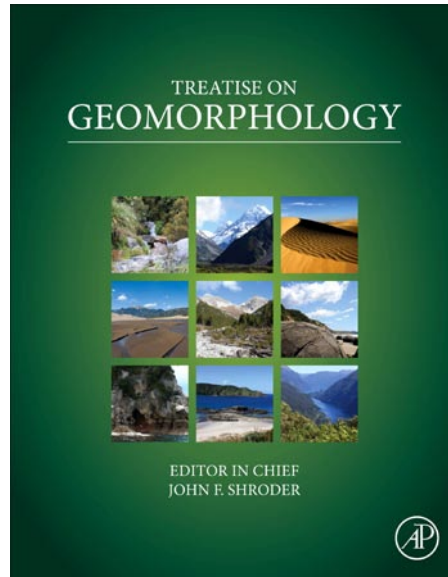


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12.5 Riparian Vegetation and the Fluvial Environment: A Biogeographic Perspective

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Abbreviations

CHILD Channel–hillslope integrated landscape development

LWD Large woody debris
TN Total nitrogen
TOC Total organic carbon

Abstract

In this chapter, we review the historical arc of research on biogeomorphic interactions between fluvial geomorphology and riparian vegetation. We then report on an examination of the past 20 years of published research on this topic. Having classified studies according to the key relationships they have identified, we map those relationships to seek spatial patterns that emerge in terms of either physiographic environment or actual geographic location. We also consider the varied patterns of causal interactions that emerge at different spatial scales.

12.5.1 Introduction

The recognition of riparian zones as biogeomorphic units in the landscape is critical both for theoretical understanding and for conservation of these high-value habitats. Since the middle of the twentieth century, study of the systematic patterns of vegetation communities in riparian zones has led to a greater

understanding of the linked physical and biotic processes that sustain them (Osterkamp and Hupp, 1984; Gregory et al., 1991; Naiman and Decamps, 1997; Naiman et al., 2005). For much of this time, emphasis was placed on the importance of understanding hydrogeomorphic influences on riparian vegetation, because fluvial forces set the physical template for ecological communities. Recently, there has been greater study of the reciprocal influence of biological organisms and processes on geomorphic processes, leading to a biogeomorphic understanding of fluvial/riparian ecosystems (Corenblit et al., 2007). This view recognizes the substantial influence that vegetation pattern and structure can have in altering the

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distribution of physical forces of flow and sediment regimes, which ultimately create feedbacks to biological communities and ecosystems (Bendix and Hupp, 2000).

Early work relating riparian ecology to fluvial processes was primarily descriptive in nature, with a common thread being the classification of riparian vegetation communities and their association with particular fluvial landforms, or even simply particular vertical locations relative to stream channels. These studies were generally place- and taxa-specific. The development of geomorphology as a more quantitative science since the middle of the last century (e.g., Leopold and Maddock, 1953; Leopold et al., 1964) laid the basis for more generality and a common biogeomorphic process approach to the study of rivers and riparian zones (Osterkamp and Hupp, 2010). Examples of this work include the hydraulic geometry approach (Leopold and Maddock, 1953), process-based classification of river environments (Montgomery and Buffington, 1997), and quantifications of interactions between sediment transport capacity and supply across a wide range of spatial and temporal scales (e.g., Howard et al., 1994).

However, much of the early work was conducted on North American streams, with particular ecological communities and physical regimes influencing a great deal of the development in early theories and empirical examples. The histories of both geomorphology and ecology include reminders of the danger of generalizing theories across dissimilar environments. Critiques of the roles of William Morris Davis in the former discipline and of Frederick C Clements in the latter have noted that theoretical models developed in distinctive geographic settings did not translate appropriately when imposed elsewhere. In a recent example, studies by Walter and Merritts (2008) in eastern North America suggest that the geomorphic context in the region where much of the early hydraulic geometry research (e.g., Leopold and Maddock, 1953) was conducted may have been in disequilibrium due to historical human influences (i.e., mill dams). These well-known examples serve as reminders that processes and relationships vary spatially. In particular, the very different environmental conditions and vegetation structure occurring in different biomes suggest that plant adaptations to hydrogeomorphic constraints, and the subsequent influence of vegetation on fluvial processes, may vary widely from one setting to another.

Another spatial complication arises when we consider the scale at which biogeomorphic relationships are observed. A variety of studies have indicated that the causal relationships observed between riparian vegetation and hydrogeomorphic processes may differ depending upon the scale of observation (Baker, 1989; Dixon et al., 2002; Petty and Douglas, 2010). In some, but not all, instances, the relationships at smaller scales may be hierarchically constrained by those operating at larger scales (Bendix, 1994a). Although there have, by now, been several case studies in varied environments of the impact of scale on riparian biogeomorphic environments, we lack a systematic review of the empirical findings regarding scale impacts – both from studies that explicitly explored scale and from those that did not but contain relevant information.

These issues raise the questions of how geography and scale influence our understanding of riparian zones and their linked physical/biological processes. For example, how do the geographic setting and scale of observation affect our

conclusions about drivers, responses, and landscape patterns in riparian vegetation communities? In which biomes and at what scales is the direction of influence primarily from the physical to the biotic, the reverse, or one of strongly linked feedbacks? How does the biome or geographic setting influence the relative strength of ecosystem drivers, including disturbance regimes (flooding, scour, and sediment deposition), abiotic stress (e.g., seasonal drought), soil chemistry, and/or limitations on life-history processes such as propagule dispersal?

We believe that a biogeomorphic approach is necessary for a legitimate understanding of either fluvial processes or the ecology of the riparian zone. The large volume of relevant empirical research since several landmark papers in the 1980s and early 1990s (e.g., Osterkamp and Hupp, 1984; Hupp and Osterkamp, 1985; Gregory et al., 1991) suggests the need to go beyond a catalog-style review to a more analytical approach to understanding the complex relationships between the ecological and geomorphic elements of the riparian environment. We therefore seek to examine the literature on the interactions between riparian plant communities and fluvial landforms/processes, within a bipartite, spatially oriented framework that emphasizes how biogeomorphic interactions between riparian vegetation and fluvial geomorphology vary with both geography and the scale of observation.

In this chapter, we begin with a condensed review of the historical arc of research on the varied fluvial impacts on vegetation, the means whereby vegetation influences fluvial geomorphology, and the feedbacks between the two. The bulk of that research has been on the specific mechanisms of hydrogeomorphic influence on riparian plant communities; therefore, these mechanisms receive particular emphasis in our review. We then report on an examination of the past 20 years of published research on this topic. Having classified studies according to the key relationships they have identified, we map both the causal directions and the mechanisms to seek spatial patterns that emerge in terms of either physiographic environment or actual geographic location. We also consider the varied patterns of causal interactions that may emerge at different spatial scales.

12.5.2 Early History: Pattern and Process in Riparian Zones

The current understanding of the physical/biological linkages in river ecosystems is inherited from a long line of conceptual and empirical work in stream ecology and river science. The issues of biogeography and scale in studies of riparian ecology date to early work relating geomorphic landforms to vegetation communities. For almost a century, scholars have acknowledged and described associations between geomorphic landforms and the distribution of vegetation communities in river and floodplain systems. More recently, researchers have investigated the specific processes that drive these vegetation associations with landform. Early studies drew on the disciplinary traditions of geography, geomorphology, and ecology, establishing strands that have persisted through time. Beginning in the 1930s, a primary focus of this work was the description and classification of riparian vegetation communities, but, even in these

early efforts, there were attempts to systematically relate vegetation communities to fluvial landforms and processes. The distinct zones of vegetation described by Hefley (1937) on the low terraces of the Canadian River in Oklahoma were subsequently attributed by Ware and Penfound (1949) to a combination of flood damage and drought.

Such studies were the precursors of later work that would use more rigorous statistical tools to document similar relationships (Hupp and Osterkamp, 1985; Harris, 1987; Shin and Nakamura, 2005). Our understanding of process and quantitative tools for testing this have evolved over time to the point that some researchers have developed and tested predictive models of vegetation response to hydrogeomorphic factors such as flood inundation (Auble et al., 1994; Dixon and Turner, 2006), flood energy (Bendix, 1999; Sandercock and Hooke, 2010; Stromberg et al., 2010), ice scour (Auble and Scott, 1998), channel meandering, and floodplain sedimentation (Harper et al., 2011). Some of these models are phenomenistic (e.g., Auble et al., 1994; Shafroth et al., 1998), whereas others are mechanistic in nature (Lytle and Merritt, 2004; Stella, 2005; Dixon and Turner, 2006; Harper et al., 2011).

12.5.3 Influence of Hydrogeomorphology on Vegetation: Evolution from Descriptive to Quantitative Studies

Hydrogeomorphic processes generally influence riparian vegetation through their contribution to the physical disturbance regime, which affects plant demography (e.g., dispersal to safe sites and flood mortality), and through their impacts on the resource environment for plant growth. These drivers interact with plant life-history processes, traits, and physiological tolerances to influence population demographics and community dynamics in riparian communities. As early as the 1930s, when plant zonation patterns on rivers were first documented, researchers had recognized that flooding regimes influence the composition, distribution, and structure of riparian vegetation. Illichevsky (1933) documented distinct cross-sectional compositional belts in the floodplain of the Dnieper River, noting differences in plant assemblages between the inundated and dry zones. Examples of similar work in the years that followed include Shelford's (1954) documentation of biotic communities in the lower Mississippi valley floodplain and their age and elevation relative to the mean low water level, and Fanshawe's (1954) use of topographic position on bars and banks as a criterion for distinguishing plant communities on river fringes in British Guiana.

Studies during this early period generally described patterns more than the processes that influenced them, although there are some notable exceptions (Hefley, 1937; Ware and Penfound, 1949), in particular, investigations relating vegetation to flood frequency and duration, and linking flood disturbance to successional zonation (Wistendahl, 1958; Lindsey et al., 1961). Sigafos (1961) took issue with successional interpretations, arguing that zonation instead reflected tolerance to flooding (see Hupp (1988) for a useful discussion of where and why successional zonation might

occur). Sigafos identified distinctive vegetation bands along the Potomac River related to inundation frequency; these observations set the stage for his groundbreaking work reconstructing past floods from dendrogeomorphological records (Sigafos, 1964). Although much of the research in this period was in the middle and eastern parts of North America, valuable research emerged in the West as well. Everitt (1968) related cottonwood regeneration on Utah's Fremont River to flood dynamics. Teversham and Slaymaker (1976) studied riparian vegetation composition in Lillooet River valley, British Columbia, documenting species groupings that were related to both sediment size and flood frequency. These examples, by no means exhaustive of the studies during this period, give an indication of the range of contemporary perspectives.

Beginning in the 1980s, interest in riparian ecology broadened greatly, leading to classification systems of vegetation communities with landforms and quantification of the physical processes that sustained them. Osterkamp and Hupp (1984) (also see Hupp and Osterkamp, 1985) investigated these relationships along northern Virginia streams and documented assemblages of woody plants on geomorphic surfaces that are distinguished by inundation frequency and duration. Similar studies using categorical classifications of landforms that are associated with different flood inundation frequencies include examples from Northern California (Harris, 1987), Central Oregon (Kovalchik and Chitwood, 1990), and Japan (Shin and Nakamura, 2005). In this approach, vegetation species presence and/or cover was recorded and associated with elevation above the active channel, and by association with flood frequency and duration. Often, some type of multivariate analysis was used to classify species into groups that sort along hydrologic gradients (Harris, 1987; Auble et al., 1994; Bendix, 1994b; Rodríguez-González et al., 2010).

Beginning in the 1990s, researchers began to develop quantitative models linking vegetation response to mechanistic, hydrological, and hydraulic drivers. In an innovative approach combining standard numerical modeling in plant ecology and river engineering, Auble et al. (1994) conducted a plant community analysis of the Gunnison River (CO), using cluster analysis in conjunction with hydraulic modeling to quantify the flood duration of distinct plant communities and model vegetation change under proposed regulated flow regimes. In California's Transverse Ranges, Bendix (1999) used hydraulic modeling, ordination, and regression to relate plant community composition to computed values of unit stream power, as opposed to earlier studies that relied on assumptions of relative flood energy inferred from landform position. His research demonstrated that variation in hydraulic parameters imposes spatial variation in the ecological impact of floods within watersheds (Bendix, 1997, 1998). In another application of hydraulic modeling, Dixon et al. (2002) integrated calculations of energy slope from a one-dimensional hydraulic model with quantitative landscape analysis to investigate the influence of physical characteristics at the local and landscape scales on the distribution of pioneer tree seedlings along the Wisconsin River. This was an extension of the approach WC Johnson used to infer maximum streamflow thresholds that cause seedling mortality from flood removal

and ice scour on both the Missouri River (Johnson et al., 1976; Johnson, 1992) and the Platte River, Nebraska (Johnson, 1994, 1998).

With the increasing emphasis on sophisticated quantitative analyses, the mechanisms of plant recruitment and mortality were studied in more detail, and species-level investigations assumed greater prominence to complement studies conducted at the whole-community level (Shafroth et al., 1998; Stella, 2005; Dixon and Turner, 2006; Shafroth et al., 2010). Riparian species differ in key life-history traits that are linked to recruitment and survival in dynamic fluvial environments, including inundation duration (Huffman, 1980; Toner and Keddy, 1997; Robertson et al., 2001; Kozłowski, 2002; van Eck et al., 2004), seed dispersal and characteristics of fecundity, release timing, seed longevity and buoyancy (Kubitzki and Ziburski, 1994; Danvind and Nilsson, 1997; Lopez, 2001; Nilsson et al., 2002; Stella et al., 2006; Gurnell et al., 2008), and those related to survival of scour and burial (Bornette et al., 2008), particularly hydraulic resistance and stem flexibility, rooting depth, and resprouting ability (Brewer et al., 1998; Levine and Stromberg, 2001; Karrenberg et al., 2002; Lytle and Poff, 2004; Renofalt and Nilsson, 2008; Rodríguez-González et al., 2010). Differences in reproductive and survival traits have been used successfully in several mechanistic, numerical approaches to predict relative abundance of species within riparian communities (Shafroth et al., 1998; Stella, 2005; Dixon and Turner, 2006; Bornette et al., 2008).

12.5.4 Specific Mechanisms of Hydrogeomorphic Impact

Hydrogeomorphic processes interact with riparian vegetation through life-history characteristics, plant traits, and physiological tolerances (Rood et al., 2003). There are many mechanisms that influence vegetation composition, distribution, and density; however, for ease of analysis we have grouped them into six main categories, all of which are consequences to some degree of periodic floods and the dynamic hydrology characteristic of near-channel environments:

1. flood energy, which exerts a limiting effect on vegetation distribution due to scour and stem breakage;
2. sedimentation, which can exert influence through creation of new habitat for plant colonization and reduction of competition, burial of existing vegetation, and/or sediment texture effects on water availability;
3. prolonged inundation, which generally reduces physiological function and survival;
4. water-table depth and dynamics, which regulate soil moisture;
5. soil chemistry influences, including mineral nutrition, salinity, and pollutants; and
6. fluvial controls on propagule dispersal.

12.5.4.1 Flood Energy

The hydraulic energy associated with flooding in dynamic river systems causes damage or mortality of plants through root zone scour and stem breakage (Hughes, 1997; Polzin and Rood, 2006; Perucca et al., 2007). Vegetation is particularly

vulnerable when plants are small relative to the magnitude of flood energy, such as during seedling establishment. This is also the case for plant removal by scour, which will generally occur when scour depth approaches the depth of coarse roots. Root or stem breakage not only is common for herbaceous vegetation during high flow but also can occur for woody plants in large floods (Chambers et al., 1991; Groeneweld and French, 1995; Gurnell et al., 2002). The energy required to remove or break plants varies with their size and flexibility, their root characteristics, and the nature of the substrate in which they are rooted (Bendix, 1999).

At the vegetation patch scale, plant removal occurs when scour depth exceeds a critical depth that is related to the size and structure of the vegetation roots. The patchy nature of riparian vegetation introduces complexities and feedbacks to flood energy because vegetation often reduces near-bed velocities and scour depths deep within a patch, but increases velocities at the upstream and outside edges of vegetation patches through flow contraction. This can create wider and deeper scour patterns than those produced around individual stems and increased susceptibility to flood mortality for exposed plants (Lightbody et al., 2008; Yager and Schmeeckle, 2007).

The impacts of flood energy on the species composition of riparian plant communities may be seen both through differential survival of the potential damage described above and through colonization by pioneers replacing the species that do not survive (Bendix and Hupp, 2000). More subtly, even floods that do not cause mortality may clear leaf litter, providing an advantage for species that require bare mineral soil for colonization (Yanosky, 1982).

12.5.4.2 Sedimentation

Sedimentation can act on plants in either positive or negative ways, and includes effects of landform construction (Cooper et al., 2003; Latterell et al., 2006), mortality due to burial (Hack and Goodlett, 1960), and sediment texture controls on water availability (McBride and Strahan, 1984a). At the landscape scale, the sediment regime has a controlling influence on plant establishment, community composition, biomass, and vegetation structure (Everitt, 1968; Hickin, 1984; Bechtold and Naiman, 2006; Naiman et al., 2010). Channel migration processes drive formation and development of geomorphic surfaces to control the establishment and spatial extent of pioneer communities (McKenney et al., 1995; Lytle and Merritt, 2004; Harper et al., 2011). Increasingly, studies have focused on description and quantification of the relative importance of different establishment pathways for riparian forest stands on alluvial surfaces, including point bars, abandoned channels, and mid-channel bars (Baker and Walford, 1995; Cooper et al., 2003, 2006; Latterell et al., 2006; Van Pelt et al., 2006; Stella et al., 2011). One of the primary influences of new landforms on colonizing vegetation is through sediment texture effects on moisture-holding capacity, which in turn controls plant survival and growth (Mahoney and Rood, 1992; Hughes et al., 2000; Hupp and Rinaldi, 2007).

At smaller spatial scales, sedimentation affects plants through mortality by burial. The severity of this effect depends on the size of the plant relative to sediment deposition rate,

which is related to the transport capacity of individual flood events, basin-scale sediment supply (Buffington and Montgomery, 1999), meso-scale influences such as bar topography (Dietrich and Whiting, 1989; Francis and Gurnell, 2006), and local roughness fields from live vegetation or woody debris (Gurnell and Petts, 2006; Yager and Schmeeckle 2007).

Many plant species can survive burial and resprout from epicormic buds (Bond and Midgley, 2001). However, the severity of impact (i.e., plant mortality rate) depends on the depth of sediment deposited during an event, as well as the plant size, season (dormant vs. active), and taxon-specific physiology. Ewing (1996) found decreased growth and physiological function by alder and sedge plants after partial sediment burial. Levine and Stromberg (2001) found increased resistance by cottonwood over tamarisk to sediment burial, and other work along the Bill Williams River, AZ, has documented substantially greater mortality of tamarisk compared to willow seedlings in response to two dam-controlled flood releases (Shafroth et al., 2010). Mortality occurred by both scour and burial and was likely nonproportional among species because of the substantially greater first-year height and diameter growth of willow relative to tamarisk (Sher et al., 2002; Shafroth et al., 2010).

12.5.4.3 Prolonged Inundation

Although temporary flooding generally increases the supply of water and nutrients to terrestrial plants (Burke et al., 1999; Clawson et al., 2001; Kozłowski and Pallardy, 2002), long-term soil saturation induces soil anoxia, which limits nutrient availability and gas exchange for plants (Mitsch and Gosselink, 2007), and soil toxicity due to reducing conditions. These negative effects are mitigated to some degree by plants' adaptive responses to prolonged flooding, including tissues to facilitate oxygen exchange such as aerenchyma and lenticel development (Blom and Voisenek, 1996; Crawford, 1996; Rood et al., 2003; Walls et al., 2005). In riparian and other ecosystems where stressful abiotic conditions may limit plants' size, life span, and/or recruitment opportunities, increased sprouting has been associated with waterlogged soils (Rodríguez-González et al., 2010), and may be an important strategy in particular for species that do not maintain a seed bank (Bond and Midgley, 2001; Nzunda et al., 2007).

Much of the research on riparian plants' physiological responses to inundation is based on laboratory experiments (e.g., Pereira and Kozłowski, 1977; Conner et al., 1997; Li et al., 2005; Day et al., 2006), with a somewhat lesser emphasis on field studies (Megonigal et al., 1997; Eschenbach and Kappen, 1999; Tardif and Bergeron, 1999). In the field, variation in vegetation across slight topographic gradients has often been attributed to differential tolerance of inundation (Bell, 1974; Nixon et al., 1977; Robertson et al., 1978). But in observational field studies, inundation duration is often correlated with other mechanisms such as maximum flood energy, sediment texture, nutrient availability, and redox potential (Rodríguez-González et al., 2010). Therefore, teasing out specific contributions of inundation alone is difficult, especially as these effects are nonlinear and in some cases contradictory. For example, various studies on the influence of inundation on tree growth have found negative effects (e.g.,

Mitsch et al., 1991; Megonigal et al., 1997; Rodríguez-González et al., 2010), whereas others have found them to be positive (Burke et al., 1999; Clawson et al., 2001; Hanson et al., 2001). Some of these contradictions may reflect geographic variation, as environments typified by prolonged hydroperiod are likely to support species that show a positive response to inundation (Hupp, 2000).

12.5.4.4 Water-Table Depth and Dynamics

Although many riparian plant species are well adapted to their dynamic river systems through traits such as abundant seed production, wind dispersal, and fast growth (Karrenberg et al., 2002; Lytle and Poff, 2004), there are generally life-history tradeoffs that include demand for abundant soil moisture and intolerance to drought. In particular, survival of seedlings in arid and semi-arid climates is a challenge because seasonally fluctuating water tables and severe vapor pressure deficits can dramatically reduce water availability during the critical establishment stage (Donovan and Ehleringer, 1991; Horton and Clark, 2001; Hughes et al., 2001; Rood et al., 2003). On snowmelt-dominated rivers, extended flow and groundwater declines typically occur in late spring and early summer, as the snowpack melts (Peterson et al., 2000). Seedlings and other shallowly rooted plants are particularly vulnerable, and seasonal water shortage can act with other stressors in the riparian zone (e.g., scour, herbivory, and competition with herbaceous species) to limit population dynamics among riparian plants (Lytle and Merritt, 2004; Scott et al., 1996; Stromberg et al., 1991).

In arid and semi-arid regions, the connection of stream to riparian water table plays a critical role in resource supply and plant survival (Zimmerman, 1969; Rood et al., 2003), and can be the limiting factor for seedling survival and the population structure of pioneer plants (Lytle and Merritt, 2004). Long-term alterations in flow magnitude, timing, and recession rate have exacerbated the effects of seasonal water limitation in these systems and threaten to further reduce the extent of riparian woodlands (Fenner et al., 1985; Rood and Mahoney, 1990; Rood et al., 1999; Stella, 2005; Braatne et al., 2007); nor is the importance of water-table proximity limited to dry environments. On the floodplain of New Jersey's Raritan River, Frye and Quinn (1979) interpreted species distributions as a function of soil texture and depth to water table. In this setting, they considered a shallow water table to be a limiting factor, arguing that it excluded deep-rooted species. Numerous studies in lowland riparian environments highlight these species-specific differences in soil saturation and toleration of root anoxia (Niiyama, 1990; Conner et al., 1997; Rodríguez-González et al., 2010).

Despite their vulnerability to drought, riparian plants demonstrate some mitigating morphological and physiological traits. Annual species avoid drought by completing their life cycle during wet seasons. For perennial plants, rapid root extension and small shoot:root biomass ratios are adaptations that potentially reduce stresses related to seasonally variable water tables (Amlin and Rood, 2002; Horton and Clark, 2001; Hughes, et al., 1997; Kranjcec et al., 1998; Segelquist et al., 1993). Other morphological responses to water stress include

reduction in leaf size (Stella and Battles, 2010), specific leaf area (Busch and Smith, 1995), crown dieback (Scott et al., 1999), branch abscission (Rood et al., 2000), and reduced diameter growth (Stromberg and Patten, 1996). Studies of physiological function in adults indicate that these species are generally intolerant of drought and have low xylem cavitation thresholds (Amlin and Rood, 2003; Cooper et al., 2003; Leffler et al., 2000; Tyree et al., 1994). Higher water-use efficiency as indicated by higher $\delta^{13}\text{C}$ values is a common response of water-stressed plants (Smedley et al., 1991) and has been observed for riparian seedlings under experimental drought (Zhang et al., 2004) and adult natural populations between wet and dry years (Leffler and Evans, 1999). Water-table manipulations in controlled mesocosms have been used to simulate dynamic riverine environments in order to study the effects of seasonal moisture stress on plant survival and growth (e.g., Cordes et al., 1997; Horton and Clark, 2001; Mahoney and Rood, 1992; Segelquist et al., 1993; Stella et al., 2010). In one study, Stella and Battles (2010) found that seedlings of related species grown under identical conditions of water stress displayed different adaptations, with cottonwood minimizing specific leaf area to a greater degree than willow, which was more effective at reducing stomatal conductance and leaf size.

12.5.4.5 Soil Chemistry

Nonhydrologic factors also contribute to riparian plant distributions, including resource competition, lack of soil fertility, and salinity (Shafroth et al., 1995; Auble and Scott, 1998; Sher et al., 2000). Detailed work on establishment processes on fluvial landforms, including point bars, banks, and abandoned channels, has highlighted the importance of the soil environment, particularly nutrients and organic matter (Van Cleve et al., 1996; Bechtold and Naiman, 2006, 2009). In a study by Kalliola et al. (1991) on riparian forest colonization in western Amazonia, distinct vegetation communities colonized four common fluvial landforms: channel bars, swales, abandoned channels, and riverbanks. These newly deposited fluvial sediments are poor in organic carbon and nitrogen, are affected by seasonal fluctuations in the rivers, and support vegetation patches that tend to be narrow, curved, or linear patches. Local site and colonizing vegetation characteristics vary considerably between the different river types (e.g., meandering or braided, rich or poor in suspended sediment).

Bechtold and Naiman (2006) studied nutrient storage and mineralization along a toposequence on the Phugwane River in South Africa, and found that total organic carbon (TOC), total nitrogen (TN), and potential N mineralization were strongly linked to particle size distributions, with TOC and TN positively correlated with silt and clay concentration. After accounting for the effect of particle size, landform differences were not predictive of nutrient dynamics; therefore, they concluded that a collinear gradient of soil texture across alluvial landforms constitutes the primary nutrient influence on riparian soil and plant community succession.

Soil salinity is commonly cited in dryland riparian systems as a driving factor determining plant distributions, productivity, and species' relative competitiveness (Di Tomaso, 1998;

Gasith and Resh, 1999; Cramer and Hobbs, 2002). Glenn et al. (1998) found higher salinity tolerance by saltcedar (*Tamarix* spp.), a non-native shrub in the US Southwest, compared to native riparian species, and concluded that this abiotic factor was important in facilitating invasion by the saltcedar throughout the region's arid and saline riparian soils. Sher et al. (2002), however, found that salinity and other soil abiotic variables were much less important in predicting the mortality rate of first-year tamarisk seedlings than the density of native competitors (cottonwood and willow), which survived across a range of substrates.

12.5.4.6 Propagule Dispersal

Hydrogeomorphic influences on plant dispersal constitute another important mechanism affecting riparian vegetation, in part, because of co-evolution of propagule traits with disturbance regimes (Lytle and Poff, 2004). Unlike in most terrestrial environments, many plants in riparian ecosystems have little dependence on a persistent seedbank, particularly where physical disturbance from periodic flooding precludes seed storage (Pettit and Froend, 2001). Lacking a mechanism for multiyear seed storage, riparian plant recruitment typically results from dispersal of short-lived seed directly from parent plants (Young and Clements, 2003a, 2003b; Stella et al., 2006), or else transport of plant fragments as propagules (Gurnell et al., 2008). For seeds, dispersal is primarily by wind (anemochory) and water (hydrochory). The latter frequently depends upon synchronization of reproduction and seed dispersal with hydrological regimes that create favorable substrate and moisture conditions for seed dispersal (Hupp, 1992), and rapid germination and recruitment (Siegel and Brock, 1990; Scott et al., 1996; Mahoney and Rood, 1998; Stella et al., 2006). Vegetative reproduction via flood dispersal of plant fragments has also been observed for a range of taxa (Gurnell et al., 2008), from willows (Duhovnikoff et al., 2005) to columnar cacti (Parker and Hamrick, 1992). Hydrochory may be most important during overbank flows when propagules are dispersed across floodplains (Schneider and Sharitz, 1988; Gurnell et al., 2006, 2008). Wind dispersal also occurs preferentially along longitudinal stream corridors because local channel topography and the morphology of riparian canopies often serve to guide prevailing winds (Devitt et al., 1998).

As a result of these patterns, hydrogeomorphic forces are highly effective at accomplishing dispersal in both longitudinal and lateral dimensions along stream channels (Merritt and Wohl, 2002). Propagule deposition is not uniform, however, because of variation in propagule source density (Clark et al., 1999), substrate exposure (Johnson, 1994), and local variations in water velocity, hydraulic roughness and form drag due to channel morphology, existing vegetation structure and density, bed and bank substrate, and large woody debris (Johansson et al., 1996; Merritt and Wohl, 2002; Pettit and Naiman, 2006). Field studies (e.g., Gurnell et al., 2008), flume experiments (e.g., Merritt and Wohl, 2002), and models (Levine, 2003) have attempted to quantify and predict patterns of riparian propagule dispersal, and the effects of dams on riparian plant distributions through interruption of dispersal patterns have been documented (Nilsson and

Jansson, 1995; Jansson et al., 2000). Although these studies have provided details from a variety of settings, the complex nature of fluvial hydrodynamics, heterogeneous riparian environments, and variation in seed sources and morphologies currently preclude a comprehensive, predictive understanding of dispersal.

12.5.5 Influence of Vegetation on Geomorphology

In contrast to the study of physical factors on vegetation, which have been conducted primarily by ecologists and biogeographers, research on the influence of vegetation on fluvial geomorphic processes and landforms has been conducted primarily in the fields of geomorphology (typically from physical geography and earth sciences) and civil and environmental engineering (Darby, 1999; Corenblit et al., 2007; Sandercock et al., 2007). A long history of research exists on vegetation influence over the hydrological cycle (e.g., Tabacchi et al., 2000), on ecophysiological fluxes (e.g., Roberts, 2000), and on water quality (e.g., Dosskey et al., 2010). However, until relatively recently, quantitative research on vegetation controls over hydrogeomorphic processes was generally descriptive (e.g., Nanson and Beach, 1977), or fairly limited in scope and in the complexity of processes observed (Murray et al., 2008).

During flooding, woody plant stems and canopies add drag to a fluvial system, influencing both hydraulics and sediment dynamics (Nepf, 1999; Lightbody and Nepf, 2006). In addition, vegetation roots increase erosion resistance of banks, and trapping sediment adds cohesion to the substrate (Knighton, 1984). Corridor-wide fluvial characteristics and processes affected by vegetation include velocity, flood stage, flow resistance, and sediment transport (Murray et al., 2008). Local geomorphic influences include bank erosion resistance, bar sedimentation, formation of logjams, and floodplain sedimentation rates (Hickin, 1984).

Efforts to predict the contribution of vegetation to velocity date back to the nineteenth century, when Manning integrated empirical research by Darcy, Weisbach, St. Venant, Ganguillet, Kutter, and others to develop his equation for flow resistance in vegetated channels (Manning, 1891). The roughness coefficient n in the Manning equation represents the collective drag exerted on the flow by surface roughness (including vegetation) and channel sinuosity. Subsequent research has disaggregated this term into the sum of various environmental components, including vegetation (e.g., Cowan, 1956). The widespread use of Manning's equation across a range of hydrological, geomorphological, and engineering applications makes the determination of Manning's n profoundly important. Of the components that contribute to n , vegetation is among the most variable and, hence, critical (Arcement and Schneider, 1989). Furthermore, the changes in resistance that accompany plant growth (or loss) mean that the roughness coefficient may be quite variable through time (Chow, 1959).

Darby (1999) modified existing hydraulic models to predict stage-discharge curves for channels with nonuniform cross sections, sand and gravel-bed materials, and flexible or nonflexible riparian vegetation. Because roughness depends on vegetation stature, density, and flexibility, empirical

estimates of n vary based on vegetation community type and time of year, and it is important to note that this method of quantifying vegetation effects is not mechanistic, nor does it take into account interactions between vegetation drag and hydrodynamic forces (Corenblit et al., 2007).

More recently, researchers have begun to quantify the effects of vegetation on flow velocities, both as one-way processes (involving rigid stems) and interactive ones (involving flexible vegetation). Experimental and theoretical work involving rigid, nonsubmerged stems approximate the effects of woody plants on overbank floods, and show that the diameter, density, and clustering of stems affect both flow velocity and stage. Stone and Shen (2002) conducted flume experiments with cylinders to represent rigid plant stems of various sizes and densities. They showed that flow resistance varies with density, length, and diameter of stems, as well as flow depth, and developed physically based formulas for resulting flow resistance and velocity. Nepf (1999) extended the work on rigid vegetation to emergent stems with feedbacks to vegetative drag and flow turbulence, and developed a model to describe the drag, turbulence, and diffusion for flow through emergent vegetation with varying properties of stem density.

The role of large woody debris (LWD) in the initiation and evolution of geomorphic landforms, first described by Keller and Swanson (1979), has received substantial attention over the last two decades (e.g., Bilby and Ward, 1991; Fetherston et al., 1995; Abbe and Montgomery, 1996; Gurnell et al., 2002; Jeffries et al., 2003; Lassetre et al., 2008; Opperman et al., 2008). Woody debris loading and transport have been correlated with in-channel sediment storage (e.g., Bilby and Ward, 1991), pool spacing (e.g., Montgomery et al., 1995), channel island formation (e.g., Gurnell et al., 2002), floodplain accretion (e.g., Jeffries et al., 2003), and increased channel complexity (e.g., Pettit et al., 2006; Abbe and Montgomery, 1996), among other features. Abbe and Montgomery (1996) documented the initiation of channel-altering jams when key-member logs become lodged in the channel. Over time, these jams collect more LWD and sediment, and form stable structures over 10^1 – 10^2 years that control local channel hydraulics and ultimately assist in riparian forest development. Jeffries et al. (2003) documented that LWD on floodplains increased the rate and the variability of overbank flooding and deposition depths.

LWD interacts with sediment to exert strong effects on alluvial channel morphology, particularly where longitudinal slopes are gentle enough to trap bedload behind logjams. In a study of LWD effects on channel habitat in the Pacific Northwest (US), Montgomery et al. (1995) found that pool spacing depended on LWD loading and channel type, slope, and width. Mean pool spacing in channels with gentle slopes decreased 13-fold with increased LWD loading, whereas pool spacing in steeper channels was not affected. From their study of sediment processes on the Tagliamento River (Italy), Gurnell et al. (2001) developed a conceptual model of island development that integrates interactions between LWD and vegetation, geomorphic features, sediment texture, and hydrological regime. Depositional and erosional processes resulted in different island types and floodplain developmental stages.

The potential for LWD to resprout or for live trees to form logjams in stream channels is another mechanism by which vegetation affects geomorphic processes, often with longer-term effects than for dead wood (Opperman et al., 2008). Following a 100-year flood on the Sabie River in South Africa, Pettit et al. (2006) found that patterns of LWD accumulation were dominated by characteristics of the trapping sites, especially trees that fell but remained rooted in place and resprouted (36% of piles surveyed). These resprouted piles supported tree seedlings (28% of piles) and created heterogeneous topography in the main channel and floodplain. Opperman and Merenlender (2007) found that living trees in Northern California streams represented a major portion of the functional in-stream large wood, was 28% more persistent than LWD, and was likely more stable than dead wood of similar size. They concluded that live wood may have a disproportionate influence on channel morphology, particularly in riparian ecosystems lacking many large diameter trees.

Bank cohesion is another important geomorphic characteristic that is at least in part a function of vegetation attributes, including erosion resistance conferred by roots and increased cohesion from fine sediment deposition induced by plant hydraulic roughness (Knighton, 1984; Murray et al., 2008). In an early example, Clifton (1989) showed that morphology of mountain streams varied with vegetation structure, in addition to physiography and land use. Abernathy and Rutherford (1998) developed a classification scheme for assessing the role of vegetation in stream bank erosion at different points throughout a catchment. Their experimental work focused on the enhancement of bank strength by reducing pore-water pressures and by directly reinforcing bank material by plant roots (Abernathy and Rutherford, 2001). Experimental work by Simon and Collison (2002) quantified bank strength effects on constituent hydrologic and mechanical processes, including soil moisture modification and root reinforcement, as well as the potentially destabilizing influence of vegetation weight, and tested their effects on the probability of bank failure. Tree and grass roots exerted species-specific increases on soil strength, and mechanical effects of plant cover increased stability by 32–71%. Martin and Church (2000) found that the addition of roots to riverbanks improved stability even under worst-case hydrological conditions, and was apparent over a range of bank geometries, with the best protection offered by trees closest to the potential bank failure locations. Much of the work on root reinforcement has been based on models derived from materials science; however, Pollen and Simon (2005) noted that the results derived can vary widely depending on the sophistication of the models used.

At a landscape scale, increased bank cohesion due to belowground vegetation effects is instrumental in controlling river meander rates (Micheli et al., 2004) and frequency of channel cutoffs (Micheli and Larsen, 2011). Hupp (1992) cited the combined impact of stabilization by roots and sedimentation due to the flow resistance from plant stems in recovery and meander initiation along formerly channelized streams. Graf (1978) found that following the introduction of tamarisk to upper reaches of the Colorado and Green Rivers, the combination of bank stabilization and overbank sedimentation led to the development of stable islands and dramatic channel

narrowing. He suggested that within 25 years after the species' introduction, it had driven the system into a new equilibrium condition. Numerous subsequent studies have also shown vegetation colonization of former active channel bars and banks to reduce channel planform width and width/depth ratios, as well as change channel cross-sectional geometry (e.g., Friedman et al., 1996a, 1996b; Johnson, 1994, 1998; Trush et al., 2000; Liébault and Piégay, 2001). Although these developments can be induced by natural processes such as temporary increases in precipitation (e.g., Martin and Johnson, 1987) and recovery from large floods (Liébault and Piégay, 2002), many are the result of dams and other human modifications to physical processes that reduce sediment supply (e.g., Kondolf et al., 2007) or magnitude and frequency of high-flow events (e.g., Johnson, 1998; Michalková et al., 2011).

Recent experimental work highlights the importance of vegetation in transforming braided streams into single-thread channels in coupled stream–floodplain systems (Tal and Paola, 2007, 2010; Murray et al., 2008; Braudrick et al., 2009). Gran and Paola (2001) and Tal and Paola (2007) have shown in flume settings that floodplains supporting vegetation (alfalfa sprouts) produced more single-thread river planforms than braided ones, and that the resulting channels were narrower, deeper, and less mobile. Furthermore, the experimental addition of vegetation to previously braided channels has induced self-organization of the channel network, including formation of a single thread, control of bend and bar migration rates, and formation of channel cutoffs (Braudrick et al., 2009; Tal and Paola, 2010).

However, the magnitude of vegetation effects is highly context dependent. Labbe et al. (2011) found that riparian vegetation was not a significant control on channel cross-section form on the Tualatin River, Oregon. Sandercock et al. (2007) noted that in contrast to humid climates, semi-arid and arid climate riparian zones are characterized by locally patchy vegetation and channel morphology influenced by extreme flood events. Therefore, the role of vegetation in bank stability in these environments is expected to be lower overall than in humid climates, and the degree of influence highly dependent on local distribution, composition, and density (Sandercock et al., 2007).

12.5.6 Feedbacks between Vegetation and Hydrogeomorphology

If, as discussed above, hydrogeomorphic factors influence vegetation, and vegetation influences hydrogeomorphic processes, then it follows that there are likely to be feedbacks between the two. Indeed, not only are there interactions between vegetation and the hydrogeomorphic mechanisms described in Sections 12.5.4.1–12.5.4.6, but many of those mechanisms also interact with each other. A diagram of these interactions serves both to summarize many of the relationships described in this chapter and to illustrate the complexities of riparian biogeomorphic feedbacks (Figure 1). The relationships shown may be briefly described as follows:

- a. Flood energy affects riparian vegetation directly, through mechanical damage or scour, as discussed in Section 12.5.4.1.

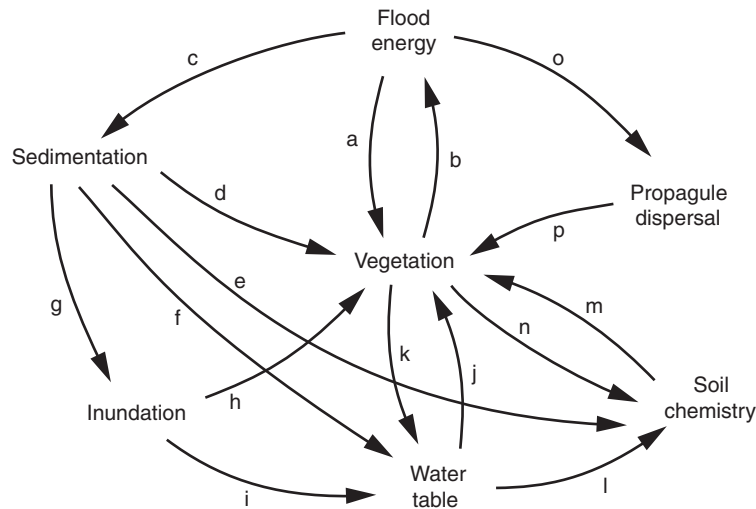


Figure 1 The network of potential biogeomorphic interactions and feedbacks that may link riparian vegetation and fluvial geomorphology. Influences represented by the arrows are discussed in the text.

- b. Riparian vegetation affects flood energy through hydraulic roughness (Section 12.5.5).
- c. Flood energy affects sedimentation, controlling the size distribution of mobilized sediment, its sorting, and the spatio-temporal patterns of deposition.
- d. Sedimentation affects riparian vegetation directly, through burial of existing plants and through creation of alluvial surfaces for colonization (Section 12.5.4.2).
- e. Sedimentation affects soil chemistry, through the composition of the alluvium deposited and particle size controls on nutrient dynamics and mineralization rate.
- f. Sedimentation affects water-table depth through the height of depositional landforms and the texture of the deposits (i.e., capillarity).
- g. Sedimentation affects inundation through the height of depositional landforms.
- h. Inundation affects riparian vegetation directly, through anoxia (Section 12.5.4.3).
- i. Inundation affects water-table depth and dynamics through contributions to groundwater.
- j. Water-table depth and dynamics affect riparian vegetation directly, through provision of water or through limiting the aerated rooting zone (Section 12.5.4.4).
- k. Riparian vegetation affects the water table through transpiration.
- l. The water table affects soil chemistry through its impact on redox potential.
- m. Soil chemistry affects riparian vegetation directly, by serving as the primary control of nutrient availability (Section 12.5.4.5).
- n. Vegetation affects soil chemistry through plant litter and mineralization rate in the root zone.
- o. Flood energy provides transport for propagules (Section 12.5.4.6).
- p. Dispersal of propagules directly affects vegetation, allowing its establishment at new sites.

It is important to note that some of the most important relationships are actually indirect. For example, riparian

vegetation, through its impact on flood energy (b) has a very strong influence on sedimentation (c). Overall, **Figure 1** serves to illustrate the centrality of feedbacks in the riparian zone. Some or all of these feedbacks have been noted in earlier reviews, including those by [Parker and Bendix \(1996\)](#), [Bendix and Hupp \(2000\)](#), [Hupp and Bornette \(2003\)](#), [Steiger et al. \(2005\)](#), and [Corenblit et al. \(2007\)](#). A limited number of empirical and review studies have specifically addressed the issue of feedbacks. Although these feedbacks were addressed in a few early studies (see below), most such work has been published since the mid-1990's. [Murray et al. \(2008\)](#) referred to the feedbacks between organisms, physical processes, and morphology as 'biomorphodynamics.' They attributed the increased attention to such interactions in a variety of environments (not limited to fluvial/riparian settings) to the increased popularity of interdisciplinary research, the challenges of realistically analyzing responses to environmental change, and to the advances in modeling capabilities at a variety of scales.

In his argument for application of complexity theory to biogeomorphology, [Stallins \(2006\)](#) argued for a focus on feedbacks, stating a need to "move beyond listbound descriptions of unidirectional interactions of geomorphic and ecological components." He emphasized the importance of recursivity, whereby the interactions between floods and vegetation constrain future development of the system, so that it becomes self-organizing. This notion is inherent in the view of [Corenblit et al. \(2009\)](#) who argued that the self-organizing properties of riparian systems reflect both contemporary feedbacks that allow for niche construction by plants and longer-term natural selection as plants evolve for specific roles within the system.

Empirical studies of feedbacks have focused primarily on pathways whereby riparian vegetation promotes sedimentation through increased hydraulic roughness by live, rooted stems, or through the role of LWD; in turn, the increased sedimentation affects the vegetation able to grow at a site. In some instances, these feedbacks become part of the mechanism whereby succession occurs.

In an early example of feedbacks centered on roughness, [Nanson and Beach \(1977\)](#) related overbank sedimentation

and forest succession on the Beatton River floodplain in British Columbia. They found that dense balsam poplar colonizing new alluvial surfaces promoted increased sedimentation, for which the poplar had a high tolerance. Eventually, however, aggradation reduced sedimentation sufficiently for shade-tolerant white spruce to replace the intolerant poplar. As the spruce matured, sedimentation declined even further because the lower-stem density of the mature spruce forest reduced hydraulic roughness. On point bars of Dry Creek in California, [McBride and Strahan \(1984b\)](#) noted that colonization of gravel substrate by willows and cottonwoods resulted in deposition of finer sediments. The finer substrate allowed for subsequent establishment of alder, which eventually formed a canopy that ultimately inhibited the shade-intolerant willows and cottonwoods. Along rivers in the Ozarks, [McKenney et al. \(1995\)](#) described models whereby channel migration was driven by the age of the vegetation on gravel bars. Young, dense stands or patches of riparian vegetation created high roughness and favored deposition and stabilization of the surface. As the vegetation aged and self-thinning led to reduced stem densities, roughness decreased, and the surfaces actually became less geomorphically stable.

[Petit and Naiman \(2006\)](#) provided an instance in which LWD is central to riparian feedback. A large flood on the Sabie River (geomorphic process) not only devastated the existing riparian vegetation, but also interacted with woody debris (vegetation influence) to create numerous LWD jams. Those LWD accumulations, in turn, mediated the geomorphic mechanisms of flood energy, water table, and soil chemistry by providing seedling germination sites that were protected from floods and had high moisture and nutrient availability.

Certain feedback scenarios may be constrained to specific biogeographic locations. In Washington's Olympic Mountains, [Latterell et al. \(2006\)](#) described a dynamic patch mosaic of fluvial landforms, including a variety of channels, bars, floodplains, and terraces, each with a characteristic vegetation assemblage. The distribution of these landform/patches was controlled by lateral channel migration, but channel behavior is influenced by LWD accumulations. Woody debris accumulations in turn require key-member logs, contributed by erosion of mature terraces (classified based on stand age and composition), along with smaller woody debris from other landforms. They cautioned, however, that their model of patch structure and dynamics would only be applicable in comparable environments, and should not be applied to dissimilar settings, such as those where vegetation distribution is constrained by water availability or where trees do not reach sufficient size for woody debris to play an important role. In the Transverse Ranges of California, [Bendix and Cowell \(2010\)](#) found that the distribution of flood depth across valley floors when integrated with species composition allowed for the determination of the distribution and rate at which burned snags fell after wildfire. This, in turn, governs the supply and distribution of woody debris, with its attendant geomorphic and ecological roles. The exogenous role of fire as a catalyst for this set of feedbacks limits the applicability of these findings to environments where riparian forests do in fact burn ([Dwire and Kauffman, 2003](#)).

Attempts to quantitatively model riparian biogeomorphic feedbacks are relatively new and typically require complex,

often recursive model structures. An analog is provided by efforts in the field of hillslope modeling, in which representations of vegetation growth are coupled with surface runoff and landscape evolution models (e.g., channel-hillslope integrated landscape development (CHILD) model, [Tucker and Bras, 1999](#); [Tucker et al., 2001](#); [Istanbulluoglu and Bras, 2005](#)). An early numerical modeling effort for river channels, about which much less work has been conducted than for hillslopes, consists of work by Murray and Paola (1994, 1997), which explored channel braiding through simple numerical feedbacks between bedload transport and channels with noncohesive banks. Over a series of modeling exercises, they found that braiding occurred under conditions of sparse or slowly growing vegetation, and high sediment fluxes were caused by high discharge and/or steep regional slopes. In their studies, the channels reorganized on time frames shorter than the riparian plants' life spans.

An alternative feedback quantification approach is provided by [Perucca et al. \(2007\)](#), who coupled a fluid dynamic model of meandering rivers with a process-based model of riparian biomass dynamics. In this approach, riparian vegetation influences channel morphology via a relationship between biomass, density, and bank erodibility. Their numerical results show a strong effect of vegetation growth on meander evolution and, like Murray and Paola (1994, 1997), they emphasized the sensitivity of their results to the relative temporal scales of plant growth versus morphodynamic processes.

12.5.7 Patterns in Published Literature

The forgoing review illustrates that a large volume of research has brought increasingly complex perspectives on ecogeomorphic interactions to the study of fluvial/riparian environments. That large volume suggests that a systematic analysis of published work might reveal underlying patterns in what has been learned to date. Accordingly, we undertook an analysis of the past 20 years of published literature relating riparian vegetation to hydrogeomorphic processes and/or specific fluvial landforms. This content analysis was designed to quantify the incidence of published content according to a scheme that was systematic and objective. Our particular interest was to discern whether certain relationships tend to be revealed in particular environments, or when studied at particular spatial scales. [Parker and Bendix \(1996\)](#) called for research examining the extent to which vegetation-landform relationships vary geographically, suggesting that some might be generalized for a variety of environments while others might be unique to certain regions. This analysis of the literature offers one approach to that challenge.

There is a danger in such a study of detecting the patterns of researchers' interests, rather than actual variation in natural processes. Nonetheless, the studies being published presumably have some relationship to the predominant processes in the locales where they are conducted, so that patterns in the types of interaction in the literature should offer some clues as to the relative import of those interactions in different locations and at different scales.

12.5.7.1 The Sample and Coding

As an initial step, we searched the Scopus and Web of Science databases for all publications from 1990 through 2009 with the term 'riparian vegetation' in the title, abstract, or keywords. This search yielded >3700 references. We examined the abstracts of these papers and retained those that met the following criteria: (1) the paper included substantive analysis of hydrogeomorphic interaction with the riparian vegetation; (2) the study was data based, rather than a review or solely theoretical discussion; and (3) the data were collected in the field, rather than laboratory, because the latter would not be inherently reflective of geographic or scalar variation.

For each of the papers that passed this filter, we recorded the year of publication, the journal (or conference proceeding), the continent and country on which the data were collected, the study region's ecological biome, the scale of observation of the study, the causal direction of the environmental relationships studied, and the causal mechanism found (for hydrogeomorphic influence only; see below). The first four of these are rather straightforward, although country was occasionally complicated by cross-boundary studies. For biome, we classified each study as being in one of the 14 biomes identified by the Millennium Ecosystem Assessment (2005; Figure 2).

Coding of biome for each study was based on the description provided in the paper's text. If such a description was lacking, we located the study site on Figure 1 to determine the appropriate biome. Scale was coded as 'site' if the data had been collected at a single cross section involving <500 m length of channel, as 'reach' if data were collected from a greater length of the river, up to 1 km, and 'watershed' if the data were from multiple sites or from >1 km length of the river. Causal direction reflected the emphasis of the study: if it focused on hydrological and geomorphic influences on vegetation, it was coded as 'geomorphic'; if it dealt primarily with the impact of vegetation on geomorphology and/or hydrology, it was coded 'vegetation'; and if the primary emphasis was on feedbacks between the two, it was recorded as 'feedback'.

Because so much research has been directed at disentangling the specific mechanisms of hydrogeomorphic influence on riparian vegetation, we further coded those studies for which the causal direction was geomorphic, focusing on the six categories of causal mechanisms described above (Table 1). In each instance, we coded for the primary influence identified in the paper. If the study did not find that a single influence predominated, but rather that multiple factors were exerting comparable degrees of influence, we coded it as 'multiple'. We tried to be parsimonious in the use of this classification, and although many papers mentioned potential

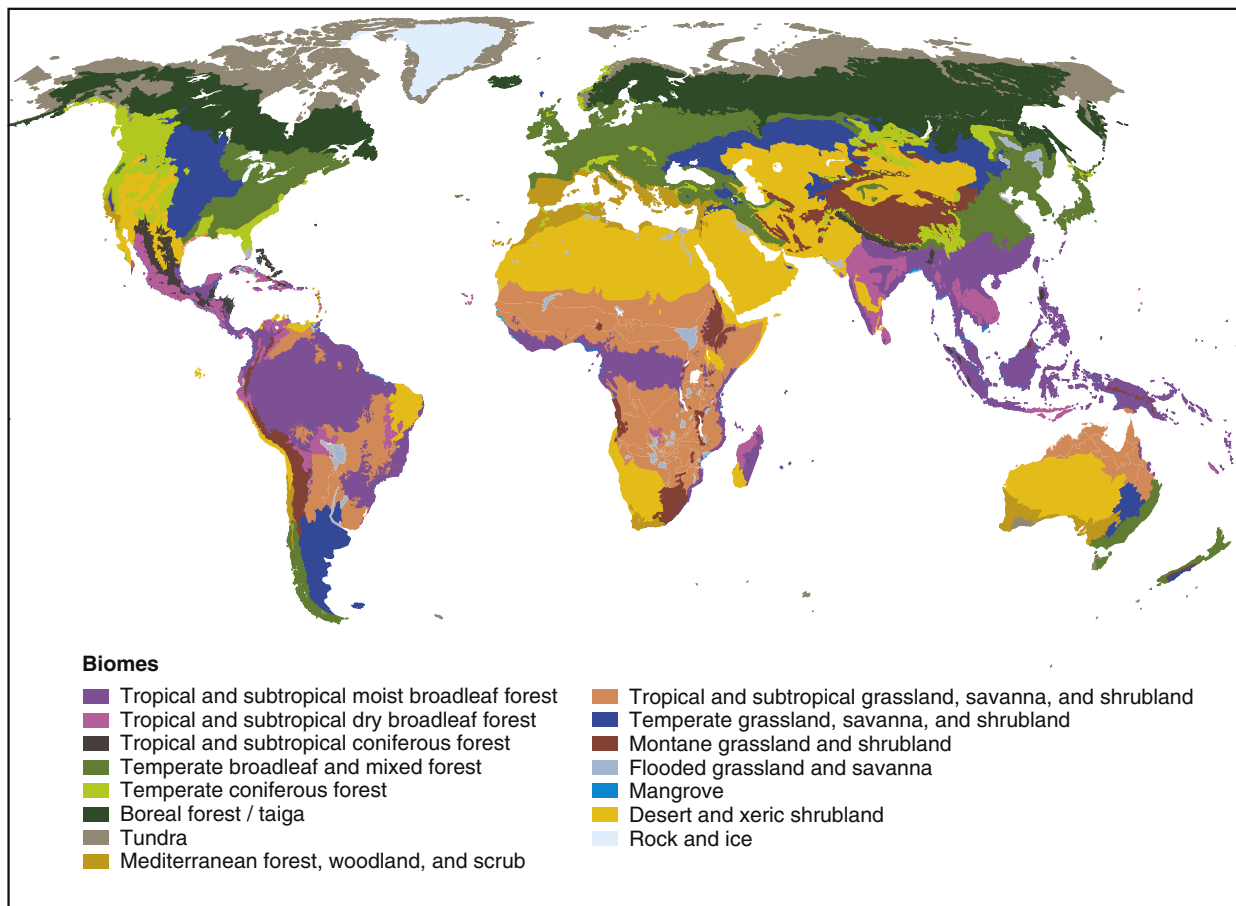


Figure 2 Biome boundaries used in the study. Based on the Millennium Ecosystem Assessment, 2005. Ecosystems and Human Well-Being: Biodiversity Synthesis. World Resources Institute, Washington, DC, 86 pp.

covariables in passing, we did not code a study as multiple if its focus seemed clearly to be on one mechanism.

12.5.7.2 General Characteristics of the Sampled Literature

There were 274 studies that met our criteria for inclusion in the sample. The papers appeared in 101 venues, but 12

journals with multiple papers accounted for almost half (136) of the total (Table 2). In general, the number of papers on the topic has increased (Figure 3), albeit with some fluctuation. Over the past 5 years, more than 20 papers per year have dealt with riparian vegetation–landform relationships. The majority of the papers (189) examined geomorphic influences, with 62 being coded as vegetation, and just 23

Table 1 Causal mechanisms coded for studies identified with the primary causal direction of geomorphic influence over vegetation

Causal mechanism code	Criteria for classification
Energy	Hydraulic energy of floodwaters, whether destroying vegetation or eroding its substrate (Section 12.5.4.1)
Sedimentation	Sediment deposition, whether by its impact on existing vegetation or by creation of new substrate (Section 12.5.4.2)
Inundation	Extended inundation by floodwaters (Section 12.5.4.3)
Water table	Depth to the water table under the landform(s) on which the vegetation was growing, and variation in water-table depth. (Section 12.5.4.4)
Soil chemistry	Soil chemistry of the landform(s) on which the vegetation was growing (Section 12.5.4.5)
Dispersal	Transport of plant propagules by floodwaters (Section 12.5.4.6)
Multiple	Multiple factors were exerting comparable degrees of influence

Table 2 Journals in which five or more of the sampled papers were published, by number and percent of the total sample, with number within each causal direction

Journal	Number (%) of papers	Geomorphic	Vegetation	Feedback
<i>River Research and Applications (and Regulated rivers)</i>	31 (11.3)	28	3	2
<i>Geomorphology</i>	19 (6.9)	3	10	6
<i>Earth Surface Processes and Landforms</i>	17 (6.2)	5	10	2
<i>Wetlands</i>	14 (5.2)	14	0	0
<i>Ecological Applications</i>	10 (3.6)	8	1	1
<i>Plant Ecology</i>	8 (2.9)	8	0	0
<i>Forest Ecology and Management</i>	7 (2.6)	7	0	0
<i>Journal of the American Water Resources Association</i>	7 (2.6)	2	3	2
<i>Journal of Vegetation Science</i>	7 (2.6)	7	0	0
<i>Physical Geography</i>	6 (2.2)	4	1	1
<i>Annals of the Association of American Geographers</i>	5 (1.8)	5	0	0
<i>Hydrological Processes</i>	5 (1.8)	1	3	1

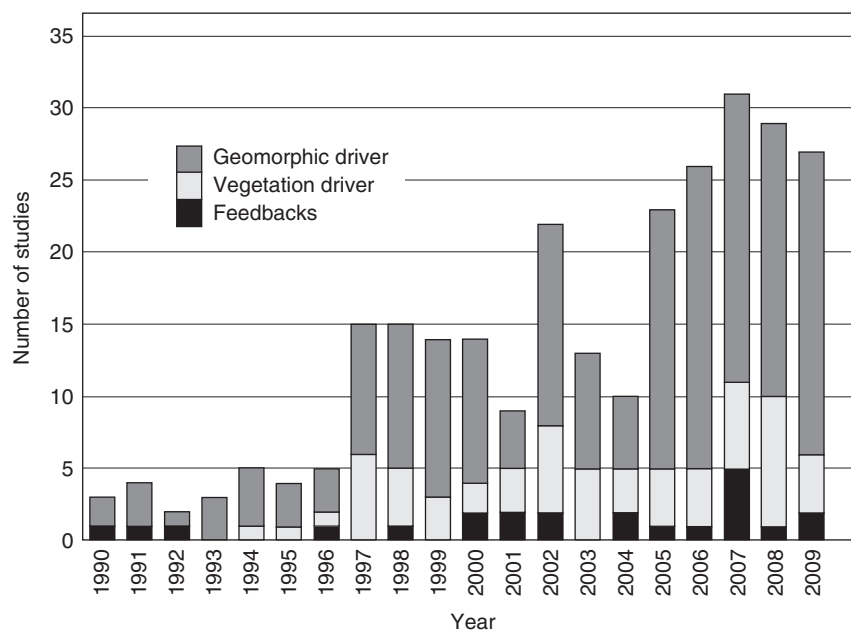


Figure 3 Year of publication of the studies included in the sample, and the causal direction examined.

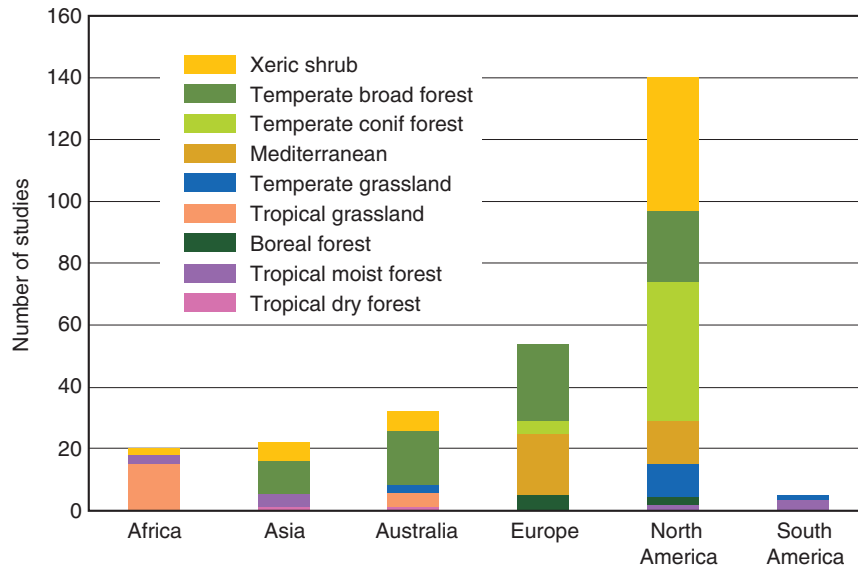


Figure 4 Number of studies conducted in each biome, on each continent.

feedback. Indeed, the interest in vegetation as driver is relatively recent, with few papers appearing before 1997. The disparity in the causal direction studied is reflected in [Table 2](#), as only four of the journals with five or more papers in the data set had a majority of their papers on vegetation's influence: *Geomorphology*, *Earth Surface Processes and Landforms*, *Journal of the American Water Resources Association*, and *Hydrological Processes*. It is logical that these journals, with their emphasis on landforms and hydrology, tended to publish studies in which the influences on those topics are examined. However, the extent to which the rest of the literature emphasizes vegetation as the dependent variable is rather striking. The smaller number of studies addressing feedbacks may well have a logistical explanation. Although most scientists working in riparian environments would probably acknowledge the importance of feedbacks, to actually study them in the field poses the challenge of incorporating two field studies (vegetation driver and geomorphic driver) into one, in order to discern their interactions. In addition, feedbacks take time to observe in the field, as there must be time for an initial process to occur, and then for a subsequent process to occur in response.

There was also a distinct geographic bias to this literature. The great majority of the studies was carried out in North America, with a secondary peak in Europe ([Figure 4](#)). Australia, Asia, and Africa were the setting for substantially fewer studies, with South America accounting for the least of all. This pattern presumably reflects the fact that the majority of the scholars publishing the studies are based at institutions in North America, Europe and, to a lesser extent, Australia. In turn, with more than 80% of the studies being conducted in Europe (primarily Western Europe), North America, and Australia, it is unsurprising that there is also an imbalance in the biomes studied. Most study areas were located in temperate broadleaf and mixed forest (fairly widely distributed), desert and xeric shrubland (mostly in North America), temperate coniferous forest (mostly in North America), and Mediterranean forest, woodland and scrub (mostly in Europe

and western North America). The relative scarcity of papers in the data set from South America, Africa, and Asia contributes to the underrepresentation of tropical biomes in our survey.

Across all of the biomes, the studies tended toward larger scales of observation, with watershed scale being the most common and site scale being the least common ([Figure 5](#)). Overall, flood energy was the most common mechanism (28%), followed by water table and multiple (both 21%), and sedimentation (12%). These were also the mechanisms that were found to operate in most biomes. There were, however, distinct differences in the spatial distribution of these mechanisms, as discussed below.

12.5.7.3 Differences among Biomes

The research within most of the biomes reflects the general tendency of the literature to focus on the geomorphic causal direction ([Table 3](#)). The two tropical and subtropical forest biomes are exceptions to this generalization, although with just 10 studies between them, they can hardly be said to constitute a regional research trend. Our discussion, then, deals primarily with the hydrogeomorphic influences on vegetation.

The number of studies within each biome that focused on each mechanism of hydrogeomorphic influence is shown in [Figure 6](#). A striking, and intuitive, feature of this graph is the prominence of depth to water table in desert and xeric shrubland (44% of the studies in the biome). Where water is the overriding limiting factor for vegetation, the proximity of subsurface water becomes all the more important. The flashy hydrology that characterizes many desert environments presumably accounts for the prominence of flood energy as a mechanism in this biome, as high-energy floods are to be expected. Conversely, flood duration in most deserts tends to be short, so that the 11% coded as inundation are more puzzling. Some authors did simply discuss inundation as an important

Table 3 Number of papers by study area biome and causal direction

<i>Biome</i>	<i>Number of papers</i>	<i>Geomorphic</i>	<i>Vegetation</i>	<i>Feedback</i>
Temperate broadleaf and mixed forest	77	44	28	5
Desert and xeric shrubland	58	45	6	7
Temperate coniferous forest	49	38	9	2
Mediterranean forest, woodland, and scrub	38	28	5	5
Tropical and sub-tropical grassland, savanna, and shrubland	21	15	4	2
Temperate grassland, savanna, and shrubland	14	11	2	1
Tropical moist forest	8	1	7	0
Boreal forest	7	6	1	0
Tropical and sub-tropical dry broadleaf forest	2	1	0	1

variable without specifying whether the impact of the inundation was through the submergence or through mechanical damage sustained during inundation, and this vagueness may account for the high numbers of inundation references.

Mediterranean forest, woodland, and scrub have much in common with desert and xeric shrubland, with the pronounced dry season making water a critical limiting resource, and characteristically with similarly flashy hydrologic regimes. In Mediterranean environments, flood energy predominated as in xeric regions, but water table was much less prominent. Many of the studies coded as multiple in this biome did include water table as one of the variables. Nonetheless, given the prominence of obligate riparian species in Mediterranean biomes, presumably present only due to the presence of a (relatively) shallow water table, it is surprising that this variable did not emerge in more studies. Sedimentation was important here, reflecting the high sediment load and sediment mobility typical of many Mediterranean streams. Sedimentation may also be important because of the impact of sediment texture on capillarity, which mediates soil moisture availability. Both the mobility of sediment and its importance for water availability are characteristic of streams in most dry environments, so that the less frequent role reported for sedimentation in desert studies is rather anomalous.

The temperate and the tropical/subtropical grassland, savanna, and shrubland had much in common. Each had flood energy as the most prominent mechanism, with water table and sedimentation also being important. Water table was, however, distinctly more important in the tropical and subtropical grasslands than those in temperate zones. This likely reflects the greater heat stress and consequent water demand in the lower-latitude biome than in temperate areas. As in other dry environments, high sediment mobility and the capillary influence of substrate texture are reflected in the importance of sedimentation.

The temperate broadleaf and mixed forest has the most heterogeneous mix of mechanisms examined. This reflects two factors acting in combination. One is simply that with so many studies having been conducted in the biome, there is an increased likelihood that most conceivable mechanisms will have been examined. It is a type of environment in which there is no overriding stressor (such as drought), allowing for a range of individual mechanisms to prevail, depending on the specific conditions in a given study area. Much the same is true of the temperate coniferous forest. In each biome, flood energy is the most notable mechanism, but is joined by water

table, sedimentation, dispersal, and inundation. The temperate broadleaf forest and the temperate grassland are the only biomes in which soil chemistry appears as an influence.

The paucity of studies from tropical forests makes it difficult to infer much about these biomes. It is perhaps unsurprising that water-table depth was important to riparian vegetation in tropical and subtropical dry broadleaf forest, but with only one study conducted there is not enough to establish a pattern. Again, with only one study from a low-order mountain stream in tropical and subtropical moist broadleaf forest, citing multiple mechanisms, it is similarly not informative.

Finally, the boreal forest/taiga, although also indicating a role for flood energy, is notable for the prominence of dispersal. In this case, the pattern is clearly a result of the sample characteristics, rather than an anomalously important role for hydrochory in boreal forests. The sample for this biome was small (**Figure 6**), and happened to be dominated by a group of scholars in Sweden who published several papers on dispersal during the time period covered by our study (e.g., [Andersson et al., 2000](#)). Indeed, this example offers a useful reminder that the interests of individual researchers have a distinct potential to skew results for any biome (or scale) in which the number of papers is limited.

12.5.7.4 Scale-Related Differences

The contrasts in mechanisms predominating in studies with different scales of observation (**Figure 7**) are less dramatic than among the varied biomes, but some differences are apparent. In keeping with their overall importance, flood energy and water table are important across all scales. But both are more prominent in studies at the site scale (<0.5 km of stream bank length) than at reach (0.5–1 km) or watershed (>1 km) scales. This is logical, as both have greater potential variance at a given cross-section than along a gradient up or downstream. Along a cross-section, they will vary from a presumed maximum energy and minimum distance to water table at or near the thalweg to zero energy and maximal water-table depth at some distance from the channel. This may also be why inundation is so much more prominent at the site scale. It is similarly logical that dispersal is irrelevant at the individual site scale, where there is no space for transport to occur, but increases in prominence with increasing scale. It is less clear why no studies at the site scale focused on multiple mechanisms.

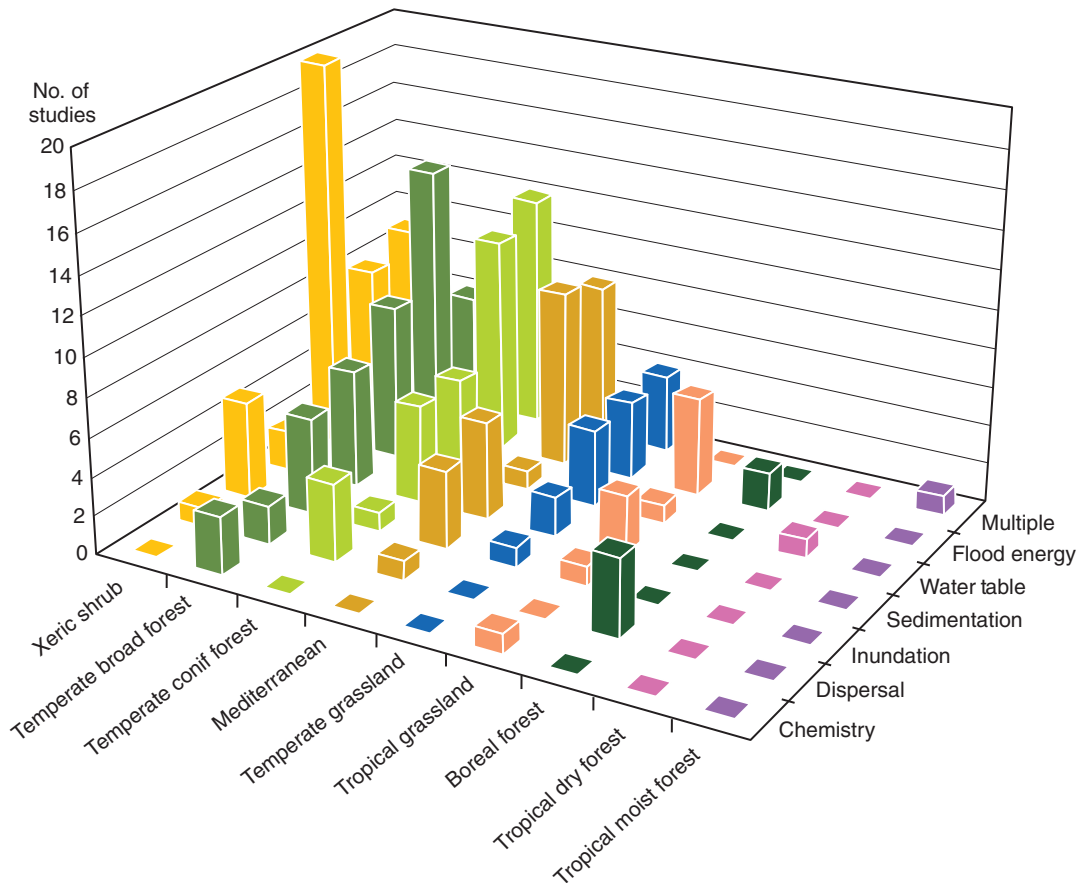


Figure 6 Mechanisms of hydrogeomorphic influence in studies within each biome.

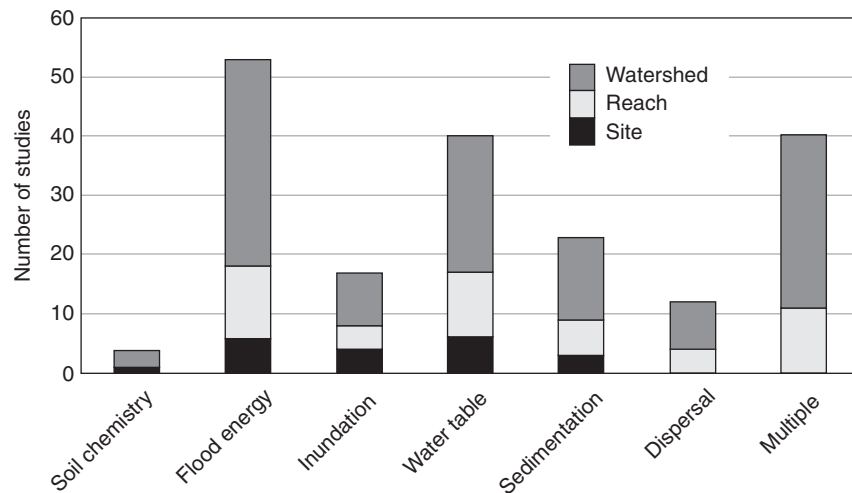


Figure 7 Number of studies emphasizing each mechanism at each scale.

12.5.7.5 Hydrogeomorphic Mechanisms in the Context of Scale and Biogeography

The broad pattern of the mechanisms acting at varied scales in different biomes can be seen in a plot of the modal mechanism for each combination of scale and biome (Figure 8). This plot serves to reinforce the primacy of flood energy as the most

common hydrogeomorphic driver affecting riparian vegetation. However, it also reveals exceptions that indicate the importance of both the setting and the scale of observation in determining which drivers will predominate. In desert and xeric shrub, although flood energy is important (Figure 6), the overriding importance of distance to the water table is present across all scales.

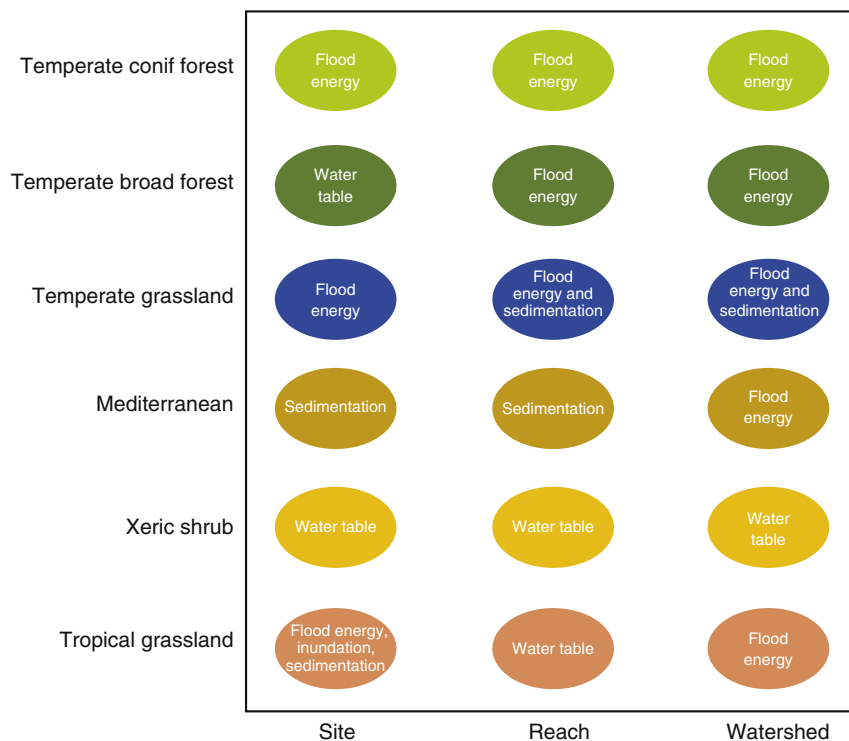


Figure 8 Modal mechanisms cited for each combination of scale and biome. Multiple mechanisms reflect scale–biome combinations for which equal numbers of studies cited the mechanisms shown. Biomes in which fewer than 10 studies had been conducted are omitted from the figure.

In other biomes, the primary mechanism shifts with the scale of the study. Flood energy appears most consistently at the watershed scale. Clearly, the downstream changes in valley morphology that can be found in many river systems across a range of environments allow for sufficient variance in flood energy for marked patterns of vegetation response to emerge (Hupp, 1982; Bendix, 1997). At the site scale, however, water table assumed the greatest importance for temperate broadleaf and mixed forest. In this humid environment, a high water table may prove to be a limiting factor, rather than a resource. Thus, when viewed in detail across a given site, species with specialized adaptations occur where the water table is highest (e.g., Nakamura et al., 2002; Sharitz and Mitsch, 1993). Sedimentation is the principal factor at the watershed scale only for temperate grassland, but at decreasing scales appears elsewhere, and is the predominant driver for the Mediterranean environment at both reach and site scale. The deposition of sediment, whether burying plants (e.g., Wang et al., 1994) or creating substrate (e.g., Greco et al., 2007), is in many instances a localized phenomenon, and its variance is likely to be more evident at the site or reach scale than across a watershed.

12.5.8 Patterns and Perceptions Revealed in the Literature

Our review of the past 20 years of research shows that there has been a steady and increasing volume of research on riparian biogeomorphic relationships. Most of the studies in our sample examined hydrogeomorphic influences on vegetation, despite

the longstanding realization that vegetation also affects fluvial processes and landforms. This disparity is in part an artifact of our sampling strategy: we included only field studies, and much of the research on vegetation as a driver has been experimental, typically using flumes. Furthermore, the use of riparian vegetation as our search term may have served to exclude some of the studies examining the impact of plants on fluvial processes. Whereas the modifier riparian is logical for a paper with an ecological or biogeographic focus, it becomes redundant as a description of vegetation in a paper on fluvial geomorphology, for which all vegetation is likely to be riparian. The scarcity of papers in the sample that address feedback is probably more representative of the overall literature, as this is a topic that received little attention until recently. The recent publication of major theoretical articles specifically advocating recognition and study of feedbacks (e.g., Stallins, 2006; Corenblit et al., 2009) may well accelerate the increase in such work that was noted by Murray et al. (2008).

The overall body of literature is dominated by empirical studies detailing the impacts of flood energy and water-table distance on riparian vegetation. But both their relative importance and the importance of other mechanisms do vary with both the biome in which studies are set and the scale of observation. This variance confirms Parker and Bendix's (1996) speculation that there is a geography of biogeomorphic interactions. Indeed, the nature of our sample may well obscure that geography. Many of the world's biomes (Figure 2) are either underrepresented or entirely absent from our sample.

The underrepresentation of key biomes is one of several reasons for caution in interpreting our findings. Our emphasis

on identifying a single key factor in as many studies as possible inevitably required simplification of what were often complex analyses. Once a key mechanism is identified from a study, the question remains of whether that mechanism was dominant in the environment (or at the scale) in which it was studied, or was simply the mechanism most easily measured or of most interest to the author(s).

Notwithstanding these caveats, we believe that there is much to learn from this survey. Clearly, some spatial patterns do exist in terms of spatial variation and the importance of different types of biogeomorphic interaction. The empty spaces in our data may be the most interesting of all: the biomes that have not been studied, and the types of interactions that have not been studied within certain biomes, point the way for future research.

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