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OPINION

A model of plant strategies in fluvial hydrosystems

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SUMMARY

1. We propose a model of plant strategies in temperate fluvial hydrosystems that considers the hydraulic and geomorphic features that control plant recruitment, establishment and growth in river floodplains.
2. The model describes first how the disturbance gradient and the grain-size of the river bed load affect the relative proportion of erosion and deposition processes, and how the frequency of flood disturbance affects the intensity of such processes.
3. Secondly, the model predicts plant strategies according to direct and indirect effects of floods (disturbances through erosion versus deposition processes, and associated nutrient excess or limitation).
4. The relevance of the model as a prediction tool is discussed. Some proposals are made to validate the model, and traits are proposed that should be considered in future research for improving the predicting value of the model.

Keywords: deposition processes, disturbance, erosion processes, life-history traits, river

Introduction

Organization and dynamics of vegetation in river floodplains have been extensively studied (Müller, 1995; Van Eck *et al.*, 2005). Many studies show that geomorphology in combination with hydrological processes control plant communities in floodplains (Naiman & Décamps, 1997; Bendix & Hupp, 2000; Amoros & Bornette, 2002). Several models of vegetation organization and dynamics have been proposed (Menges & Waller, 1983; Van Coller, Rogers & Heritage, 1997), but only a few deal with the consequences of floods on plant strategies (Amoros & Bornette, 1999; Hupp & Bornette, 2003). Moreover,

they typically apply only to a particular set of rivers, flood conditions or plant communities and are not broadly applicable (Franz & Bazzaz, 1977; Lenssen, Van De Steeg & De Kroon, 2004).

This lack of a general model can be partly explained by contradictions among authors. If we consider, for example, literature on river connectivity (permanent or temporary links between the river and the wetlands of the floodplain, Amoros & Bornette, 2002) and plant communities in riverine wetlands, several authors noticed a decrease in abundance of aquatic vegetation as a result of increasing surface connections between the river and the wetlands, which lead to increasing inputs of suspended matter that increase turbidity (Sparks *et al.*, 1990; Van Den Brink *et al.*, 1993). Conversely, other authors found an increase in plant species richness when flood frequency increases, because of the limitation of competition processes because of scouring flood disturbances (Bornette,

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Amoros & Lamouroux, 1998; Pollock, Naiman & Hanley, 1998; Tabacchi & Planty-Tabacchi, 2005). In another study, the absence of a significant trend was attributed to regulatory processes that decrease flood frequency (Tiegs *et al.*, 2005).

Flood disturbances may scour substrate (Henry, Amoros & Bornette, 1996; Matthaei, Guggelberger & Huber, 2003) or deposit sediment of various size classes (Schwarz, Malanson & Weirich, 1996; Olde Venterink *et al.*, 2006). Consequently, a shifting mosaic of landforms characterizes river systems, and considerable variation in hydrogeomorphic processes can occur across a single fluvial landscape (Ward *et al.*, 2001; Poff, Bledsoe & Cuhaciyan, 2006a). Floods may also create new patches in contrasting habitats (e.g. on point bars versus floodplains). Depending on their erosional or depositional nature, floods induce either plant breakage and uprooting, or plant burial by sediment deposits, and consequently select for plant species tolerant of such events, and affect species colonization patterns (Hupp & Osterkamp, 1985; Sparks *et al.*, 1990). These disturbances are abiotic factors that partly control the pattern and intensity of biotic interactions (mainly, competition and facilitation), and are consequently a major driving force in vegetation development on river floodplains (Riis & Biggs, 2001; Lenssen *et al.*, 2004; Tiegs *et al.*, 2005). The consequence is the great diversity of vegetation patterns that may occur in river systems (Ward, Tockner & Schiemer, 1999; Bornette *et al.*, 2001).

A broadly useful model predicting the organization of plant communities on river floodplains should consider the following factors and their effects on habitat characteristics and plant communities: (i) the nature of the physical constraints that affect plant communities (the scouring or depositing character of flood disturbances); (ii) the frequency and intensity of disturbances that limit competitive interactions and create gaps for recruitment for new individuals, and ultimately impede plant colonization and (iii) the specific life-history traits that allow plant maintenance, recruitment and colonization in the variously disturbed riparian systems.

The present paper proposes a model of physical factors that affect plant communities in river floodplains. This model predicts plant species diversity and life-history traits. It is illustrated with several contrasting examples in selected temperate areas.

Physical factors that organize river floodplains

Erosion and deposition patterns

Large rivers that drain alpine areas and their piedmonts (e.g. Europe and Northwestern North America) tend to have relatively high energy, abundant gravel bed load, and straight, braided or wandering channel patterns (Piégay *et al.*, 2000; Poff *et al.*, 2006b). Lateral instability and avulsion during flows promote the development of abandoned channels in these systems, such as chute cut offs, oxbows and cut-off channels (Gilvear & Bravard, 1996; Ward *et al.*, 1999). These lateral movements of the main channel promote a high biodiversity in these floodplains by creating a mosaic of coincident patches with different ages and hydrological characteristics (Amoros & Bornette, 2002; Ward *et al.*, 2002). In these areas, a few authors have identified distinct erosional and depositional zones along the river gradient (Sullivan *et al.*, 1987; Tabacchi *et al.*, 1998). Where there is a decrease in coarse material or alteration of river transport (common in European regulated rivers), erosion processes can lead to the incision of the main channel and the progressive decrease of connectivity between the river and its floodplain (Bornette & Heiler, 1994; Kondolf, Piégay & Landon, 2002; Hupp & Rinaldi, 2007).

Large upland rivers draining relatively moderate gradient areas (e.g. Eastern North America) tend to carry considerable silt/clay sediment loads and may be relatively stable with large, fine-grained floodplains (Hupp & Osterkamp, 1985; Hupp, 2000). Floodplains aggrade either through lateral accretion or point-bar extension where coarse material is deposited on the inside bank of channel bends, or by vertical accretion where suspended sediment is deposited over the floodplain during over-bank flows. The often drastic and sudden reduction in flow velocity after leaving the main channel and entering the hydraulically rough floodplain environment facilitates deposition of fine sediment.

Conceptual scheme

Deposition and erosion processes are the two main types of process that occur in the river landscape during floods (Hupp & Bornette, 2003). Floodplains or floodplain reaches can be plotted on this curve that represents erosion and deposition processes (Fig. 1).

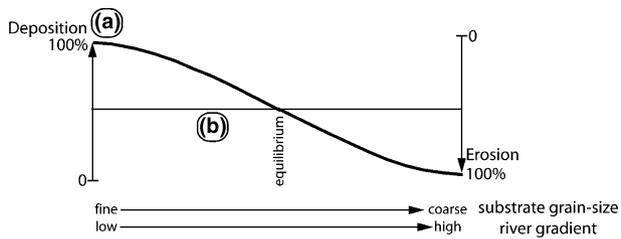


Fig. 1 Conceptual scheme of erosion and deposition processes in river floodplains. Each floodplain or floodplain reach can be plotted on a curve that represents intensity of erosion or deposition processes. The position along the curve depends on the dominant process [vertical (a) axis], and on the river gradient and grain size of the bed load [horizontal (b) axis]. At the extremes of the gradient, the proportion of the river reach subjected either to erosion or to deposition processes is the highest (close to 100%). Near the centre (equilibrium) of the curve, the surface areas of river reach subjected to erosion and deposition processes tend to be equal, leading to the same proportion of eroded and deposited patches.

The position along this curve depends on the dominant process [vertical (a) axis]. In rivers strongly dominated by aggradation processes, extensive depositional areas may be generated during each flood. In rivers where erosion processes predominate, large eroded zones may be generated, and the river is progressively less hydraulically connected to its floodplain. Most fluvial systems occur between these two extremes, where the partitioning between erosion and deposition processes varies from steady state equilibrium (where erosion and deposition processes are of equal importance) to disequilibrium situations (where either erosion or deposition processes predominate). The curve on Fig. 1 simulates the variation of the floodplain area experiencing a given process according to the grain-size of the river bed load and the river gradient [horizontal (b) axis]. Indeed, for a given hydrological event, the contribution of deposition versus erosion processes depends strongly on flow velocity during floods (Wu, Shen & Chou, 1999; Samani & Kouwen, 2002). When stream gradient (or power) is high, the flow velocity during floods tends to be high, and the bed load grain size is at a maximum, the finest grain sizes being washed away during each flood event. In such situations, erosion processes dominate (e.g. low-order high mountain cascades), and the substrate grain size is predominantly coarse, with only scarcely distributed patches subjected to deposition processes. Conversely, along low gradient reaches, flow velocity during floods is

comparatively low, and the grain size of the bed load is fine [horizontal (b) axis]. In such situations, depositional processes usually dominate (e.g. coastal plain rivers during periods of rising sea level), and substrate grain size of the river reach is predominantly fine, with only small patches experiencing erosion processes.

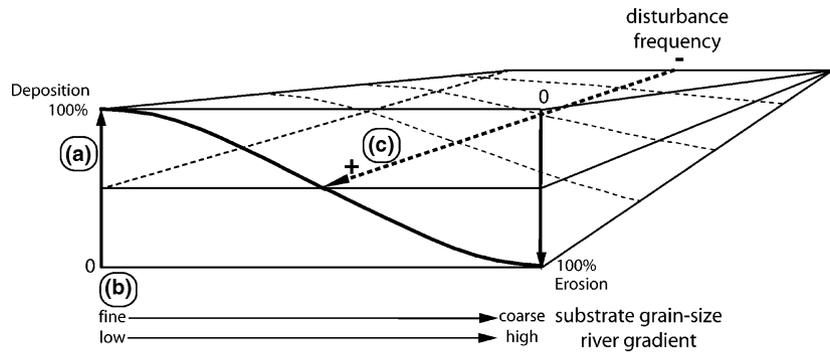
The position of a given river or river reach on the curve of intensity of erosion versus deposition processes is determined by the relative amount of surface area experiencing each of these two processes. At equilibrium, the area of the floodplain landscape subjected to deposition processes is similar to the one subjected to erosion processes. In such a situation, the habitat tends to be patchily organized as a mosaic of deposited and eroded patches of various sizes, but the patch sizes tend to be rather small in comparison to the total area of the floodplain reach. This state represents the highest level of habitat heterogeneity because of the co-occurrence of patches subjected to erosion and deposition processes even at the scale of short river sections. This highest heterogeneity is potentially associated with the highest biodiversity.

When one of the two processes becomes increasingly dominant, the proportion of the floodplain area subjected to this process increases. At the extremes of the gradient, the highest patch size occurs (ultimately, patch size corresponding to the entire river or river reach).

Most temperate rivers or river reaches can be plotted somewhere along the curve in Fig. 1, symbolizing erosion and deposition processes. However, rivers or river reaches located at the equilibrium point become increasingly less common in temperate areas, because of the often frequent and heavy impacts of human activities that disrupt and drive fluvial processes toward one of the ends of the curve. At the scale of an entire river, some reaches may be subjected to migrating deposition processes (e.g. lag or 'legacy' deposition processes), and others to erosion processes (e.g. nickpoint migration). Thus, it is at the reach scale where disruption of equilibrium may be most easily observed.

Figure 1 is drawn for a given frequency of flood disturbances, that is, for a given turnover rate of patches subjected to erosion and deposition processes. However, flood frequency is a major determinant of the rate of habitat reworking in the floodplain. Consequently, it is necessary to add a third axis,

Fig. 2 Conceptual model of the dominant processes that determine habitat heterogeneity in river floodplains. Axes (a) and (b) are the same as in Fig. 1. Axis (c) indicates the frequency of flood disturbances. As the frequency of disturbances decreases [axis (c)], the intensity of erosion and deposition processes decreases [axis (a)].



which accounts for the frequency of flood disturbances [i.e. frequency of sediment reworking or burial; axis (c), Fig. 2]. The intensity of erosion and deposition processes decreases when the flood frequency decreases along axis (c), but patterns indicated along axes (a) and (b) remain the same.

Plant strategies in the conceptual model

Flood patterns in the three-dimensional model of disturbance

The three axes of the model can be easily assimilated by the three theoretical dimensions of disturbances (sensu Pickett *et al.*, 1989; Grime, 2002). Indeed, the intensity of disturbances (called magnitude in Pickett *et al.*, 1989, and related to the severity of plant destruction) can be assimilated along the (a) axis. The spatial scale of disturbances occurs along the (b) axis, as river slope and grain-size determine the relative portion of landscape that is submitted to erosion or deposition processes. The temporal scale of disturbances (i.e. frequency) can be assimilated along the (c) axis.

Most models that relate plant strategies to abiotic factors stress a major role for disturbances in

controlling plant life-history traits (Kautsky, 1988; Mc-Intyre *et al.*, 1999). For example, Glenn-Lewin & Van Der Maarel (1992) suggested that recolonization of cleared patches should involve contrasting life-history traits, according to the position of the cleared patch in this three-dimensional space.

Processes involved in species maintenance according to disturbance frequency

High frequency and intensity of disturbances, whatever their nature, should select species according to their ability to tolerate the high instability of the habitat [dominance of allogenic processes, Fig. 3, axis (c)]. At the proximal extremity of this axis, biological interactions should be the lowest, and the disturbance level the highest, selecting disturbance-tolerant or opportunist species (Holm, 1988; Ackerly, 2004). As disturbance frequency decreases, biological interactions increase (e.g. competition and herbivory, Weiher & Keddy, 1995; Elger *et al.*, 2004), favouring competitive species (or a resistance strategy, Holm, 1988). Disturbances by floods no longer dominate plant communities at this end of the gradient, where autogenic processes dominate. Other driving forces, such as nutrient limitation, fluxes of propagules and biological interactions become

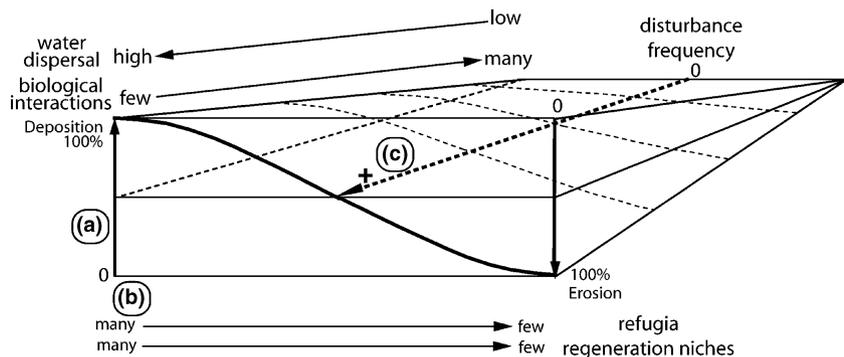


Fig. 3 Ecological processes that hypothetically control plant communities and related strategies in the conceptual model.

the main structuring forces (Whittaker & Goodman, 1979; Taylor, Aarssen & Loehle, 1990).

Plant dispersal via water fluxes is expected to be highest when disturbance frequency is highest, as water is a very efficient dispersal agent during floods (Boedeltje *et al.*, 2004; Jansson *et al.*, 2005). Conversely, the lowest disturbance frequency corresponds to low water dispersal. However, other agents (e.g. wind, birds; Figuerola & Green, 2002; Leyer, 2006) also contribute to diaspore dispersal, sometimes leading to a dispersal peak in sites flooded at an intermediate frequency (Abernethy & Willby, 1999; Tabacchi *et al.*, 2005). Furthermore, empty gaps can also be colonized by vegetative spread from the border of the gap (e.g. Noble & Slatyer, 1980; Paine & Levin, 1981; Henry *et al.*, 1996), and by propagules that were preserved from disturbances in the bank (Leck & Brock, 2000; Brock *et al.*, 2003). The occurrence of these refuges and regeneration niches for plant recruitment depends on the partitioning between erosion and deposition processes involved in gap creation. Consequently, regenerative strategies depend also on this partitioning.

Processes involved in species maintenance according to disturbance frequency and intensity

When disturbance frequency increases, the nature (erosion versus deposition processes) and size of patches increasingly control plant strategies. Highly erosional or depositional situations correspond to the highest habitat homogeneity, with large eroded or deposited patches. Consequently, the highest habitat specialization is expected among plants colonizing either strongly depositional or strongly erosional reaches. The ability of communities to survive a disturbance event, and the importance of resistance (i.e. the ability of the community to avoid displacement during period of disturbances) versus resilience (i.e. its ability to return to normal after the disturbance; sensu Webster *et al.*, 1983; Mitchell *et al.*, 2000) in maintenance of communities should vary according to the process involved (deposition versus erosion processes).

In heavily eroded situations, coarse substrate dominates in most patches, and consequently few refuges occur. Furthermore, where fine substrate is chronically lacking, there is a decrease in soil moisture and nutrient availability (Stromberg *et al.*, 2007). Thus, nutrient limitation should be highest in heavily eroded areas. The opportunity for plant species to

survive through the preservation of at least a part of the individual (e.g. roots, rhizomes or preserved individuals), and to resprout after disturbances should consequently be low. However, some species with deep tap roots or dense canopy may be instrumental in trapping fines and stabilizing substrate, potentially facilitating the anchorage and growth of other species (Madsen *et al.*, 2001; James, Barko & Butler, 2004). Consequently, community maintenance in such situations would rely predominantly on processes related to resilience, whereas resistance should be low.

In situations where deposition processes dominate, plants may be exposed to long-term inundation and partial burial by fine sediment. Because flow velocity is usually low in such situations, biomass losses through breakage are low, but plants must resist anoxia and burial. In such situations, plant maintenance would rely predominantly on traits conferring resistance. Deposition-dominated areas should be nutrient-rich, as deposits of fine sediment in the riparian zone may supply organic material and nutrients, and potentially create eutrophic conditions (Johnson, 1994; Schwarz *et al.*, 1996). In some cases, however, ruderal strategists can be recruited in such habitats, at least in the first stages following massive deposition of fine sediment (Tabacchi & Planty-Tabacchi, 2005), but this recruitment may be strongly limited by competition with established dominants and vegetative propagules from the local vegetation.

The equilibrium point should correspond to the highest habitat heterogeneity, with similar proportions of the floodplain area subjected to deposition and erosion processes. Because of the close juxtaposition of patches subjected to erosion and deposition processes, both nutrient-rich and nutrient-poor patches may occur. Consequently, species growing in these habitats should be tolerant to these various habitat conditions.

Life-history traits and flood disturbances

Traits related to disturbance frequency and intensity

The opportunistic strategy should be selected in the more disturbed situations [i.e. proximal extremity of the (c) axis, Fig. 3]. In this part of the scheme, the occurrence of any plant species should be determined mostly by an ability to tolerate disturbances and to

regenerate in gaps. Traits allowing survival during disturbances are usually grouped under the 'ruderal' or 'r' strategy. Several authors have defined the key-traits of this strategy:

1 The 'r' strategists of Southwood (Southwood, 1988) have a large number of small seeds with wide dispersal ability, and early maturation (i.e. small size and lack of vegetative spread).

2 Ruderals of the Grime model are of small size with a limited lateral spread, a short life cycle and a high frequency of flowering. These species have numerous small seeds or spores dispersed by wind, and should be able to persist in the seed bank in a dormant form for long periods (Grime, 2002).

3 Ruderals of the Kautsky model are of small size, with a limited lateral spread, and have a short life-span with a large proportion of the annual biomass production spent on sexual reproduction, with no vegetative propagules, but numerous dormant seeds or zygotes (Kautsky, 1988).

4 Traits related to the 'explerent' explorative strategy (Rabotnov, 1975; in Onipchenko, Semenova & Van Der Maarel, 1998) include a high production of small seeds, a large seed bank and a high relative growth rate, which leads to rapid growth if nutrients are available.

Connell & Slatyer (1977) suggested that large highly disturbed patches should be recolonized mainly by external colonizers, whereas the less disturbed patches should be partly re-colonized by seeds and propagules from the soil reservoir. Field observations partially confirm this prediction, although similarities between seed bank and established vegetation remain relatively high in areas frequently exposed to disturbances (Tabacchi *et al.*, 2005).

When sexual reproduction is effective, seeds are expected to have a high dispersability. In the Salicaceae, for example, dispersability is efficient through small wind-dispersed seeds that must reach suitable habitats rapidly after release in order to compensate for low viability of the diaspores (Guilloy *et al.*, 2002). Mahoney & Rood (1998) developed a model showing that the efficiency of dispersal of such species depends on a narrow timeframe. As a consequence, their recruitment is highly variable from year to year. Water dispersal should be highly favoured, as it increases the opportunity for propagules to reach gaps immediately after the disturbance, but such dispersal requires high buoyancy of propagules

(Andersson, Nilsson & Johansson, 2000; Boedeltje *et al.*, 2004; Riis & Sand-Jensen, 2006). Seeds of the helophytes *Alisma plantago-aquatica* L., *Carex flava* L. and *Cladium mariscus* (L.) Pohl., like seeds of the hydrophyte *Hippuris vulgaris* L., are able to float for >1.5 years (Praeger, 1913). Seeds of the disturbance-tolerant species *Berula erecta* (Hudson) Coville and *Myriophyllum spicatum* L. are able to float for about 7 days (Guppy, 1906; Praeger, 1913), while fragments of several species that colonize disturbed habitats are able to float for several weeks (Barrat-Segretain, Bornette & Hering-Vilas-Bôas, 1998; Boedeltje *et al.*, 2003). Conversely, seeds and fragments of plants species that colonize undisturbed habitats tend to have low buoyancy: seeds of *Baldellia ranunculoides* (L.) Parl., *Oenanthe fistulosa* L., *Oenanthe aquatica* (L.) Poir. and *Nuphar lutea* (L.) Sm. (I. Combroux & G. Bornette, pers. obs.), or fragments of *Potamogeton coloratus* Hornem. sink immediately or very soon after release (Barrat-Segretain, Henry & Bornette, 1999).

Seeds of plants that colonize disturbed habitats tend to have no dormancy, or dormancy breakage depending on a signal from the disturbance itself (Thompson & Grime, 1979; Jutila, 2001; Karrenberg, Edwards & Kollman, 2002), which enables them to be immediately available when gaps are created. For example, Charophytes are pioneer species, which usually bloom after disturbance (Bornette & Arens, 2002), suggesting that the disturbance itself induces oospore germination. During floods, the abrasive effects of sediment movement can break cuticular dormancy. Seeds of several species that colonize disturbed habitats [*Luronium natans* (L.) Raf., *Potamogeton pectinatus* L., and *Potamogeton pusillus* L., Bornette *et al.*, 1998] show increasing germination if they are scarified (S. Greulich & G. Bornette, pers. obs. for *L. natans*, and Teltscherova & Hejny, 1973).

Vegetative regeneration is a key function for the maintenance of species subjected to recurrent disturbance, particularly in infertile situations that can prevail in the most disturbed floodplain habitats (Bellingham & Sparrow, 2000; Klimešová & Klimeš, 2007). Several authors have demonstrated the prevalent role of clonal growth in species maintenance after disturbances through survival of deeply anchored roots or rhizomes, spreading from refuges or sprouting from vegetative propagules (Prach & Pyšek, 1994; Henry *et al.*, 1996; Barsoum, 2002). As an example, along U.S.A. rivers, two shrubs common on

the channel shelf (a bank feature), *Alnus serrulata* (Ait.) Willd. and *Cornus amomum* Mill., are relatively resistant to destruction by flooding because of small, highly resilient stems and the ability to sprout rapidly from damaged stumps (Hupp & Osterkamp, 1985). This high capability of regrowth is also facilitated by the production of adventitious roots that utilize nutrients in alluvial material deposited by floods, allowing for rapid rooting of flood-detached branches (Hupp & Osterkamp, 1996). Plants that produce rhizomatous systems resist flood disturbance by vegetative production of new shoots from resistant rhizomes (Bartley & Spence, 1987; Willby, Abernethy & Demars, 2000; Kotschy & Rogers, 2008). Plants having a high growth rate should also be selected when disturbance frequency increases. High growth rate would be important not only for seedlings, but also for plants that regenerate from plant fragments, or that colonize empty patches by growing in from the edge (Barrat-Segretain & Amoros, 1996; Henry & Amoros, 1996).

Disturbance affects the size of eroded versus deposited patches, as patches tend to be larger when disturbances increase in intensity. Traits linked to vegetative and to sexual reproduction are involved differently in the recolonization process, depending on patch size (Miller, 1982; Belsky, 1986). The growth rate of plants at the patch edge, as well as patch size, determine the contribution of vegetative propagation to recolonization (Connell & Keough, 1985). In large patches, seed colonization tends to dominate, whereas the edge effect tends to be low (Vandvik, 2004). Further, Miller (1982) also suggested that large patches should be colonized mostly by species having high rates of reproduction and high dispersal ability, whereas small patches should be colonized mostly by more competitive species with a high growth rate located around the patch perimeter (edge effect). Consequently, even if the regenerative strategies involved in the colonization process vary according to patch size, large patches (i.e. patches that are usually generated by a high frequency and/or intensity of disturbances) should be colonized mainly by seeds with high dispersal ability.

Traits related to the deposition versus erosion nature of disturbance

Traits increasing resistance. The type of disturbance greatly influences which species attributes are most

important (Armesto & Pickett, 1985; Pickett *et al.*, 1989). Resistance to flood disturbances should involve different adaptations depending on the deposition versus erosion nature of floods. A resistance strategy should be particularly efficient for depositional floods. Indeed, such events usually do not lead to mechanical destruction of vegetation, but to burial, elevated turbidity and long inundation periods (lasting months in some cases, e.g. southeastern U.S.A. coastal plain). Consequently, the duration of inundation is a highly influential factor that controls lowland floodplain vegetation patterns. Recurrent flood inundations reduce substrate porosity through deposition of fine sediment, which leads to disconnection between surface water and ground water, increase of eutrophication and substrate anoxia. Such processes result frequently in low species richness of both hydrophytes and helophytes (Brock, Van Der Velde & Van De Steeg, 1987; Van Geest *et al.*, 2005). The tallest plants, able to remain emerged during floods or that have sufficiently high biomass, are more probably to tolerate long-term submersion (Mommer *et al.*, 2006). The coincident high turbidity and deposition of fine particles should favour floating species (Kalliola *et al.*, 1991; Bini *et al.*, 1999), species able to anchor themselves in sediment of low cohesive strength (Hanley & Lamont, 2002), or species able to produce adventitious roots or to spread laterally close to the surface of the newly deposited sediment or at the surface of the water (Sorrell *et al.*, 2000; Xiong *et al.*, 2001). Rapid adventitious root formation allows the rooting of the elongated stems lacking support tissues when water level decreases. Ultimately, deposition processes can impede regrowth of Nymphaeaceae species from rhizomes. As seeds of these species require early supply of light to hypocotyls (Smits *et al.*, 1990), their growth could be impeded in frequently turbid habitats. Species able to survive should have storage systems (e.g. large rhizomes or tubers), making them able to generate vegetative parts of the individuals destroyed by long-term submersion (Brock *et al.*, 1987). For example, *Nymphoides peltata* (S.G. Gmelin) Kuntze rapidly produced new leaves able to reach the water surface during a long-duration inundation (>3 weeks), but disappeared as the water level decreased, because its storage system was insufficient to produce subsequent new leaves over such a short time frame. Conversely, *N. lutea* and *Nymphaea alba* L., with their low growth rates and large storage systems,

may survive long inundation. More generally, herbaceous plants tend to be intolerant of prolonged inundation (Grimoldi *et al.*, 1999). Species that survive can be described as plastic, with morphological and/or metabolic adaptations to deal with inundation and anoxia, such as aerenchyma formation, adventitious root formation, increasing specific leaf area and leaf and stem elongation (Vartapetian & Jackson, 1997; Jackson & Colmer, 2005; Voeselek *et al.*, 2006). Aerenchyma formation, and leaf and stem elongation should increase the plant capacity to reach the water surface, and thus to survive anoxia (Grimoldi *et al.*, 1999; Lenssen *et al.*, 2000).

Resistance to scouring floods should be limited, because such disturbances may remove substrate and plants (Riis & Biggs, 2003). Traits that reduce the hydrodynamic forces encountered by plants or increase mechanical resistance to breaking and uprooting enable them to reduce the risk of being damaged (Schutten & Davy, 2000; Puijalon *et al.*, 2008). Willows, as well as many aquatic plants, are small to intermediate-sized species with highly flexible stems and strong anchorage, which decrease the risk of uprooting or breakage during floods (Karrenberg *et al.*, 2003; Lytle & Poff, 2004). Some species also have breaking points (*Salix fragilis* L., *Hottonia palustris* L.) that enable a self-thinning of the crown and may thereby reduce resistance to floods (Brock, Mielo & Oostermeijer, 1989; Beismann *et al.*, 2000) but also favour the dispersion of vegetative propagules produced by the flood itself (Cellot, Mouillot & Henry, 1998). Plastic responses, leading to small-sized, very flexible growth forms, or to an increasing allocation of resources to anchorage, also decrease the uprooting or breaking risk during floods. This ability to bend under moderate and high flows has direct feed-back consequences on siltation (Tsujimoto, 1999) and geomorphic processes (Kouwen & Li, 1980), and probably facilitates the anchorage of riverside plants.

Traits increasing resilience. Many plants have few or no specific morphological adaptations allowing them to resist disturbances, and their maintenance relies mainly on an ability to colonize the disturbed patch immediately after the disturbance.

Depositional floods strongly control recruitment of plants, as seeds and seedlings exhibit various tolerances to anoxia and low light conditions, and thus

require particular water levels to germinate (Voeselek, Degraff & Blom, 1992; Smits *et al.*, 1995; Middleton, 2000). Consequently, most aquatic species in such habitats are able either to germinate in turbid and oxygen-poor conditions and to rapidly reach the water surface, or to spread laterally. It is presumed that the interval between successive floods is sufficient for newly recruited individuals to reach the water surface, allowing sexual or at least vegetative reproduction. Clonal growth should also increase survival of individuals after disturbance, and increase recruitment success by maintaining a physiological relation between the parent plant and the newly produced ramets (Shumway, 1995; Pennings & Callaway, 2000; Yu, Chen & Dong, 2002). Because of these major restraints, resilience processes should be less involved in community maintenance in hydrosystems characterized by inundation.

In habitats with moderate frequency and intensity of erosional floods, perennial species may be broken (but rarely completely uprooted) by flood events. Such fragments should contribute to recolonization of disturbed patches (Henry *et al.*, 1996), as long as they are able to disperse and regrow efficiently (Cellot *et al.*, 1998; Karrenberg *et al.*, 2002; Boedeltje *et al.*, 2003). When scouring intensity and frequency are distinctly high, only annuals that are able to grow and reach reproductive maturity over a short period should occur (Schippers *et al.*, 2001; Tabacchi *et al.*, 2005). When normal flows alternate with highly scouring events, plants regrowing from diaspores may establish. Charophytes, as well as plants germinating from light diaspores (*Zannichellia palustris* L., *P. pusillus*, *Nasturtium officinale* R. Br.) can reach high cover in the newly scoured substrate of cut-off river channels (Bornette & Arens, 2002; Combroux & Bornette, 2004).

Conclusion

The response of riverine vegetation to floods appears complex, resulting from the interaction of diverse effects such as nutrient inputs, propagule inputs, scouring effects, suspended matter inputs and depositional processes. The present work is a first attempt to propose a broadly applicable model of plant traits depending on flood restraints in river hydrosystems. In contrast to models previously proposed, the present model asserts that two types of disturbance could

select for contrasting adaptive strategies, based mainly on the ability of a plant to resist the disturbing event and to colonize new patches.

Most traits may be easily documented, and the predictions offered by this framework are applicable to various hydrosystems, and should be testable in different geographical areas because they are not based on a given list of species.

The quantification of disturbances would require the documentation of disturbance intensity and nature (erosion or deposition processes) in the floodplain patches. As it is rather difficult to document disturbance frequency, because habitats are frequently not accessible during floods, the organic carbon content of the substrate could be a proxy of the frequency of sediment reworking. Indeed, carbon content has been previously demonstrated to be linked to the disturbance level of floodplain habitats (Rostan, Amoros & Juget, 1987; Schwarz *et al.*, 1996). This proxy would allow researchers to plot on the same scale habitats subjected to erosion processes and those subjected to deposition processes. Erosional processes export organic matter that accumulates between flood events, and deposition of mineral particles leads to a decreased proportion of organic matter in the substrate.

The substrate grain size of habitat patches could be considered as a proxy of the nature of disturbance (erosional or depositional processes) that affects each of these patches, as grain size is usually coarse in erosional situations, and fine in depositional ones. The analysis of vegetation patterns in contrasting situations according to these two parameters would permit validation of the model, and potentially identify the presently obscure points that should be considered in future research.

Among traits that should be considered more specifically are those involved in plant resistance to flow. Indeed, some studies have demonstrated that significant differences in tolerance to flow velocity exist among species colonizing running habitats (Riis & Biggs, 2003), but the traits involved in these contrasting patterns of resistance could be more clearly elucidated, although some preliminary studies exist (Schutten & Davy, 2000; Sand-Jensen, 2003). Furthermore, plastic responses to flow velocity, at the individual (Puijalón *et al.*, 2008) or at the clone scale (Sand-Jensen *et al.*, 1989), could increase resistance to mechanical damages, and thus, may influence the

future development of the habitat and its susceptibility to flood disturbance.

The predictions presented in this model may also fail to encompass the full range of traits that are involved in plant regeneration (e.g. seed production and germination requirements, capability of regeneration from fragments, patterns of vegetative propagation). Although some experimental studies deal with such questions, either they typically focus on a small number of species (Voesenek & Blom, 1992; Lenssen *et al.*, 2000) making generalizations of the trends observed difficult, or they do not encompass a sufficiently long gradient of physical constraints (Schutten & Davy, 2000). Future developments of this model would benefit by including such traits, which are potentially specifically screened by the abiotic conditions generated by floods in river hydrosystems.

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