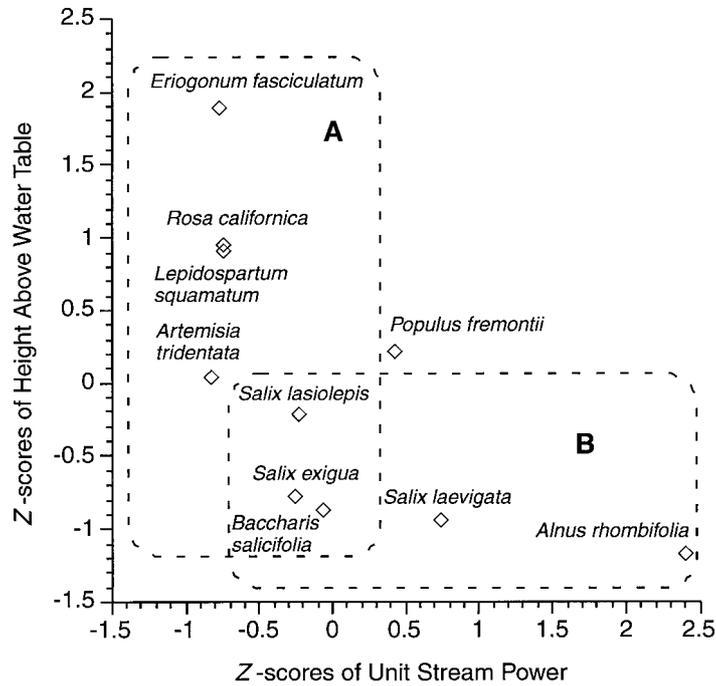


Figure 3. Relationship of 10 common southern California riparian species to unit stream power and height above the water table. Plotting positions reflect the median values for sample positions in which that species had 25% cover. Box A encloses species plotting at less than the mean for unit stream power, box B encloses species plotting below the mean for height above the water table. Modified from Bendix (1999). Reproduced by permission of the International Association for Vegetation Science and Opulus Press Uppsala.

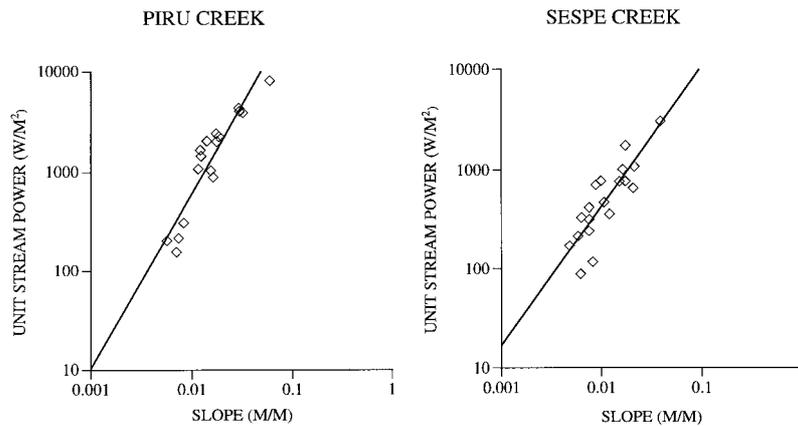


Figure 4. Relationship of unit stream power to gradient in two southern California streams. Values for unit stream power are averages for the 20-year recurrence interval flood, across cross-sections of the 20-year floodplain. R^2 for Piru Creek is 0.86, R^2 for Sespe Creek is 0.72; both are significant at the 0.001 level. Modified from Bendix (1997). Reproduced by permission of the American Geographical Society.

In arid, bedload-laden streams, an increase in gradient is often associated with a shift to a braided channel pattern (Graf, 1988a). The result is that a higher proportion of the valley floor is occupied by relatively unstable, shifting islands and bars, relative to the more permanent floodplain surface. The potential for disturbance is thereby magnified, as powerful floods (owing to the steep gradient) are combined with an unstable substrate. Offsetting this tendency is the presence in some bedrock gorges of boulders (possibly present due to mass wasting from adjacent slopes) which are immovable by moderate floods that would have reworked smaller sediments (Bendix, personal observation). A complicating factor is that the distribution of stream power through alluvial watersheds is not constant through time, as changes occur in response to erosional events (Graf, 1983).

Flood impacts also vary through watersheds as a simple function of changing discharge. In two southern California streams, a flood with negligible upstream impacts was found to have a significant impact at downstream sites where its discharge had been greater (Bendix, 1998). In arid regions, there may also be reach-to-reach variation between perennial and ephemeral flow; the consequences of this variation for vegetation may be independent of, or interactive with, the flood regime (Zimmerman, 1969; Zimmerman and Thom, 1982; Birkeland, 1996).

Non-hydrogeomorphological environmental influences that vary between reaches and watersheds may limit the pool of species available to respond to the hydrogeomorphological factors within a given reach (Baker, 1989; Malanson, 1993). Environmental influences may include temperature and precipitation (both of which often vary with elevation within a watershed) and non-flood disturbance history (Bendix, 1994a), as well as the longer term history of climate change and species' dispersal (Baker, 1989).

The simultaneous action and interaction of different-scaled variables affecting riparian vegetation means that the interpretation of data from any given scale must be undertaken in a multidimensional context. In analysing vegetation on a given landform (e.g. floodplain or terrace), it is common to think in two dimensions — how far is it from the channel horizontally, and how high is it above the channel, vertically. But other dimensions (either geometric or conceptual) may be critical: the longitudinal position in the watershed, the characteristics of the watershed itself, and the site history may all constrain both flood magnitude and severity at that point in the valley bottom and the species available to respond to floods. This explains at least some of the variation we see in vegetation occurring on seemingly comparable landforms — the actual species composition reflects the unique intersection of environmental influences acting at varied scales (Bendix, 1994b).

COLONIZATION OF RIPARIAN SITES

Floods play at least a three-fold role in the establishment and survival of riparian plants. First, most riparian plants germinate in alluvium that is deposited during floods. Fresh deposits provide sites for colonization, and the energy conditions of the floods determine the texture of the new substrate. Second, floods may create colonization sites by destroying pre-existing vegetation. Third, the occurrence or lack of floods subsequent to germination may determine whether seedlings survive to maturity. In some cases, floods may also play a significant role in dispersing propagules to colonization sites. The propagules may be clonal segments (Douglas, 1989; Parker and Hamrick, 1992), or seeds, including some that are more often thought of as wind-dispersed (Thébaud and Debussche, 1991; Hupp, 1992; Johnson, 1994; Rood *et al.*, 1998).

A number of studies have examined the role of floods, and more generally of discharge and stage variation, in the establishment of various species of cottonwood (*Populus*). Although there is substantial agreement that cottonwood establishment occurs following floods (e.g. Scott *et al.*, 1997; Mahoney and Rood, 1998; Stromberg, 1998), the actual timing of establishment may vary from the flood year itself (Rood *et al.*, 1998) to a window of several post-flood years (Merigliano, 1998). In some instances, high water during the spring seed dispersal period may still cover the cleared surfaces, preventing cottonwood germination (Bendix, 1998) or limiting it to gravel substrates — which in turn restricts moisture availability as a result of limited capillary rise (McBride and Strahan, 1984a). Much of the variation in the timing of post-flood seedling

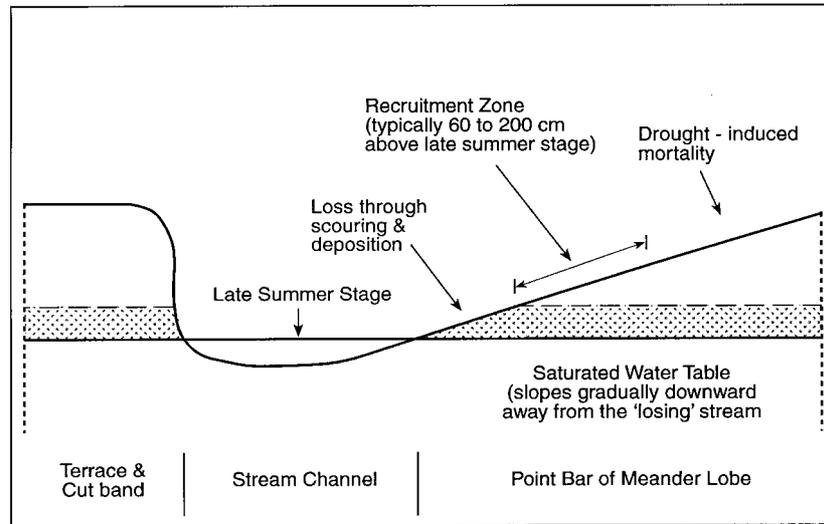


Figure 5. Schematic cross-section showing ideal location for germination and survival of cottonwood seedlings. Modified from Mahoney and Rood (1998). Reproduced by permission of the Society of Wetland Scientists

establishment is probably due to seedling requirements for enough water to survive coupled with vulnerability to excess flows. In Colorado, Baker (1990a) related stand establishment of *Populus angustifolia* to years in which high peak discharges (floods large enough to clear sites) coincided with climatic conditions favourable to seedlings: cool winters, wet springs, and cool, wet autumns. Mahoney and Rood (1998) summarize an extensive literature on cottonwood recruitment to identify the intersection of the timing of declining discharges and seed release that would most favour seedling establishment. They also identify the geomorphological position in which seedlings are most likely to germinate and survive (Figure 5), where they are low enough for their roots to reach capillary moisture, but high enough to survive ongoing fluvial processes.

There are, of course, species other than cottonwoods that may colonize alluvial surfaces. Although there are sometimes observable differences in the sites at which various species germinate (e.g. substrate texture; McBride and Strahan, 1984a; Niiyama, 1990), it remains unclear the extent to which these differences reflect habitat requirements versus the times at which different species disperse seed relative to the time of surface exposure by receding water levels. Friedman *et al.* (1996) found that, although the establishment of different species along a Great Plains stream in Colorado was strongly linked to elevation above the channel, that distribution could be related to a complex mix of flood disturbance, seed dispersal, and moisture and nutrient availability. The interaction of environmental gradients and timing may explain why Shafroth *et al.* (1998) found little evidence that seedling species were sorted by local environmental conditions, and Malanson and Butler (1991) concluded that dispersal history and founder effects were more important than local environmental variables in determining which species become established.

VEGETATION DYNAMICS

Much of the research on riparian vegetation has been directed at relating site history to successional status of vegetation. The term succession is much used in ecology, often with conflicting meanings. The classic meaning implies a directional sequence of changes in species composition and other plant community

characteristics (productivity, biomass, diversity, etc.) that occurs as vegetation colonizes an open site and then changes through time (Clements, 1916; Odum, 1969). A variety of other theoretical perspectives suggest less deterministic pathways, involving multiple endpoints or unpredictable, contingent change (Vale, 1988). A significant element in interpretation of the literature on this topic is recognition of the meanings applied by different scholars. In most riparian studies, the term succession seems to be applied to sequential changes in species composition.

Some of the examples of successional studies have linked successional status to specific landforms. In this approach, fluvial landforms are identified by their established or assumed age. The vegetation found on the landforms can then be placed on a temporal gradient, and interpreted in terms of successional change. In some studies the chronosequence of landforms has been a series of terraces, with the highest being oldest, and the lowest youngest (Fonda, 1974; Smith, 1980); in others, the lateral migration of stream channels has provided a horizontal sequence of different-aged sites (Nanson and Beach, 1977). In the Missouri River floodplain, Johnson *et al.* (1976) combined the two, with progressively older stands along a gradient from the edge of point bars to their interior and up on to terraces. They found young stands dominated by cottonwood (*Populus deltoides*) and peach-leaved willow (*Salix amygdaloides*). These were gradually replaced in older stands by green ash (*Fraxinus pennsylvanica*), American elm (*Ulmus americana*), box elder (*Acer negundo*) and bur oak (*Quercus macrocarpa*).

Other successional studies have emphasized flood history rather than landform position. In this approach, the temporal starting point is the last stand-clearing disturbance, rather than the date of landform creation. In the Rhine Valley, Schnitzler (1995) found that pioneer 'softwoods' (*Salix* and *Populus*) give way, absent disturbance, to 'hardwoods' (*Fraxinus*, *Quercus* and *Ulmus*). Baker and Walford's (1995) assessment of Colorado's Animas River was less deterministic: they emphasized that the interjection of allogenic factors ranging from varying intensity of disturbance to substrate changes makes the course of vegetation change unpredictable.

An underlying question in all of these studies relates to the appropriateness of applying successional concepts to riparian communities. As noted earlier, several authors have suggested that riparian communities should be considered compositionally stable, maintained by periodic flooding, rather than successional, recovering from floods (Sigafos, 1961; Yanosky, 1982; Hupp, 1983; Bendix, 1998). Although the distinction is largely semantic, the conceptual implications may be important, given the modern tendency of ecological theory to translate (perhaps erratically) into environmental policy (Zimmerer, 1994; Baker and Walford, 1995).

RIPARIAN BIODIVERSITY

Although the discussion thus far has emphasized the species composition of riparian plant communities, flood disturbance is also relevant to the diversity of plant species present (Décamps and Tabacchi, 1994; Patten, 1998). Although some explanations of riparian diversity depend more on dispersal patterns and history than on disturbance (Nilsson *et al.*, 1991; 1994), many others call on the intermediate disturbance hypothesis, which suggests that species diversity should be greatest where there are intermediate levels of disturbance (Connell, 1978; Petraitis *et al.*, 1989). According to the hypothesis, intermediate magnitude and frequency of disturbance allow for the maintenance of multiple vegetation patches on sites with varying degrees of disruption and at varying successional stages.

At a regional scale, Baker (1990b) concluded that the intermediate disturbance hypothesis could not explain the regional distribution of riparian species richness in western Colorado. At watershed and smaller scales, conclusions have been more variable. In France, Tabacchi *et al.* (1990) found support for the intermediate disturbance hypothesis in vegetation along the Adour River, but Nilsson *et al.* (1989) were unable to relate species richness patterns on the Torne and Kalix Rivers in Sweden to disturbance variables.

Bendix (1997) noted that the distribution of disturbance-related diversity within watersheds may be controlled by the systematic downstream variation of the hydraulic variables depth, slope and velocity, but

cautioned that the resulting patterns will depend on the scale of the watershed and the severity of its flood regime. In his analysis of two California streams, he found that richness increased in a downstream direction, and attributed the finding to downstream increases of stream power imposed by bedrock slope control. This finding parallels that of Hupp (1982) in Virginia, who found increases in diversity in severely flooded, high gradient reaches of Passage Creek. In both instances, diversity seems to be maximized at high, rather than intermediate, levels of disturbance, recalling Bendix's (1997) concern that intermediacy may be disguised by the scale of observation.

CONCLUSION: QUESTIONS OF CAUSALITY

It is clear that the distribution of plant species, and of species diversity, within watersheds is not random, and is linked to the distribution of hydrogeomorphological processes and landforms. We caution, however, that the understanding of these linkages is still far from complete. Because of the complexity of fluvial systems in which floods, landforms and vegetation interact, there are causal linkages and feedbacks that have yet to be clarified.

A species found to be dominant on the recent terrace (I) in Figure 2a might be thriving there because of temporal factors, as a result of succession since the terrace was abandoned. It might be there for hydrological reasons, because floods up on the 100-year floodplain are shallower and less destructive than those on the 50-year floodplain (Figure 2b). Or it might be there because the well-drained middle-terrace soils (Figure 2c) maintain the moisture and/or nutrient conditions required by the species. None of these 'independent' variables are independent, of course. The geomorphological evolution of the valley was presumably in response to hydrological changes in flood regime, and the soil characteristics reflect the hydrogeomorphological conditions in which the alluvium was deposited, overbank deposition of sediment by the rare floods that reach that terrace, and the pedogenic processes that have been allowed for by the geomorphological history of the terrace. Because our primary clue is the location of the species, the fact that multiple, potentially significant, variables coincide at any given location makes interpretation a formidable, interdisciplinary task.

It is also misleading to think of riparian vegetation as a purely dependent variable in our studies (Hickin, 1984). Although floods may affect vegetation, they are also affected by it (Tabacchi *et al.*, 2000, this issue), owing to the contribution of vegetation to hydraulic roughness. The importance of this is reflected in the prominent role of roughness (n) in the widely used Manning equation. Dense riparian vegetation can have an extraordinary impact on hydraulic roughness, increasing values of n by as much as an order of magnitude (Arcement and Schneider, 1989). In assessing the relationship between vegetation and floods, it is therefore necessary to recognize that flood velocities at any point in the valley bottom may be substantially decreased as vegetation grows, or abruptly increased if the vegetation is destroyed. Similarly, although substrate undoubtedly has an impact on riparian vegetation, the vegetation in turn affects the substrate when its roughness contributes to the deposition of sediment (e.g. Graf, 1978). These feedbacks become particularly complex when vegetation-induced sedimentation changes the nature of the vegetation that can be supported on a landform (McBride and Strahan, 1984b), or when successional changes in the vegetation alter its contribution to sedimentation (McKenney *et al.*, 1995).

These complexities serve to underscore the need for process-oriented, scale-conscious interdisciplinary studies integrating plant ecology and biogeography with hydrology and geomorphology (Hupp, 1988). It is only through analyses incorporating the subtleties of each that we will continue to elucidate the impacts of hydrogeomorphological processes on riparian vegetation.

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